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Greater sexual reproduction contributes to differences in demography of invasive plants and their noninvasive relatives

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Abstract. An understanding of the demographic processes contributing to invasions would improve our mechanistic understanding of the invasion process and improve the efficiency of prevention and control efforts. However, field comparisons of the demography of invasive and noninvasive species have not previously been conducted. We compared the in situ demography of 17 introduced plant species in St. Louis, Missouri, USA, to contrast the demographic patterns of invasive species with their less invasive relatives across a broad sample of angiosperms. Using herbarium records to estimate spread rates, we found higher maximum spread rates in the landscape for species classified a priori as invasive than for noninvasive introduced species, suggesting that expert classifications are an accurate reflection of invasion rate. Across 17 species, projected population growth was not significantly greater in invasive than in noninvasive introduced species. Among five taxonomic pairs of close relatives, however, four of the invasive species had higher projected population growth rates compared with their noninvasive relative. A Life Table Response Experiment suggested that the greater projected population growth rate of some invasive species relative to their noninvasive relatives was primarily a result of sexual reproduction. The greater sexual reproduction of invasive species is consistent with invaders having a life history strategy more reliant on fecundity than survival and is consistent with a large role of propagule pressure in invasion. Sexual reproduction is a key demographic correlate of invasiveness, suggesting that local processes influencing sexual reproduction, such as enemy escape, might be of general importance. However, the weak correlation of projected population growth with spread rates in the landscape suggests that regional processes, such as dispersal, may be equally important in determining invasion rate.

Key words: *demography; invasive species; life table response experiment; matrix population model; phylogeny.*

Introduction

A major goal of conservation biology is to understand mechanisms of biological invasion, defined here as rapid spread in the landscape (sensu Richardson et al. 2000), due to both local-scale demographic factors and regional-scale processes, such as dispersal (reviewed in Rejmánek 2011). Attempts to identify correlates of invasion have included trait-based approaches (e.g., Rejmánek and Richardson 1996, Pheloung et al. 1999, Daehler and Carino 2000, Van Kleunen et al. 2010), demographic analyses (e.g., Parker 2000, Schutzenhofer et al. 2009, reviewed in Ramula et al. 2008), and spread rate models that include dispersal information (Neubert and Caswell 2000). All of these approaches typically

compare invasive and native species. Here we present two methodological advances in the identification of correlates of invasiveness: (1) we compare invasive species to noninvasive introduced species, rather than to native species, because traits that differ between invasive and noninvasive species should more accurately reflect correlates of invasiveness, and (2) we parameterize matrix population models in the field for invasive species and their noninvasive relatives, to evaluate why some introduced species are highly invasive, while their introduced close relatives might be less invasive.

Comparison of invasive species to their introduced noninvasive relatives is the most appropriate study design for identifying mechanisms governing invasiveness, yet this approach is still rare (but see, e.g., Grotkopp et al. 2002, Burns 2008). Because both invasive and noninvasive introduced species have had the same potential for population spread in the novel range, comparisons between them reveals more about the potential mechanisms of invasiveness than comparisons with native species (Rejmánek and Richardson 1996). Meta-analyses have demonstrated that invasive

populations have higher projected population growth than native populations, and the difference was correlated with greater importance (elasticities) of growth and fecundity for invaders and greater importance of survival for natives (Ramula et al. 2008). However, because there are no in situ demographic studies of noninvasive introduced populations of which we are aware (as pointed out in Rejmánek 2011), the extent to which conclusions can be generalized from the native population comparison is unknown. We present a demographic comparison of invasive populations with noninvasive introduced populations to identify vital rates correlated with invasiveness.

The study of invasions using demographic approaches is powerful because matrix population models provide a snapshot estimate of fitness that integrates across the life cycle (McGraw and Caswell 1996), and creating demographic models from static life table data is considerably more efficient than following cohorts from birth to death. Matrix population models are a widely used tool for projecting dynamics of structured populations (Caswell 2001) and have been used to understand the population dynamics of invasive plant species (reviewed in Ramula et al. 2008). Individual vital rates, such as growth, survival, and fecundity, are incorporated into these models and are used to project population growth (Caswell 2001). The dominant eigenvalue of the matrix, λ, projects how fast the population would grow if conditions remained the same as when the demographic parameters were measured. Lambda values >1 (ln $\lambda > 0$) project that a population will experience net positive growth, and lambda values <1 (ln $\lambda < 0$) project that the population will decline. While lambda is not an explicit prediction of future population size, it is a powerful tool for comparing the behavior of different populations (Crone et al. 2011), such as in our present analysis of 17 co-occurring species. By decomposing demographic matrix models using retrospective sensitivity analysis (Life Table Response Experiments, LTRE) (Caswell 2001), one can quantify how transitions in the life cycle contributed to differences in λ for invasive as compared to noninvasive species.

This approach will yield insights into the relative importance of local and regional processes in invasiveness. If regional processes are more important in determining invasiveness, we would expect no difference between invasive and noninvasive species in λ, reflecting similar local processes and implicating regional processes like dispersal in governing spread rates. Alternatively, if local processes, such as habitat filtering, herbivory, and competition, are important determinants of invasiveness, we might find that invasive species have consistently higher λ. This could be a result of species-specific patterns in the underlying vital rates. For example, it is possible that invasive species are better able to increase their fitness in the introduced habitat than their noninvasive relatives, but one invasive species might succeed because of its high fecundity, whereas

another might have high adult survivorship. Alternatively, invasive species could show consistent patterns in demographic strategies, in which case invasiveness might be due to differences in life history between invasive and noninvasive species. For example, invasive species might have greater constitutive allocation to fecundity, or might have greater plasticity in fecundity, a vital rate that demographic analyses suggest is highly variable (Morris and Doak 2004, Burns et al. 2010).

We examined the demography of 17 species that co-occurred in a single study location to control for as much environmental variation as possible. Controlling for environmental variation is essential for determining correlates of invasiveness, because temporal and spatial variation contribute to a large amount of the variation in demographic projections (Buckley et al. 2010). When environments are inconsistent across populations, environmental variance might obscure correlates of invasiveness. For example, in a greenhouse study that controlled for environmental variation, projected population growth was significantly associated with invasiveness in the Commelinaceae, but only in high-nutrient environments, in which consistently greater vegetative reproduction in the invasive species contributed to their larger λ (Burns 2008). Here, we present the first in situ comparison of the demography of invasive and noninvasive species; recent meta-analyses have found no such comparisons (Ramula et al. 2008, Buckley et al. 2010, Burns et al. 2010). This comparison has the advantage of realistic measures of demographic parameters in the field, while controlling for some environmental variance by conducting the in situ study at a single location.

To compare demographic contributions to invasiveness, we conducted a field study of population growth and dynamics of 10 invasive and 7 noninvasive introduced species at a single field site in Missouri, USA. We simultaneously tested whether phylogeny improved model fit for vital rates and λ, to determine whether comparative studies of invasive plant demography might benefit from incorporating phylogeny (Felsenstein 1985, Martins and Garland 1991, Martins and Hansen 1997). Finally, in order to identify the demographic patterns leading to invasiveness, we used LTRE to decompose the demography of these species and evaluate what demographic transitions contributed to differences in projected population growth rates between invasive species and their noninvasive relatives.

METHODS

We quantified the demography of 17 introduced species in a small geographic area within Tyson Research Center (Tyson), an ~800-ha field station in St. Louis County, Missouri, USA (38°30′ N, 90°30′ W) (Fig. 1; Appendix A). We chose a sample of introduced species that (1) occurred at the study site in sufficient numbers for demographic monitoring, (2) represented a broad phylogenetic sampling of the angiosperms, (3) could be classified as invasive or noninvasive based on
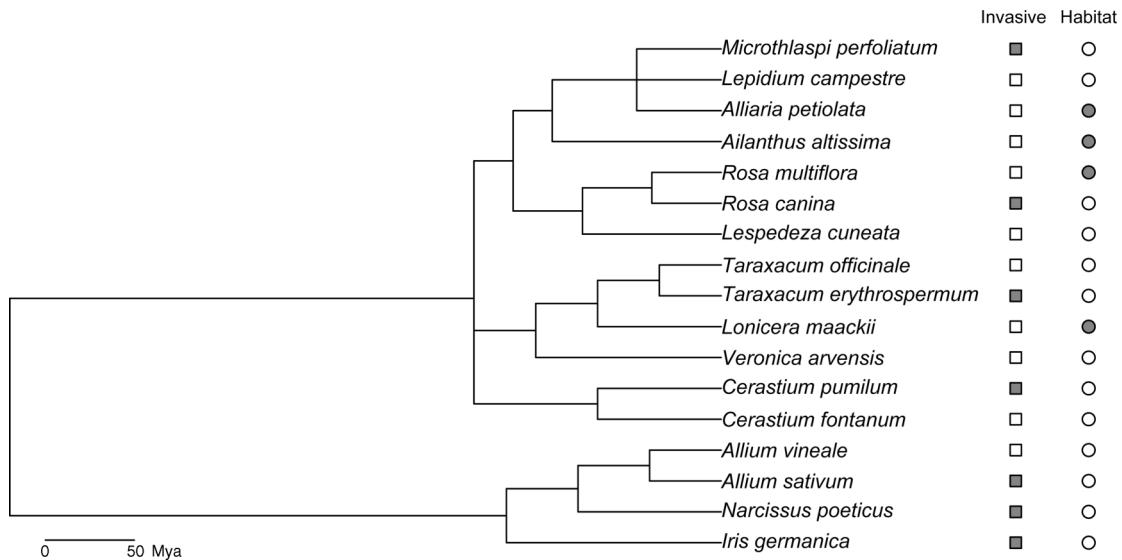
Fig. 1. The phylogenetic relationships among introduced terrestrial plant species in this demographic study estimated with Phylomatic (Webb and Donoghue 2005). Symbols are as follows: invasive species by a priori classification, open squares; noninvasive introduced species, gray squares; old-field species, open circles; forest species, gray circles. Mya stands for millions of years ago.

expert classifications, and (4) had occurred in Missouri for at least 30 years, minimizing the chances of misclassifying a future invasive species as noninvasive. We also estimated the date of first appearance in Missouri, based on herbarium records (Appendix B). Further, to determine whether habitat classification was a useful covariate in explaining demographic patterns, we classified the habitat association for each species as either forest or old field (Fig. 1).

Species were classified a priori as invasive or noninvasive using the USDA Plants Database and the Missouri EPPC list (MEPP 2002, USDA 2010). *Rosa canina* is invasive in Australia (cf. Parsons and Cuthbertson 2001), but not in Missouri (MEPP 2002), and it was classified as noninvasive in this study. Because "invasiveness" is most often defined by ecologists as rapid spread in the introduced range (Richardson et al. 2000), we also measured local invasiveness by estimating the empirical rate of spread in the landscape based on herbarium records (sensu Lonsdale 1993; see Appendix B for additional details). We then compared to what degree invasive and noninvasive species differed in empirical spread rates as an independent check of the a priori classifications.

To quantify demographic parameters, individuals were marked and followed in the field from 2007 to 2008, with the exceptions of *Lespedeza cuneata* and *Alliaria petiolata*, where demographic information was estimated at the same field site but in different years (Schutzenhofer and Knight 2007, Pardini et al. 2009, 2011). Details of how each matrix was constructed can be found in Appendix C. The population projection matrix for *Lespedeza cuneata* was taken from the control treatment (no artificial herbivory) from Schutzenhofer

and Knight (2007), which was parameterized at Tyson Research Center in 2005 and 2006. The density-independent population projection matrix for *Alliaria petiolata* was parameterized at Tyson in 2003 and 2004, except for one parameter, early seedling survivorship, which was parameterized in 2006 (Pardini et al. 2009). Estimates were extracted from data in Pardini et al. (2009, 2011), except for the seed bank transitions, which were modified for consistency with the models presented here (Appendix C: Tables C3 and C4, and footnotes therein). Density-independent vital rates for *Alliaria petiolata* were estimated for summer survival, winter survival, and fecundity from plots with <10 adult plants/m^2 (Appendix C: Table C4).

We classified individuals as seeds in the seed bank, seedling, nonreproductive, or reproductive, where appropriate, in order to build a stage-based matrix population model across a broad sample of species, with modifications as appropriate for each life cycle (Fig. 2; Appendix C: Table C4). Seedlings were defined by size for in situ populations for *Ailanthus altissima*, *Lonicera maackii*, and *Rosa multiflora* with size cut-offs of heights 10, 20, and 50 cm, respectively. *Lespedeza cuneata* is a long-lived perennial with multiple size classes of reproductive individuals and multiple seed types (cleistogamously and chasmogamously produced seeds [Schutzenhofer and Knight 2007]). *Ailanthus altissima* is a dioecious species, and the matrix model describes dynamics of the female plants. We attempted to sample ~90 individuals in each stage class to estimate stage transition probabilities (Appendix C: Tables C3 and C4), which simulation studies suggest is sufficient for most demographic parameters (Fiske et al. 2008). Survival and transitions among life stages (e.g., nonre-

$$\mathbf{A} = \begin{bmatrix} v_2(1-e_2) & 0 & 0 & f_3v_1(1-e_1) \\ v_2e_2 & 0 & 0 & f_3v_1e_1 \\ 0 & s_2g_2 & s_3(1-g_3) & s_4r_4 \\ 0 & 0 & s_3g_3 & s_4(1-r_4) \end{bmatrix}$$

Fig. 2. The demographic matrix models followed the general format of a four-stage model with seed bank, seedlings, nonreproductive, and reproductive stage classes (subscripts 1, 2, 3, and 4, respectively), with several exceptions (Appendix C). Vital rates were viability, v; emergence, e; fecundity, f; survival, s; growth, g; and retrogression, r.

productive-to-reproductive) were recorded for all individuals.

Survival, growth, and retrogression transitions were empirically estimated, with a few exceptions (Appendix C: Table C4). For example, the population of *Taraxacum officinale* experienced a catastrophic flood in the winter of 2007 and all marked reproductive individuals died or tags were washed away. However, anecdotal evidence at Tyson (J. H. Burns, *personal observation*) suggests that this species does not have a survival rate of 0 at this site. To add biological realism, we estimated survival of reproductive individuals and transitions from nonreproductive to reproductive of *T. officinale* at 0.01 rather than the observed 0. Because survival of its noninvasive relative *T. erythrospermum* Andrz. ex Besser (syn. *T. laevigatum* (Willd.) DC.) was 0.55 at Tyson and nonreproductive-to-reproductive transition was 0.13, using an estimate of 0.01 should result in a conservative estimate of λ for the more invasive species, *T. officinale*. We refer to this as the "conservative" parameterization for *T. officinale* in the results. Comparable models with survival of reproductive individuals and nonreproductive-to-reproductive transition for *T. officinale* set equal to the estimates of 0.55 and 0.13 (as for *T. erythrospermum*), respectively, yielded a higher estimate of λ for the invasive *T. officinale*. We refer to the latter as the more "realistic" parameterization for *T. officinale*. Lambda was 10.06 with survival of reproductive individuals set to the more realistic *T. erythrospermum* rates, compared with λ = 2.87 in the more conservative case (Appendix C: Table C4). Analyses that follow use the more conservative λ = 2.87 estimate, unless otherwise specified.

Fecundity was estimated as the average number of seeds produced per individual (see Appendix C: Table C1 for vital rate definitions). For species with many fruits, fruit number per plant was counted, and fecundity was estimated by multiplying fruit number by the number of seeds per fruit, which was estimated for a subsample of 30 representative fruits per species. For the *Taraxacum* species, which fruit throughout the season, fecundity was estimated as the product of the

number of seeds per inflorescence and the number of inflorescences per plant, counted twice per week, over the course of a field season. For *Iris germanica*, *Narcissus poeticus*, and *Rosa canina*, we observed no sexual reproduction over the course of three field seasons, probably as a result of self-incompatibility (East 1940, Wissemann and Hellwig 1997), and thus we only included asexual reproduction in models for these species, which was included in the nonreproductive-to-nonreproductive transition (Appendix C: Table C2).

To estimate germination transitions, field germination trials were conducted for each species in the demographic comparison in a common garden from 2007 to 2009. Seeds were placed on top of the soil in fine mesh bags that allowed light penetration and were buried under a layer of litter approximating the average litter in the surrounding habitat (sample sizes in Appendix C: Table C3). Seed bags were checked for new germination and seedlings removed each week from 15 May 2008 to 24 June 2008. The germination probability for seeds produced that year was estimated as the proportion of seeds germinating in 2008, g_{erm1}/p_1, = seeds germinating in 2008/seeds planted in 2007. Seeds remaining after this trial were split into two samples, one for seed viability estimates ($n = 20$), and a second that was reburied for a second germination trial to quantify seed transitions out of the seed bank (Appendix C: Table C3). To estimate germination out of the seed bank, we monitored germination from May to June 2009 using identical methods on the subset of seeds reburied from the first germination experiment, and again estimated the probability of germinating as the proportion of seeds that germinated in this trial. The probability of germinating out of the seed bank was estimated for seeds germinating in 2009 as g_{erm2}/p_2 = seeds germinating in 2009/seeds replanted in 2008 (see Appendix C: Tables C1–C3).

To estimate survival of seeds after a single year in the seed bank, we conducted tetrazolium-staining (Baskin and Baskin 2004, Peters 2004) tests to determine seed viability on seeds from the 2007–2008 germination experiment. This estimate of viability, v_t, was calculated as the proportion of viable seeds. The seed bank was modeled with exponential decay with an empirically estimated, constant rate of decline (Appendix C: Fig. C1) (e.g., Kalisz 1991, Auld 1995, but see Meyer et al. 2006). No germination was observed in the experiment for *Ailanthus altissima*, and in 2008 tetrazolium staining (Baskin and Baskin 2004) found 0.90 viability for these seeds. Therefore, germination was assumed at a low level of 0.001 for this species, less than the minimum value it was possible to observe (1/400 = 0.0025). (See italicized parameters in Appendix C: Table C4 for estimates that were assumed.)

If there are consistent demographic correlates of invasiveness, then we expect vital rates such as sexual reproduction to be different between invasive and noninvasive species. We used Phylogenetic Generalized Least Squares (PGLS) to determine whether invasive

and noninvasive species differed in vital rates, i.e., sexual reproduction, seed viability, and proportion germination. In PGLS, the phylogeny is incorporated into the error structure of the model as a variance–covariance matrix (Martins and Hansen 1997). The phylogenetic relationships among the species in this study were estimated using Phylomatic (version 4.0.1b, Webb and Donoghue 2005) with reference tree R20080417 and branch lengths estimated following Wikström et al. (2001) (Fig. 1). To create the variance–covariance matrix, we tested among models of evolution (Brownian motion, Ornstein-Uhlenbeck, and Grafen models) and used AIC to choose the best model of evolution (Burnham and Anderson 2002). We then compared models with and without phylogeny in the error structure by AIC and chose the model with the lowest AIC. After choosing the best model by AIC, we then tested for an effect of invasive status by conducting a chi-square test on the likelihood ratio of models with and without the tested effect. For single-effect models, the model without the tested effect was fitted with an intercept only. These tests could only be conducted for vital rates that were consistently present for most species in the study. For example, survival of reproductive individuals was only relevant for longer-lived species, and we had nonzero estimates of this parameter for only 6 out of 17 species; therefore this parameter could not be used in this analysis.

We presented density-independent stage-based demographic models here for two reasons. First, density-independent processes are expected to be most important at the early stages of the invasion process (Neubert and Caswell 2000, Parker 2000), and thus maximum population growth rate of low-density populations might best correlate with invasiveness. This is true for species like *Cytisus scoparius* and *Alliaria petiolata*, which are known to exhibit density dependence that varies across the range (Parker 2000, Pardini et al. 2009, 2011). Second, there was minimal evidence for density dependence in vital rates for most species in these populations, in spite of the broad range of densities sampled (Appendix B: Figs. B1 and B2). The exceptions were fecundity for *Microthlaspi perfoliatum* and *Taraxacum erythrospermum*, survival for *Ailanthus altissima* (Appendix B: Figs. B1and B2), and rosette survival and sexual reproduction for *Alliaria petiolata* (Pardini et al. 2009, 2011), which all exhibit significant density dependence. For these species, we parameterized the stage-based density-independent demographic matrix models at low density to model dynamics at the invasion front (Neubert and Caswell 2000, Parker 2000), following Caswell (2001) with a one-year projection interval (see Appendix C for additional information).

To determine whether invasive species had higher projected population growth rates than their noninvasive relatives, we modeled ln λ as a function of a priori invasive status, and considered models that incorporated the phylogenetic dependence of the sampled species (Felsenstein 1985). We chose the model with the lowest AIC among P/GLS models with Brownian, OU, and Grafen models of evolution (Paradis et al. 2004) or without phylogenetic information in the error structure of the model (Burnham and Anderson 2002). Next, we tested the main effect of a priori invasive status on ln λ, starting with the full model, including invasiveness category and covariates (i.e., date of first appearance in the herbarium records, rate of spread, habitat) and possible interactions, tested among all possible models, and again chose the optimal model by AIC (Burnham and Anderson 2002). We also presented analyses with rate of spread as an independent test of the hypothesis that population growth rate correlates with rate of spread in the landscape, both with and without bird-dispersed species (*Lonicera maackii*, *Rosa canina*, *R. multiflora*) included in the analysis (Appendix D). Lambda was natural log transformed before all analyses, and ln λ are presented throughout for consistency. If expert classifications of invasiveness are accurate, and if demography is sufficient to predict invasiveness, then we expected that ln λ will be consistently greater for invasive species than their noninvasive relatives. If there is not a consistent relationship between spread in the landscape and ln λ, it would suggest that regional (dispersal) processes are at least equally important, compared with local (demographic) processes, in determining invasiveness.

To determine how differences in demographic transitions contributed to differences in λ between invasive and noninvasive relatives, as in Burns (2008), we also conducted a Life Table Response Experiment (LTRE) analysis (Caswell 2001). Species were paired by relatedness, creating five pairs of invasive (I) and noninvasive (N) closely related species: (1) *Allium vineale* (I) and *A. sativum* (N), (2) *Cerastium fontanum* (I) and *C. pumilum* (N), (3) Brassicaceae: *Lepidium campestre* (I) and *Microthlaspi perfoliatum* (N), (4) *Rosa multiflora* (I), and *R. canina* (N), and (5) *Taraxacum officinale* (I) and *T. erythrospermum* (N). All five pairs were more closely related to one another than to other species in the LTRE (Fig. 1). For the purposes of the LTRE, all matrices were coerced to a 4×4 format (e.g., we added a 0-valued transition for seedling and nonreproductive stages to *Cerastium* species) to create matrices of comparable form, allowing LTRE calculations, such as matrix addition, to be conducted. Deterministic λ values were identical for original and coerced matrices (Supplement). We tested whether invasive species differed in ln λ from their noninvasive relatives with a paired *t* test, in two separate analyses: for both the conservative and realistic parameterizations of *Taraxacum officinale*. LTRE contributions to the difference in λ were calculated, and noninvasive contribution matrices were subtracted from invasive contribution matrices within each pair. Average contributions, and their associated standard errors, were calculated across the five pairs (Supplement). Larger LTRE effect sizes contributed
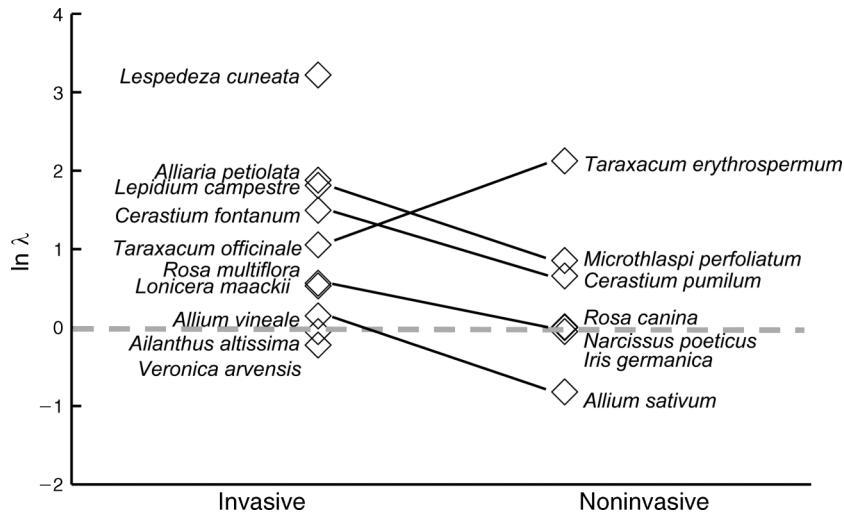
FIG. 3. The projected population growth of ten invasive and seven noninvasive species at Tyson Research Center, St. Louis, Missouri, USA. The dashed line is ln λ = 0, where ln λ > 0 indicates projected population growth, and ln λ < 0 indicates projected population decline. Species were classified a priori as invasive or noninvasive introduced, based on expert classifications (MEPP 2002, USDA 2010) and did not differ significantly in λ between categories ($\chi^2 = 2.11$, $P = 0.15$). Lines are drawn between taxonomic pairs used in the Life Table Response Experiment.

positively to a greater λ for the invasive species compared with its noninvasive relative. All analyses were conducted in R (Paradis et al. 2004, R Statistics 2008).

RESULTS

The maximum spread rate of invasive species was on average three times higher than that for noninvasive species (Appendix D, Fig. D1, Invasive = 73.0 ± 22.3 km/yr, Noninvasive = 21.7 ± 4.6 km/yr; GLS, $\chi^2 = 3.16$, $P = 0.08$). Average spread rate was also higher for invasive species than noninvasive species, though not significantly so (Invasive = 22.4 ± 5.7 km/yr, Noninvasive = 9.38 ± 1.8 km/yr; GLS, $\chi^2 = 2.62$, $P = 0.11$). Invasive and noninvasive species did not differ significantly in date of first appearance in Missouri ($P > 0.25$; Appendix D).

Invasive species differed from their noninvasive relatives in fecundity (sexual reproduction), with more invasive species exhibiting greater fecundities (Appendix D: Fig. D2, Table D1). Models with phylogeny were also preferred to models without phylogeny for fecundity and proportion germination (Appendix D: Table D1), meaning that phylogeny explains some of the error variance in these traits. This can be seen in the taxonomic patterns. For example, *Taraxacum* had very high fecundity, whereas *Allium* had among the lowest fecundity values (Appendix D: Fig. D2). Also, *Taraxacum* had higher germination of newly produced seeds than *Cerastium* (Appendix C: Table C3). Seed viability and germination proportion did not differ significantly between invasive and noninvasive species (Appendix D: Table D1).

Many invasive species had larger projected population growth rates (ln λ) than their noninvasive relatives (Fig. 3). For the conservative parameterization of *T. officinale* (Appendix C: Table C4), the most likely model was the model with invasiveness as a predictor of natural-log-transformed lambda (loglikelihood = −23.675), while the comparable model with just the intercept was not significantly worse (loglikelihood = −24.732, $\chi^2 = 2.11$, $P = 0.15$; Appendix D: Table D2). For the alternative more realistic parameterization of *T. officinale*, again the model with invasiveness was slightly, though not significantly, more likely (loglikelihood = −24.359) than the model with just an intercept (loglikelihood = −24.732, $\chi^2 = 0.75$, $P > 0.39$). Eight out of 10 invasive species had a ln λ greater than 0, projecting that, assuming that conditions remain the same in the future, the populations would grow (Fig. 3). Two invasive species had ln λ <0 (Fig. 3), projecting that the populations would decline. Three of the seven noninvasive species had ln λs ≤0, and four noninvasive species had ln λ >0 (Fig. 3). The model without phylogeny was preferred to the model with phylogeny for analyses on ln λ ($\chi^2 = 1.48$, $P < 0.05$). There were no effects of observed spread rate on ln λ and no interactions between invasiveness category and spread rate on ln λ, as chosen by AIC, though power to detect such interactions might be low (Appendix D: Table D2). There was also no evidence for a significant relationship between maximum spread rate and ln λ across all 17 species ($n = 17$ species; GLS, $\chi^2 = 0.55$, $P > 0.25$) (Fig. 4). The relationship between spread rate and ln λ was also not significant when bird-dispersed species (*Lonicera maackii*, *Rosa canina*, *R. multiflora*) were excluded ($n = 14$ species; PGLS, $\chi^2 = 2.68$, $P = 0.10$), though there
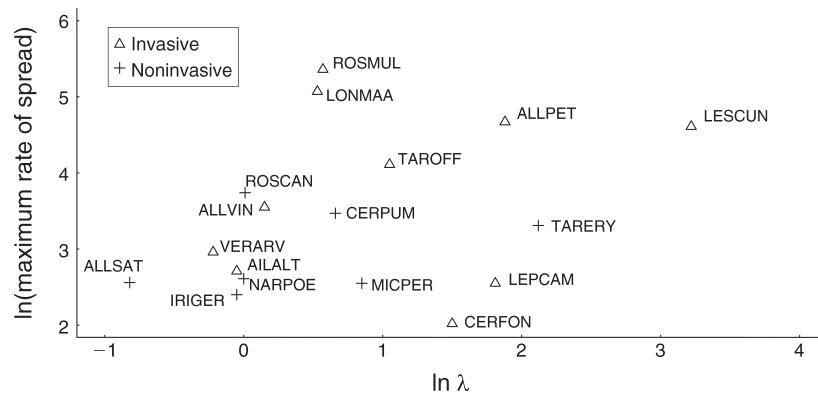
FIG. 4.   There was no significant relationship between ln λ and the maximum rate of spread (in kilometers per year; $n = 17$, generalized least squares [GLS], $\chi^2 = 0.55$, $P > 0.25$), suggesting that spread in the landscape is a function of more than just local demography. This relationship was also not significant when bird-dispersed species (*Lonicera maackii*, *Rosa canina*, *R. multiflora*) were excluded, although there was a marginally significant positive trend ($n = 14$; GLS, $\chi^2 = 2.68$, $P = 0.10$). Abbreviations are the first three letters of the genus and species epithet (see *Methods* and Appendix A).

was a marginally significant positive trend (estimate = 0.39, $t_{1,12} = 2.17$, $P = 0.051$) (Fig. 4). Habitat (forest vs. old field) was also not a covariate in the model chosen by AIC (Appendix D: Table D2).

Five taxonomic pairs were used for further LTRE analysis, where one species in each pair was invasive and one noninvasive. When using the more conservative parameterization of *T. officinale*, projected population growth was greater for four out of five invasive species than their noninvasive taxonomic pair ($t_4 = 1.17$, $P = 0.31$). Alternatively, when using the more realistic parameterization of *T. officinale*, five out of five invasive species had a higher ln λ than their noninvasive taxonomic pair ($t_4 = 4.75$, $P = 0.009$). The LTRE suggested that greater sexual reproduction of the invasive species than their noninvasive taxonomic relative had the largest contribution to the greater ln λ observed for some invasive species (Appendix D: Table D3). The reproductive-to-seed-bank transition, which includes fecundity, and reproductive-to-nonreproductive transition, which often involves the production of seeds that germinate in a single season, exhibited large LTRE effect sizes (Appendix D: Table D3), and this result was the same for both parameterizations of *T. officinale* (Appendix D: Table D3).

DISCUSSION

We compared the in situ demography of 17 introduced populations that differ in invasiveness to determine whether local processes governing demography are sufficient to explain differences in invasiveness among species. The comparison of invasive species to noninvasive introduced species we present here is important because traits and vital rates that differ between invasive and noninvasive species should more accurately reflect demographic correlates of invasiveness than would comparisons of invasive to native species. A priori classifications of invasiveness, based on independent expert classifications, were associated with the observed rate of spread in the landscape, the most widely accepted definition of invasiveness (Richardson et al. 2000), confirming the USDA expert classification (USDA 2010). These invasive species did not always have higher projected population growth than their noninvasive relatives, suggesting that invasiveness was not solely a function of demography, which is consistent with arguments that invasiveness is a function of both local and regional processes (Neubert and Caswell 2000).

The consistent correlation of high sexual reproduction with invasiveness suggests that life history strategies with high allocations to fecundity, either via constitutively higher fecundity or greater resource opportunism, are more likely to become invasive (Burns 2008, Van Kleunen 2010, Davidson et al. 2011). Our comparison of invasive and noninvasive introduced species is broadly consistent with comparisons of invasive and native species, which also suggest that high fecundity might be correlated with invasiveness (e.g., Daehler 2003). Fecundity tends to be a highly plastic life history trait, and demographic meta-analyses have identified it as highly temporally variable within species, compared to survival, which is much less variable across years (Morris and Doak 2004, Burns et al. 2010). Local processes such as escape from herbivory or competition could free resources, allowing more opportunistic invaders to allocate those resources to fecundity (Davidson et al. 2011). Alternatively, invasive species may be those with constitutively higher expression of fecundity in the native range, potentially allowing fecundity to be used as a predictive trait for invasiveness (sensu Pheloung et al. 1999). The current study, however, cannot distinguish between constitutively high fecundity or plasticity in fecundity as driving the observed correlation.

The greater contribution of sexual reproduction to projected population growth rate for some invasive species found here differs from results in Burns (2008),

where vegetative reproduction contributed more consistently to the greater λ of invasive Commelinaceae (dayflower family) species than did sexual reproduction. This difference may be due to differences in life history of the species considered. Commelinaceae have many vegetative members and some self-incompatible invaders (e.g., *Tradescantia fluminensis*). Some of the species in this study (e.g., *Rosa canina*) had vegetative reproduction, but the magnitude of this mode of reproduction was relatively small in this study (Appendix C: Table C3). These differences among taxa in reproductive strategy suggest that sexual and asexual reproduction may be alternative mechanisms leading to the same demographic consequences for invasiveness.

Close relatives were similar in some vital rates (fecundity and proportion of germination) but not in projected population growth rate. Phylogeny did not improve model fit on ln λ, consistent with demographic meta-analyses, which have also failed to detect a phylogenetic signal on λ (Buckley et al. 2010), perhaps because the strong signal of the environment on demography obscures the signal of phylogeny (Burns 2008, Buckley et al. 2010). If integrated fitness measures, such as λ, have little phylogenetic signal, it suggests that within a clade there is considerable variation in factors that influence population dynamics. This is consistent with the long-held observation that close relatives, such as congeners, are often very different in their population dynamics (e.g., Fiedler 1987, Byers and Meagher 1997).

These estimates of ln λ might be best interpreted as a snapshot estimate of fitness (McGraw and Caswell 1996) and are based on a single set of vital rates, which are known to vary among years (e.g., Parker 2000, Burns 2008, Buckley et al. 2010). Thus measuring demography under the appropriate environmental conditions and at the appropriate stage of invasion is essential to understanding demographic mechanisms of invasiveness. Further, studies of invasion phase have determined that λ decreases with time since invasion, because density-dependent processes are expected to act later in the invasion process (Parker 2000, Pardini et al. 2009). Some of the estimates of population growth rate were quite large in this study (e.g., *Lespedeza cuneata*, ln λ = 3.22) and are not sustainable over the long term. Projections for a newly introduced species are most likely to be meaningful at the early, density-independent phase of invasion, because it is the low-density population growth rate that is expected to result in invasiveness. Individual populations may be in different phases of invasion locally, but by conducting demographic studies at a single location and incorporating time since introduction as a covariate, we attempted to minimize some of this environmental variation.

The disproportionately large rate of spread that defines invasive species is a product of both local, demographic processes and regional dispersal processes (Neubert and Caswell 2000). In our study, there were no effects of spread rate (average or maximum) on ln λ across all 17 species (Appendix D: Table D2), in spite of the greater magnitude of spread rates of more invasive species (Appendix D: Fig. D1), suggesting that regional processes such as dispersal and propagule pressure are essential to predict spread rates. Some of our highly invasive species (*Lonicera maackii*, *Rosa multiflora*) had relatively low ln λ values (Fig. 3) and are bird dispersed (Ingold and Craycraft 1983, McDonnell and Stiles 1983, respectively), suggesting that dispersal might play a greater role than demography in governing the spread rate of these invaders. The marginally significant positive relationship between ln λ and maximum spread rate (Fig. 4) when the bird-dispersed species were excluded from the analysis is consistent with this hypothesis. Therefore, spread rate might be better explained by a combination of demography and dispersal, rather than by demography alone. This study is the first comprehensive data set of local population dynamics for both invasive and noninvasive introduced species, and demonstrates significant differences in life history between these groups, especially in sexual reproduction. Demography is a product of local conditions and is dependent on local mechanisms such as habitat filtering, enemy release, competition, and soil feedbacks, and the greater sexual reproduction of invasive species here suggests an important role of such local mechanisms in determining invasiveness. Future work will determine the relative importance of local and regional mechanisms in determining invasiveness.

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SUPPLEMENTAL MATERIAL

Appendix A

Species descriptions for 17 introduced species at Tyson Research Center, St. Louis, Missouri, USA (*Ecological Archives* E094-088-A1).

Appendix B

Supplemental methods for estimating rates of spread in the landscape and density dependence for 17 introduced species at Tyson Research Center, St. Louis, Missouri, USA (*Ecological Archives* E094-088-A2).

Appendix C

Demographic matrix models and details of their construction (*Ecological Archives* E094-088-A3).

Appendix D

Analyses and figures of vital rates, spread rates, and demographic transitions associated with invasiveness for 17 introduced species at Tyson Research Center, St. Louis, Missouri, USA (*Ecological Archives* E094-088-A4).

Supplement

R code for demographic analysis of 17 species of introduced plants at Tyson Research Center, St. Louis, Missouri, USA (*Ecological Archives* E094-088-S1).