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Spatial structure in invasive *Alliaria petiolata* reflects restricted seed dispersal

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Abstract

Identification of processes that shape the spatial structure of invasive species has important implications for understanding population regulation. In invasive *Alliaria petiolata* we quantified (i) spatial scale of seed dispersal under field conditions, (ii) spatial structure of rosette and adult density and (iii) the relative importance of environmental filtering, propagule pressure and adult-rosette interactions in shaping rosette and adult density. We conducted a seed dispersal experiment under field conditions; and in a three year field survey we measured quadrat-level rosette and adult density, adult seed production and soil moisture and light along transects in three *A. petiolata* populations at Koffler Scientific Reserve in Southern Ontario, Canada. Propagule pressure was estimated based on quadrat-level seed production and neighbourhood seed production. We found that seed dispersal of *A. petiolata* followed a lognormal distribution with a mean dispersal distance of 1.82 m, and that spatial structure in both adults (Moran's I : 0.30 – 0.56) and rosettes (0.48 – 0.57) was significant up to 2 m. Propagule pressure and adult-rosette interactions were significant processes associated with rosette density, whereas propagule pressure was the most important process associated with adult density. However, due to the observational nature of the data, it is difficult to determine whether the observed negative association between adult and rosette density is related to competition or to temporal variation in density-dependent seed production. Overall, we conclude that spatially restricted seed dispersal is the most important factor underlying this species' patchy distributions.

Key Words: *Alliaria petiolata*; seed dispersal; spatial autocorrelation; spatial processes

Introduction

In natural landscapes, many invasive species show patchy spatial distributions. Since processes shaping the dynamics of ecological populations often leave their signatures in the spatial structure of populations and communities (Powell 1990; Seabloom et al. 2005), analysis of spatial structure may offer useful insights into the mechanisms of species' spatial organization (Fortin and Dale 2005; McIntyre and Fajardo 2009). Such knowledge is crucial to devise appropriate management strategies for invasive populations. However, identifying important processes creating spatial structure in ecological populations may be challenging because numerous processes interactively shape ecological populations and we rarely know about all processes (Fortin et al. 2012). Furthermore, a single process may create varying spatial structure (Pielou 1960; Powell 1990) and different processes may create similar spatial structure (Fortin and Dale 2005; Malkinson and Jeltsch 2007; Dray et al. 2012).

One way to deal with these challenges is to simultaneously quantify the relevant processes as identified by theories on spatial organization, such as metapopulation theory or the metacommunity concept. The latter emphasizes three key process: (i) environmental filtering, (ii) dispersal and (iii) species interactions (Gilpin and Hanski 1991; Leibold et al. 2004; Biswas and Wagner 2012). These three processes may be a good starting point (Legendre 1993; Dorman et al. 2007), whereas any remaining residual spatial structure after accounting for these processes may point towards additional important processes (Wagner and Fortin 2005; Dray et al. 2012).

Since lack of a unique signature of each process makes the task of inferring processes from spatial structure challenging (McIntyre and Fajardo 2009), attempts should be made to quantify them directly if possible. While many studies quantify environmental conditions and biotic interactions directly, dispersal is often either approximated by geographic distance or introduced as a post-study explanation for residual spatial structure (Cottenie 2005). However,

dispersal is a central process of species spatial organization (Nathan and Muller-Landau 2000; Nathan et al. 2000). In real landscapes, species dispersal may be a highly complex process (Biswas and Wagner 2012), so that approximation of species dispersal based on variance explained by 'space' as commonly done (Cottenie 2005) may be insufficient. Empirical assessment of seed production, dispersal and resulting propagule pressure is important to understand species' spatial organization (Nathan and Muller-Landau 2000; Colbert 2001). This is even more important for invasive species, as propagule pressure is a major factor underlying successful invasion (Lockwood et al. 2005; Colautti et al. 2006). Yet, there is a paucity of studies that measured dispersal and resulting propagule pressure directly together with other processes (Nathan and Muller-Landau 2000; Colbert et al. 2001; Colautti et al. 2006).

Alliaria petiolata (M. Bieb.) Cavara and Grande, an invasive forb in North America, is ideally suited for studying the relative importance of processes because this species generally occurs in patches (see Online Resource 1), and the processes shaping population dynamics of this biennial species are relatively well known (e.g., Davis et al. 2006). In forest understory, *A. petiolata* can be very dominant (Luken and Thieret 1997; often covering 80-100% of a quadrat), so that interspecific interactions may have negligible effects on the dynamics of *A. petiolata* (Biswas and Wagner 2014). While considerable research has been conducted on autecology and population dynamics of *A. petiolata* (see review by Rodgers et al. 2008), its dispersal ability and resulting propagule pressure, as well as the relative importance of processes shaping the spatial distribution of adults and rosettes density, are still poorly understood.

In this study we experimentally assessed the spatial scale of seed dispersal under natural field conditions, and analyzed three-year permanent plot data on adult and rosette densities to examine whether the patchiness in adult and rosette densities corresponds to the spatial scale of seed dispersal and to assess the relative importance of processes shaping adult and rosette

densities by relating density data to quadrat-level environmental site conditions (environmental filtering), life-stage interactions (adults vs. rosette densities), and propagule pressure. We thus asked three questions: (i) What is the spatial scale of seed dispersal in *A. petiolata*? (ii) What are the degree and spatial extent of spatial structure of adult and rosette density in *A. petiolata*? (iii) What are the effects of environmental factors, propagule pressure and life-stage interactions on adult and rosette density in *A. petiolata*? We hypothesized that: (i) *A. petiolata* is characterized by short dispersal, as its seeds lack morphological adaptation for seed dispersal and are thus expected to disperse through gravity, potentially followed by secondary dispersal through animal vectors. (ii) Spatial structure in rosettes is characterized by higher intensity of spatial autocorrelation than the spatial structure in adults. We expect this because short range dispersal creates patchiness in rosettes, whereas density-dependent effects are expected to reduce patchiness in adults (Powell 1990; Winterer et al. 2005). (iii) Propagule pressure and biotic interactions have a larger effect on the density of both adults and rosettes than environmental filtering, because *A. petiolata* occurs in a wide range of environmental site conditions (Cavers et al. 1979), which suggests a weak role of environmental filtering (Winterer et al. 2005).

Methods

Study species and site

Alliaria petiolata is a Eurasian native and an invasive forb in North America (Rodgers et al. 2008). The species occurs in diverse habitat types such as in forest understory, forest edges, along roadside verges, in open grasslands, and along stream bank riparian areas (Cavers et al. 1979; Meekins and McCarthy 2001). *Alliaria petiolata* is a biennial species with two distinct life stages: first year rosettes and second year adults. Seeds germinate in early spring and develop

into rosettes, which grow during summer and fall and survive winters under snow cover with some green leaves (Cavers et al. 1979).

In the second year after spring snowmelt, *A. petiolata* quickly grows stalks and produces flowers, which may self-pollinate or be pollinated by generalist pollinators such as solitary bees, honey bees and syrphid flies (Cruden et al. 1996; Rodgers et al. 2008). *Alliaria petiolata* then produces siliques (seed capsules), each containing 10-20 seeds of 2.5-3 mm length (Cavers et al. 1979). After release of seeds in June – September, which generally occurs through bursting of siliques, adults die (Anderson et al. 1996). *Alliaria petiolata* does not possess any specialized dispersal mechanism, and most seeds disperse by gravity. Yet, some seeds may disperse further by wind, deer, small mammals, water current and humans (Cavers et al. 1979; Evans et al. 2012). It is generally assumed that most *A. petiolata* seeds fall within a few meters of the mother plant (Rodgers et al. 2008). Approximately 5 - 70% of seeds germinate in the next spring and develop new rosettes; the remaining seeds stay viable in the seed bank up to 5 – 10 years (Cavers et al. 1979, Evans et al. 2012).

Our study site was the Koffler Scientific Reserve at Jokers Hill (KSR), a University of Toronto field site near King City, Ontario, Canada. Here *A. petiolata* occurs in mesic forest understory, in moist grasslands and along trails. Detailed topographic, edaphic and vegetation maps of the study area are available at www.ksr.utoronto.ca. The first record of *A. petiolata* in Canada by J. Fletcher dates back to 1879 (Cavers et al. 1979). The history of *A. petiolata* invasion at KSR is not well documented, but is estimated to be at least 20-25 years old (Biswas and Wagner 2014).

Seed dispersal experiment

We selected five replicate point sources on relatively flat slopes (< 5 degrees) in forest understory for seed trap placement in natural populations of *A. petiolata*. At each point source, we selected 2 – 3 adult *A. petiolata* (average height 1.2 meters) as source plants to ensure that there were enough seeds to be dispersed. In June 2010, we removed additional seed sources by manually clipping siliques of *A. petiolata* that occurred within a radius of 10 m from the point source. We only clipped the siliques but kept the plants to simulate natural dispersal conditions. Our choice of a 10 m radius was driven by a plan to place seed traps up to 4 m from the point source with a buffer of 6 m. We considered 4 m for seed trap placement because we expected that seeds would stay within few meters (Rodgers et al. 2008). Outside each 10 m experimental zone, we flattened all standing adults of *A. petiolata* within the next 2-3 m to the ground.

Seed traps were manufactured in-house (Mechanical Department; University of Toronto, Mississauga). Each seed trap had an area of 78.54 cm^2 and consisted of three parts: the base, the seed holder and the cover (Fig. 1). The base (3 cm height) offers a stable point to place the seed holder (6 cm height), and a 0.5 inch wire mesh cover protects seeds from predation by small animals. Both base and seed holders were built from poly-vinyl-chloride (PVC) pipe, which was circular in shape with a diameter of 10 cm. The bottom of each seed holder was netted with fine steel mesh (mesh window net) so that water could pass through but seeds not. Each seed trap was established in the field as follows: the base was inserted fully into the ground using a hammer, the seed holder was then placed on the base, and finally a cover was placed on the top of the seed holder (Fig. 1).

In July 2010, when most adults had developed siliques and there was little indication of developing further flowers or siliques, we clipped any new siliques in the non-source plants. We then counted the number of siliques for each point source (average: 102.6; range: 82 – 128). We

151 did not open siliques of the source plant but opened five siliques from nearby non-source plants
152 and counted the number of seeds per silique (average: 15.796). From the product of the number
153 of siliques at each point source (2-3 source plants) and average number of seeds per silique, we
154 estimated available seeds at each point source. The average number of seeds at each point source
155 ($N = 5$) was estimated as 1617 with a range of 1312 – 2004. We then placed 55 seed traps around
156 each point source, starting from 0.5 meters and extending up to four meters, with an interval of
157 0.5 meters, so that seed traps were placed at: 0.5, 1, 1.5, 2, 2.5, 3, 3.5 and 4 meters away from a
158 point source. The area around each point source was divided into four quadrants and seed traps
159 were placed approximately equally spaced within each quadrant (Fig. 1). Because the probability
160 of seed travel decreases with increasing distance from the seed source, we increased the number
161 of seed traps at each interval with increasing distance (Bullock and Clarke 2000).

162 In late October 2010, when seeds from source points were dispersed, we collected seeds
163 from each trap and counted them in the laboratory. During seed collection from the traps, we
164 noticed minor disturbance: several traps were displaced (2 – 13 per site) and several contained
165 full siliques with stalks that were likely dispersed by animals; we excluded those traps from
166 analysis.

167 *Field survey*

169 In August 2009, we established transects of permanent plots and collected demographic
170 and environmental information in three comparable populations of *A. petiolata* occurring in
171 forest understory at KSR. For each field population, we laid out four perpendicular radial
172 transects of contiguous 1 m² quadrats extending from the center to the edge of the *A. petiolata*
173 patch (see Online Resource 1). The number of quadrats in each transect was variable (range: 12
174 to 25; on average 17 quadrats per transect). In each quadrat ($N = 196$), we collected data on (i)

number of adults (A_t), (ii) number of rosettes (R_t) and (iii) mean seed production per adult (S_t), for three years (August 2009, June 2010 and 2011). To quantify the number of seeds per adult plant, we counted the number of siliques (n_{siliques}) in each of three (2010) or five (2009) randomly selected adults in each quadrat (if a quadrat had fewer individuals, we measured all); we opened three randomly selected siliques from each plant to count the number of seeds per silique (n_{seed}). Quadrat-level seed production (qS) was quantified for each quadrat as the product of its average number of seeds per silique, its average number of siliques per plant, and its observed number of adults (i.e., $qS = n_{\text{seed}} \times n_{\text{siliques}} \times A_t$).

As environmental variables, we measured (in August for the year 2009 and in June for years 2010 and 2011) leaf area index (LAI) as a proxy for light, and soil moisture content (M) annually for each quadrat ($N = 196$). For soil moisture, we took three measurements (using a TDR probe) within each quadrat and averaged them to represent a quadrat (median 19%, range: 7 – 30%). All soil moisture measurements were taken within a period of three days without any rainfall event seven days prior to sampling days. For light, we took a canopy image at breast height (using a Digital Plant Canopy Imager CI-110) in each quadrat and analyzed the image for leaf area index (LAI).

Statistical analyses

Quantifying the spatial scale of seed dispersal

Separately for each replicate point source ($N = 5$), we used the function ‘fitdistr’ from R library “MASS” (Venables and Ripley 2002) to fit a Weibull, a lognormal, an exponential and a half normal model to the average number of seeds (S_d , rounded to the nearest integer) recovered per seed trap for each distance level d from the point source, where $d = \{0.5 \text{ m}, 1 \text{ m}, \dots, 4 \text{ m}\}$. We extracted model parameter and model log-likelihood values for each point source. Based on

the log-likelihood ($\ln(L)$), the number of parameters in a model (k), and the number of observations ($S = \sum_d S_d$), we quantified AIC_c (Akaike Information Criterion with a correction for small samples) for each model, separately for each point source as:

$$AIC_c = 2k - 2 \ln(L) + \frac{2k(k+1)}{S-k-1}.$$

The log-normal model was consistently identified as the best fitting model, as it had the lowest AIC_c for each data set (Table 1). We used the “transectHolder” function in R library “spuRs” (Jones et al. 2012) to average parameters of the log-normal model across the five replicates. The “transectHolder” function fits the same nominated probability density function to each point source, then averages the fitted parameters across point sources (Jones et al. 2009). It returns an averaged transect probability density function (transect pdf), $f_T(r)$ with parameters μ_T and σ_T , giving equal weight to each point source and accounting for trap size.

The mean displacement of a seed from a point source is given by the radial pdf, $f_R(r)$, which accounts for the radial diffusion effect. For the log-normal model, $f_R(r)$ is approximated by $r f_T(r)$, and the parameters μ_R and σ_R of the radial pdf can be estimated by $\mu_R = \mu_T + \sigma_T^2$ and $\sigma_R = \sigma_T$ (Jones et al. 2009). Mean seed displacement distance was estimated by the mean of the log-normal distribution, $\exp(\mu_R + \sigma_R^2/2)$.

Quantifying spatial structure of *Alliaria petiolata*

We quantified spatial autocorrelation in *A. petiolata* density, separately for each life stage and year, using Moran’s spatial correlogram (Moran 1948). As implemented in the function “sp.correlogram” in R library “spdep” (Bivand et al. 2012), spatial autocorrelation, $I(d)$, for each lag (d) was calculated as:

$$I(d) = \frac{\frac{1}{W} \sum_{i=1}^n \sum_{j=1}^n w_{ij} (x_i - \bar{x})(x_j - \bar{x})}{\frac{1}{n} \sum_{i=1}^n (x_i - \bar{x})^2},$$

where W is the number of pairs of quadrats considered in a particular lag class d , and w_{ij} is the spatial weight between observations i and j . In defining spatial relationships (i.e., the spatial weight matrix $\mathbf{W}$), adjacent quadrats were considered as neighbors (rooks connection; binary neighbor list, weights = row standardized).

To improve residual distribution, density data were transformed to square roots. Since spatial analysis is sensitive to broader-scale patterns, all transformed variables were detrended (i.e., we retained the residuals of a linear regression of each transformed variable against x and y coordinates of transect positions) and scaled to zero mean and unit variance, separately for each population (Legendre and Legendre 1998; Dale and Fortin 2005; Wagner and Fortin 2005; Schlup and Wagner 2008). Using these transformed, detrended and standardized variables, we computed Moran's I correlograms over nine lag classes. The number of lags was determined on the basis of Sturge's rule (Legendre and Legendre 1998; Fortin et al. 2002) and kept constant between populations to facilitate comparison. If the overall test for the correlogram was significant, we tested statistical significance of the correlogram statistic in each lag distance using progressive Bonferroni correction (Hewitt et al. 1997). This procedure, where the first lag is tested with $\alpha = 0.05$ and subsequent lags k are tested with $\alpha = 0.05/k$ if and only if all previous lags were significant, is recommended for determining the extent of positive spatial autocorrelation with an *a priori* hypothesis that patchiness would be in the smallest distance classes (Legendre and Legendre 1998).

Comparing importance of processes

We quantified each process hypothesized to shape adult and rosette densities of *A. petiolata* with 1 – 2 variables measured in the field (Table 2). Based on the results from the seed dispersal experiment (*see below*), we created a new variable to represent the seed dispersal from neighboring quadrats (*nbS*) as the average of seeds from adjacent quadrats. We did not include second neighbor quadrats in the estimation of *nbS*, as results from the dispersal experiment suggested that the nearest neighbors would be most important, and second-neighbor quadrats are not well represented in linear transect data. Repeating the analysis including second neighbors did not change the result, and second neighbors were not significant after accounting for first neighbors. To compare the effect of each process shaping adult and rosette densities, we predicted adult (A_t) and rosette (R_t) densities at time t as functions of factors representing the three main processes (Table 2). We conducted spatial regression analyses using the function “errorsarlm” in R library “spdep” (Bivand et al. 2012), separately for adults and rosettes and for two years t (2010 and 2011), each with a spatially autocorrelated error term to account for potential spatial autocorrelation in the residuals. To facilitate comparison among processes, all transformed variables (discussed below) were standardized (mean = 0, variance = 1), and thus no intercept was required. Spatial regression models were defined as follows:

$$R_t \sim Pop + \beta_1 M + \beta_2 LAI + \beta_3 qS_{t-1} + \beta_4 nbS_{t-1} + \beta_5 A_t + \lambda \mathbf{W} + \varepsilon$$

$$A_t \sim Pop + \beta_1 M + \beta_2 LAI + \beta_3 R_{t-1} + \lambda \mathbf{W} + \varepsilon,$$

where ‘Pop’ refers to a random population effect, β refers to the regression coefficients (slope parameter) associated with the explanatory variables (see Table 2 for the definition of variables), λ is the coefficient of the spatial error term (a significant λ indicates significant residual spatial autocorrelation), which was defined by a spatial weight matrix $\mathbf{W}$ (where adjacent quadrats were neighbors; binary neighbor list, weights = row standardized), and ε is the

independent error term. Correlations among predictors were non-significant, except a moderately significant correlation among qS and nbS . To improve residual distribution, density data were transformed to square roots, and quadrat-level seed production qS , seeds from neighbors nbS , soil moisture M and light LAI to natural logarithm. Residual analyses showed that transformations were successful, as the distributions of non-spatial residuals ε were approximately normal and variances were relatively homogeneous. The proportion of variance explained by each spatial regression ($pseudo-R^2$) was computed as the squared correlation of the fitted values predicted from the non-spatial predictors in the model (i.e., without the spatial error term) and the original transformed variable (Biswas and Wagner 2014, Biswas et al. 2014). We performed all analyses in R 2.14.2 (R Development Core Team 2011).

Results

Spatial scale of seed dispersal

The lognormal model provided the best fitting dispersal kernels for *A. petiolata* (Table 1, Fig. 2). After correcting for the radial diffusion effect, the averaged model (radial pdf) with parameters $\mu = 0.407$ and $\sigma = 0.620$ resulted in an estimated mean seed displacement distance from a point source of 1.82 m. This means that 3.8% of seeds are expected to fall within 0.5 m, 49.9% within 1.5 m, and 79.4% within 2.5 m. In the context of our transects with 1m^2 quadrats, 3.8% of seeds are expected to stay within the quadrat, 46.1% go to direct neighbor quadrat, 29.5% to second neighbor, and 20.6% go beyond the second neighbor. Point source 5 showed a high level of disturbance with 13 displaced seed traps. Excluding this replicate from averaging resulted in a radial pdf (Fig. 2) with parameters $\mu = 0.427$ and $\sigma = 0.646$ and a mean displacement distance of 1.89 m.

Spatial structure of rosettes and adults

For both adults and rosettes, we found significant positive spatial autocorrelation up to the second lag (i.e., 2 m), except for adults in 2011, where only the first lag was significant (Fig. 3). In rosettes, global Moran's I (which is equivalent to the first lag, $I(1)$) was +0.59 ($P < 0.01$) in 2009, +0.57 ($P < 0.01$) in 2010 and +0.48 ($P < 0.01$) in 2011. In adults, global Moran's I was +0.66 ($P < 0.01$) in 2009, +0.56 ($P < 0.01$) in 2010 and +0.31 ($P < 0.01$) in 2011. There was some variation in patterns (intensity and range of autocorrelation) among the three replicate populations: for rosettes, spatial autocorrelation in the first distance class was consistently significant for all three populations in all three years (2009, 2010 and 2011), whereas for adults, it was significant for all three populations in 2009 and 2010 and only for one in 2011 (Online Resource 2).

Relative importance of processes

For rosettes in 2010 (R_{2010}), propagule pressure in terms of previous year's quadrat-level seed production (qS_{2009}) and seeds from neighbouring quadrats (nbS_{2009}) showed significant positive effects on rosette density, and same years' adult density A_{2010} had a significant negative effect (Table 3). The standardized β coefficients indicated that propagule pressure ($\beta = 0.48$ for qS_{2009} and $\beta = 0.26$ for nbS_{2009}) was the most important process compared to interactions among life stages ($\beta = -0.28$ for A_{2010}) and environmental filtering (ns). In 2011, only propagule pressure had a significant positive effect on rosette density ($\beta = 0.26$ for qS). In adults, previous year's rosette density R_{t-1} was the only significant process in both years (Table 3). The effects of environmental factors were not significant in either rosettes or in adults (Table 3), but random population effects were significant. Notably, there was significant spatial autocorrelation in the residuals for adult and rosette density in both years (see values of λ in Table 3).

Discussion

Seed dispersal and the spatial structure of rosettes and adults

Based on a fitted lognormal dispersal kernel, seed dispersal of *A. petiolata* under field conditions is spatially restricted with a short mean dispersal distance of 1.82 m. The spatial structure of both rosette and adult densities, as assessed by spatial autocorrelation, was significant at a small spatial scale of 1-2 m, which is consistent with the results from the seed dispersal experiment. Spatial regression analysis of survey data on rosette density revealed propagule pressure from within the same quadrat ($\beta = 0.48, 0.26$) as the most important process structuring within-quadrat rosette density in both 2010 and 2011, while the importance of dispersal from adjacent quadrats was confirmed for 2010 by a significant effect ($\beta = 0.26$) of neighboring seed production (*nbS*). Based on the independent evidence from the dispersal experiment and the survey data, we conclude that seed dispersal is important, but occurs mostly at a very small scale. Short-range dispersal may thus largely be responsible for spatial structure of rosettes in the studied populations of *A. petiolata* (Fig 3).

Some caveats need to be considered when interpreting the results from our dispersal experiment. The fact that we recovered seeds up to the maximum distance of seed traps from the point sources (4 m), with no other potential sources within at least 6 m, indicates that seeds may travel further, and hence the full tail of the dispersal kernel is not captured in this experiment. Given the estimated dispersal kernel, it is unlikely that many seeds would have dispersed by gravity from sources outside our experimental plots. However, secondary dispersal by animal vectors may have occurred. We noticed animal disturbance, resulting in displacement of several seed traps and deposition of uprooted stalks with entire siliques attached. These problems occurred mostly in one of the five replicates, and we estimated dispersal kernel both with and

without this replicate. Overall, the results provide a much needed first empirical estimate of a seed dispersal kernel in *A. petiolata* under natural field conditions.

The overall patchiness (i.e., spatial autocorrelation) in both adult and rosette densities was similar from 2009 to 2011 (Fig 3), except for a slight reduction in patchiness in adults in 2011. The result that both adults and rosettes showed similar degree of patchiness (~2m) despite demographic thinning (mortality) in rosettes suggests that the legacy of seed dispersal on the spatial structure of individuals, both adults and rosettes, is very strong. On the other hand, the observed reduction in patchiness in adults in 2011 may not be surprising because ecological processes are dynamic, and the presence of multiple processes acting at local or broader scales may produce varying degrees of spatial structure over time (Levin 1992). We identified short-range dispersal and the resulting propagule pressure as the key process that creates spatial structure in *A. petiolata* density. Factors such as animal and human movement in an *A. petiolata* patch may affect dispersal (Cavers et al. 1979) and thus spatial structure of rosettes and adults. In addition and at broader spatial scales, annual variation in weather patterns, including discrete climatic events such as timing of the first rain storm of a season or cold storm temperature, may strongly affect demography, especially seed germination, of short-lived plants (Levine et al. 2011). In *A. petiolata*, dramatic variations in demographic parameters between sites and between study years associated with environmental heterogeneity and stochasticity in weather such as rain and drought have been reported (Evans et al. 2012; Biswas et al. 2014). Finally, the ongoing research resulted in a considerable increase in human movement from 2009 – 2011 in our study populations, which may have affected dispersal patterns and thus introduced noise in the spatial structure, potentially resulting in an overall reduction of the explanatory power of the measured variables from 2010 to 2011 (Table 3).

360 *Relative importance of propagule pressure, environmental filtering and competition between life*
361 *stages*

362 Previous year's rosette density was the most important predictor of adult density in both
363 years ($\beta = 0.81$ in 2010 and $\beta = 0.45$ in 2011), which implies that adult density is strongly
364 related to propagule pressure. Similarly for rosette density, propagule pressure was the most
365 important predictor ($\beta = 0.48$ for qS_{2009} , 0.26 for nbS_{2009}), though the effect was weaker in 2011
366 ($\beta = 0.26$ for qS_{2010}). We suspect that weakening of the effects of dispersal (nbS) in 2011, and the
367 reduction of pseudo- R^2 from 0.58 in 2010 to 0.09 in 2011, may be related to year-to-year
368 variation in demographic parameters as observed in Meekins and McCarthy (2002) and in
369 Winterer et al. (2005), variability in seed production in unmeasured neighboring quadrats, the
370 ignoring of second neighbor quadrats as potential seeds sources, soil seed bank, or to disturbance
371 of seed dispersal patterns resulting from the ongoing research as discussed above. However, our
372 overall results highlight the importance of propagule pressure or colonization in shaping patterns
373 of density in *A. petiolata*, and this is consistent with a general prediction of invasion ecology that
374 propagule pressure is a key driver of biological invasion (Colautti et al. 2006).

375 As hypothesized, we found non-significant effects of environmental filtering for adult or
376 rosette density (Cavers et al. 1979; Winterer et al. 2005). However, we found that negative
377 association between life stages was the second most important process to the explanation of
378 rosette density (Winterer et al. 2005; Bauer et al. 2010; Evans et al. 2012): same year's adults
379 had a strong, significant negative correlation with rosette density in 2010 ($\beta = -0.28$, $P < 0.01$). In
380 2011, however, the life stage interaction was not significant ($P = 0.73$), which may be due to
381 strong spatio-temporal segregation between rosettes and adults (in 2010) followed by a hole-
382 filling effect (2011), i.e., a phase when rosettes and adults mix (Meekins and McCarthy 2002;
383 Winterer et al. 2005; Bauer et al. 2010). Although competitive interactions between adult and

rosette life stages of *A. petiolata* has been reported earlier (Meekins and McCarthy 2002, Winterer et al. 2005; Bauer et al. 2010; Evans et al. 2012), we are not able to determine a causal role of competition between life-stages from this observational data, because negative correlation between the life-stages could also be driven by temporal variation in density-dependent seed production (i.e., areas with high adult densities in 2010 likely had low seed production in 2009, and thus low rosette densities in 2010). While our spatial regression accounts for some sources of seed production (within the quadrat and the two neighboring quadrats), substantial seed rain is likely to come from adjacent quadrats that remains unaccounted. Further research is required to determine the causality underlying negative association between adult and rosette density; and if competition prevails, the conditions for strong competition between life stages and how the strength of competition changes from seed germination in spring to seed shed in summer, so as to identify optimal timing for management interventions.

Nevertheless, we found significant spatial autocorrelation in the residuals (λ) in both adult and rosette density for both 2010 and 2011, which may indicate the presence of unaccounted processes. Density and spatial structure in a population may be generated through demographic processes (Powell 1990), and based on existing literature on *A. petiolata*, density dependence or herbivory are likely confounding processes (Davis et al. 2006; Evans et al. 2012; Biswas and Wagner 2014; Biswas et al. 2014). Further research should thus include quantification of these processes.

Implications for management

Our results have implications for the life stage to target and the timing of management in controlling this species. First, our assessment of the relative importance of processes revealed that propagule pressure is the strongest factor governing rosette density, i.e., rosettes grow where

seeds land, and adult density is governed by rosette density, i.e., adults are still living primarily where the seeds landed despite thinning effects. The adult life stage should be targeted for management to cut off propagule supply and thus regulate the population. Interestingly, we also found that adult density was negatively correlated with the density of rosettes; this result suggests a benefit of late removal of adults to suppress rosette survival, though adults should be removed or their inflorescences cut before seeds are developed. However, this strategy should be further tested over multiple years in replicate sites to account for the potential confounding by a cyclical alternation of adult- and rosette-dominated years and a legacy effect of the soil seed bank.

To conclude, the first available estimate of *A. petiolata* mean dispersal distance under field conditions will provide important guidance for empirical studies and computer simulation modeling aimed at developing optimal management strategies. Overall, the results from this study together with earlier studies on *A. petiolata* suggest that rosette density is positively related to propagule pressure but negatively related to adult density (Meekins and McCarthy 2002; Winterer et al. 2005; Bauer et al. 2010; Evans et al. 2012). In contrast, fine-scale variation in environmental site conditions does not seem to matter for structuring this species. Our results suggest that the adult life stage should be targeted for management, the strong negative effect of adult density on rosette density suggests removing adults later, before seed shed, rather than early in spring, to benefit from this intraspecific interaction.

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References

- Anderson RC, Dhillon SS, Kelley TM (1996) Aspects of the ecology of an invasive plant, garlic mustard (*Alliaria petiolata*), in central Illinois. *Restoration Ecology* 4: 181-191
- Bauer JT, Anderson RC, Anderson MR (2010) Competitive interactions among first-year and second-year plants of the invasive, biennial garlic mustard (*Alliaria petiolata*) and native ground layer vegetation. *Restor. Ecol.* 18:720–728
- Biswas SR, Kotanen PM, Kambo D, Wagner HH (2014) Context-dependent patterns, determinants and demographic consequences of herbivory in an invasive species. *Biological Invasions* DOI: 10.1007/s10530-014-0715-0
- Biswas SR, Wagner HH (2012) Landscape contrast: a solution to hidden assumptions in the metacommunity concept? *Landscape Ecology* 27: 621-631
- Biswas SR, Wagner HH (2014) A temporal dimension to the stress gradient hypothesis for intraspecific interactions. *Oikos* DOI:10.1111/oik.00878
- Bivand R, Altman M, Anselin L, Assunção R, Berke O, Bernat A, Blanchet G, Blankmeyer E, Carvalho M, Christensen B, Chun Y, Dormann C, Dray S, Halbersma R, Krainski E, Legendre P, Lewin-Koh N, Li H, Ma J, Millo G, Mueller W, Ono H, Peres-Neto P, Piras G, Reder M, Tiefelsdorf M, Yu D (2012) spdep: Spatial dependence: weighting schemes, statistics and models. R package version 0.5-46/r430. <http://R-Forge.R-project.org/projects/spdep/>

- 455 Bullock JM, Clarke RT (2000) Long distance seed dispersal by wind: measuring and modelling
456 the tail of the curve. *Oecologia* 124: 506-521
- 457 Cavers P, Heagy M, Kokron R (1979) The biology of Canadian weeds. 35. *Alliaria petiolata* (M.
458 Bieb.) Cavara and Grande. *Canadian Journal of Plant Science* 59: 217–229
- 459 Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) *Dispersal*. Oxford University Press, UK
- 460 Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological
461 invasions. *Biological Invasions* 8: 1023–1037
- 462 Cottenie K (2005) Integrating environmental and spatial processes in ecological community
463 dynamics. *Ecology Letters* 8: 1175–1182.
- 464 Cruden RW, McClain AM, Shrivastava G (1996) Pollination biology and breeding system of
465 *Alliaria petiolata* (Brassicaceae). *Bulletin of the Torrey Botanical Club* 123: 273-280
- 466 Dale MRT (1999) *Spatial pattern analysis in plant ecology*. Cambridge University Press,
467 Cambridge, UK
- 468 Davis AS, Landis DA, Nuzzo V, Blossey B, Gerber E, Hinz HL (2006) Demographic models
469 inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). *Ecological*
470 *Applications* 16: 2399–2410
- 471 Dormann CF, McPherson J, Araújo MB, Bivand R, Bolliger J, Carl G, Davies RG, Hirzel A, Jetz
472 W, Kissling WD, Kühn I, Ohlemüller R, Peres-Neto P, Reineking B, Schröder B, Schurr FM,
473 Wilson R (2007) Methods to account for spatial autocorrelation in the analysis of
474 distributional species data: a review. *Ecography* 30: 609–628.
- 475 Dray S, Pellissier R, Couteron P, Fortin MJ, Legendre P, Peres-Neto P, Bellier E, Bivand R,
476 Blanchet FG, Caceres M, Dufour AB, Heegaard E, Jombart T, Munoz F, Oksanen J,
477 Thioulouse J, Wagner HH (2012) Community ecology in the age of multivariate multiscale
478 spatial analysis. *Ecological Monographs* 82: 257–275

- 479 Evans JA, Davis AS, Raghu R, Ragavendran A, Landis DA, Schemske DW (2012) The
480 importance of space, time, and stochasticity to the demography and management of *Alliaria*
481 *petiolata*. *Ecological Applications* 22: 1497–1511
- 482 Fortin MJ, Dale MRT (2005) *Spatial Analysis: A Guide for Ecologists*. Cambridge University
483 Press
- 484 Fortin M-J, James PMA, MacKenzie A, Melles SJ, Rayfield B (2012) Spatial statistics, spatial
485 regression, and graph theory in ecology. *Spatial Stat* 1:100–109
- 486 Gilpin ME, Hanski I (1991) *Metapopulation dynamics: empirical and theoretical investigations*.
487 Academic press, London
- 488 Hewitt JE, Legendre P, McArdle BH, Thrush SF, Bellehumeur C, Lawrie SM (1997) Identifying
489 relationships between adult and juvenile bivalves at different spatial scales. *Journal of*
490 *Experimental Marine Biology and Ecology* 216: 77–98
- 491 Holt RD, Hoopes MF (2005) Food web dynamics in a metacommunity context. In: Holyoak M,
492 Leibold MA, Holt RD (eds) *Metacommunities: Spatial Dynamics and Ecological*
493 *Communities*. University of Chicago Press, Chicago and London, pp. 68–93
- 494 Jones O, Maillardet R, Robinson A, Borovkova O, Carnie C (2009) *Introduction to Scientific*
495 *Programming and Simulation Using R*. Taylor and Franchis Group, LLC, USA
- 496 Jones O, Maillardet R, Robinson A, Borovkova O, Carnie C (2012) *spuRs: Functions and*
497 *Datasets for "Introduction to Scientific Programming and Simulation Using R"* R package
498 version 1.0.5
- 499 Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74: 1659–1673
- 500 Legendre P, Legendre L (1998) *Numerical Ecology*. Elsevier

- 501 Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin
502 JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a
503 framework for multiscale-community ecology. *Ecology Letters* 7: 601–613
- 504 Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur Award
505 Lecture. *Ecology* 73: 1943–1967
- 506 Levine JM, McEachern AK, Cowan C (2011) Seasonal timing of first rain storms affects rare
507 plant population dynamics. *Ecology* 92: 2236–224
- 508 Lockwood J, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species
509 invasions. *Trends in Ecology and Evolution* 20: 223–228
- 510 Luken JO, Thieret JW (1997) Assessment and management of plant invasions. Springer series on
511 environmental management. New York: Springer. pp117
- 512 Malkinson D, Jeltsch F (2007) Intraspecific facilitation: a missing process along increasing stress
513 gradient – insights from simulated shrub populations. *Ecography* 30: 339–348
- 514 McCann KS, Rasmussen JB, Umbanhowar J (2005) The dynamics of spatially coupled food
515 webs. *Ecology Letter* 8: 513–523
- 516 McIntire EJB, Fajardo A (2009) Beyond description: the active and effective way to infer
517 processes from spatial patterns. *Ecology* 90: 46–56
- 518 Meekins JF, McCarthy BC (2001) Effect of environmental variation on the invasive success of a
519 nonindigenous forest herb. *Ecological Applications* 11: 1336–1347
- 520 Moran PAP (1948) The interpretation of statistical maps. *Journal of Royal Statistics Society B*
521 (Methodological) 10: 243–251
- 522 Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and
523 consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285

- 524 Pielou EC (1960) A single mechanism to account for regular, random and aggregated
525 populations. *Journal of Ecology* 69: 575–584
- 526 Powell RD (1990) The role of spatial pattern in the population biology of *Centaurea diffusa*.
527 *Journal of Ecology* 78: 374–388
- 528 R Development Core Team (2011) R: A language and environment for statistical computing.
529 Viena: R Foundation for Statistical Computing.
- 530 Rodgers VL, Stinson KA, Finzi AC (2008) Ready or not, garlic mustard is moving in: *Alliaria*
531 *petiolata* as a member of eastern north American forests. *BioScience* 58(5): 426–436
- 532 Schlup B, Wagner HH (2008) Effects of the study design and analysis on the spatial community
533 structure detected by multiscale ordination. *Journal of Vegetation Science* 19: 621–632
- 534 Seabloom EW, Bjornstad ON, Bolker BM, Reichman OJ (2005) Spatial signature of
535 environmental heterogeneity, dispersal, and competition in successional grasslands.
536 *Ecological Monographs* 75: 199–214
- 537 Venables WN, Ripley BD (2002) *Modern Applied Statistics with S*. Fourth Edition. Springer,
538 New York
- 539 Wagner HH, Fortin MJ (2005) Spatial analysis of landscapes: concepts and statistics. *Ecology*
540 86:1975–1987
- 541 Williamson M (1996) *Biological Invasions*. Chapman Hall, London UK, 244 pp
- 542 Winterer J, Walsh MC, Poddar M, Brennan JW, Primak SM (2005) Spatial and temporal
543 segregation of juvenile and mature garlic mustard plants (*Alliaria petiolata*) in a central
544 pennsylvania woodland. *The American Midland Naturalist* 153: 209–216
- 545

546 **Table 1**547 Fits of the dispersal kernels models (transect probability density functions) for *Alliaria petiolata*;

548 models are ranked on the basis of the AICc.

Function	Model	AICc of replicate point sources (1 – 5)					Rank
		1	2	3	4	5*	
Lognormal	$f(x) = \frac{1}{x \cdot \sigma \sqrt{2\pi}} e^{-\frac{(\ln(x)-\mu)^2}{2\sigma^2}}$	84.0	85.8	61.6	73.1	127.3	1
Weibull	$f(x) = \begin{cases} \frac{k}{\lambda} \left(\frac{x}{\lambda}\right)^{k-1} e^{-\left(\frac{x}{\lambda}\right)^k} & x \geq 0 \\ 0 & x \leq 0 \end{cases}$	97.6	104.1	63.0	78.8	136.0	2
Exponential	$f(x) = \lambda e^{-\lambda x}$	108.5	113.0	70.7	83.0	180.7	3
Half-normal	$f(x) = \frac{\sqrt{2}}{\sigma \sqrt{\pi}} e^{-\frac{x^2}{2\sigma^2}} \quad x > 0$	121.9	136.6	69.5	94	151.2	4

549 * A large number of seed traps were displaced (by animals) in this replicate.

550

551 **Table 2**

552 Ecological processes and measured variables known to be relevant to processes

Ecological processes	Variables hypothesized to be associated with each process	
	Rosette density (R_t)	Adult density (A_t)
Environmental filtering	• Soil moisture (M), • Light (LAI)	• Soil moisture (M), • Light (LAI)
Propagule pressure	• Quadrat-level seed production (qS_{t-1}), • Neighboring seed production (nbS_{t-1})	• Rosette density (R_{t-1})
Biotic interactions	• Adult density (A_t)	-

553

554

555 **Table 3**556 Parameter estimates from spatial regression predicting rosette R_t and adult density A_t as a

557 function of environmental filtering, propagule pressure and life-stage interactions.

Response	Processes	Factor	Estimate	SE	Z	Model diagnostics
Rosettes ₂₀₁₀	Random population effects	Pop 1	0.438	0.116	3.763	
		Pop 2	-0.536	0.145	-3.690	
		Pop 3	-0.081	0.110	-0.742	
	Environmental filtering	Soil moisture	-0.005	0.053	-0.104	$pseudo-R^2 = 0.58$
		Light	-0.030	0.048	-0.630	$\lambda = \mathbf{0.399}$
	Propagule pressure	Quadrat-level seed production ₂₀₀₉	0.489	0.057	8.533	AIC = 339.73
		Seed from neighbor ₂₀₀₉	0.264	0.059	4.411	
	Life-stage interactions	Adults ₂₀₁₀	-0.285	0.057	-4.989	
Adults ₂₀₁₀	Random population effects	Pop 1	-0.490	0.083	-5.891	
		Pop 2	0.485	0.105	4.623	
		Pop 3	0.159	0.080	1.976	$pseudo-R^2 = 0.76$
	Environmental filtering	Soil moisture	0.003	0.039	0.076	$\lambda = \mathbf{0.380}$
		Light	-0.038	0.036	-1.050	AIC = 233.62
	Rosettes	Rosettes ₂₀₀₉	0.819	0.040	20.032	
Rosettes ₂₀₁₁	Random population effects	Pop 1	0.088	0.194	0.452	
		Pop 2	-0.078	0.225	-0.346	
		Pop 3	-0.057	0.182	-0.314	
	Environmental	Soil moisture	-0.086	0.074	-1.158	$pseudo-R^2 = 0.09$

Response	Processes	Factor	Estimate	SE	Z	Model diagnostics
	filtering	Light	0.015	0.067	0.234	$\lambda = \mathbf{0.476}$
	Propagule pressure	Quadrat-level seed production ₂₀₁₀	0.265	0.076	3.468	AIC =463.8
		Seed from neighbor ₂₀₁₀	0.009	0.084	0.108	
	Life-stage interactions	Adults ₂₀₁₁	0.025	0.077	0.334	
Adults ₂₀₁₁	Random population effects	Pop 1	0.427	0.110	3.860	$pseudo-R^2 = 0.49$
		Pop2	0.311	0.138	2.251	$\lambda = \mathbf{0.216}$
		Pop3	-0.597	0.102	-5.811	AIC =398.41
	Environmental filtering	Soil moisture	0.007	0.058	0.124	
		Light	0.044	0.056	0.792	
	Rosettes	Rosettes ₂₀₁₀	0.455	0.063	7.164	

558 SE = standard error; Z= Z-score; †significant ($\alpha=0.05$) values are shown in bold faces; ‡ λ =
559 coefficient of the spatial error term; AIC = Akaike Information Criteria

Figure legends

Fig. 1 Design of a seed trap set (*a*) showing its parts, the base (*b*), the bottom netting (*c*), and seed trap placement in the field (*d*). Seed traps were placed 0.5 m apart, up to 4 m from point source (*e*). Increasing number of seed traps were placed as the distance from point source increased (*f*).

Fig. 2 Seed shadows (*a-e*) and estimated seed dispersal kernels (*f*) in *Alliaria petiolata* for five point sources (= replicates). For each point source, each bar represents the average number of seeds per trap per distance class. In *f*, the transect pdf and the radial pdf are the average dispersal kernel ($n = 5$) before and after correcting for the radial diffusion effect. The dotted lines (in *f*) indicates transect and radial pdfs, the average dispersal kernels ($n = 4$) without point source 5.

Fig. 3 Moran's *I* correlograms showing spatial structure of rosettes (left) and adults (right) of *Alliaria petiolata* averaged over all three populations in 2009 (top), 2010 (center) and 2011 (bottom). A filled circle in each lag indicates statistically significant autocorrelation following a progressive Bonferroni correction (Hewit et al. 1997).

578

579

580

Fig. 1

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582

Fig. 3

Online Resource 1:

Patches of *Alliaria petiolata* after winter snowmelt - an example of spatial structure in the studied populations. The inset shows sampling design illustrating layout of transects and quadrats.

Online Resource 2:

Population-wise spatial correlograms for rosettes and adults for yrs. 2009-2011. A filled circle in each lag indicates statistically significant autocorrelation following a progressive Bonferroni correction (Hewitt et al. 1997).