No release for the wicked: enemy release is dynamic and not associated with invasiveness

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Abstract. The enemy release hypothesis predicts that invasive species will receive less damage from enemies, compared to co-occurring native and noninvasive exotic species in their introduced range. However, release operating early in invasion could be lost over time and with increased range size as introduced species acquire new enemies. We used three years of data, from 61 plant species planted into common gardens, to determine whether (1) invasive, noninvasive exotic, and native species experience differential damage from insect herbivores and mammalian browsers, and (2) enemy release is lost with increased residence time and geographic spread in the introduced range. We find no evidence suggesting enemy release is a general mechanism contributing to invasiveness in this region. Invasive species received the most insect herbivory, and damage increased with longer residence times and larger range sizes at three spatial scales. Our results show that invasive and exotic species fail to escape enemies, particularly over longer temporal and larger spatial scales.

Key words: biological invasion; browsing; enemy release hypothesis; exotic species; herbivory; introduced plants; invasion biology; invasive species.

Introduction

Most introduced species do not establish, and even fewer become invasive (Williamson and Fitter 1996). Although invasive species have fascinated scientists for decades (Darwin 1859), the causal mechanisms of invasiveness are still undetermined. Some of the earliest writers on invasiveness predicted that loss of enemies in the introduced range might drive the success of invasive species over natives (Thellung 1912, Kowarik and Pyšek 2012). Today, the Enemy Release Hypothesis (ERH) is the predominant, and most extensively tested, mechanism addressing the success of invasive species, and posits that invasive species gain a competitive advantage in their introduced range by escaping enemies that constrained their growth in their native range (Elton 1958, Callaway and Aschehoug 2000, Keane and Crawley 2002). An extension of the ERH is that invasive species are expected to receive reduced damage from enemies compared to co-occurring native species in their introduced range. Enemy release may result in increased population densities, and could explain how invasive species overcome usual controls on population growth such as density dependence and life history trade-offs (Blair and Wolfe 2004, Martin et al. 2010).

Species introduced into new ranges sometimes experience reduced enemy diversity and attack compared to

their native ranges (Mitchell and Power 2003, Torchin et al. 2003, Liu and Stiling 2006), and this reduced damage may translate into increased performance (Maron and Vila 2001). For example, parallel experiments in the native and introduced ranges of *Cynoglossum officinale* found that reduced insect herbivory in the introduced range led to increased performance and population growth rates for this species (Williams et al. 2010, see also DeWalt et al. 2004). Similarly, a review of 473 species found that plants were attacked by 24% fewer virus and 84% fewer pathogen species in their introduced range, compared to their native range, and those species with a lower diversity of pathogens were more invasive, supporting ERH (Mitchell and Power 2003).

However, release from enemies found in the native range does not mean complete release from all enemy pressures. While enemy release may play a role in the explosive population growth rate of invasive species, the acquisition of new enemies in the introduced range could explain why so many introduced species fail to become invasive (Carpenter and Cappuccino 2005, Hawkes 2007). Elton (1958) was the first to describe the dual roles played by enemies during biological invasions: an introduced species leaves behind many of its enemies, but is immediately met with a novel set of potential enemies in its introduced range. These new interactions could be just as important as those initially lost, limiting the establishment and geographic spread of an introduced species, preventing it from becoming invasive (Elton 1958, Maron and Vila 2001). Introduced species released from enemy pressures are likely to experience

increased population growth and competitive ability and as a result become invasive, while introduced species that do not experience release should not (Keane and Crawley 2002).

In this paper, we will follow the conventions used in previous studies (Cappuccino and Carpenter 2005, Liu et al. 2007, Parker and Gilbert 2007, Jogesh et al. 2008) and consider the following patterns of enemy damage evidence for ERH: (1) if enemy release explains the success of invasive species in their introduced range, we expect invaders to receive reduced damage compared to the native species with which they now compete (invasives < natives) and (2) if enemy release explains the differential success between introduced species that become invasive and introduced species that fail to become invasive (i.e., noninvasive exotics), we expect invasives to receive less damage than noninvasive exotics (invasives < noninvasive exotics). These same patterns would hold for ERH studies looking at other responses to enemies, such as enemy effects on plant performance and survival.

Many previous studies on ERH do not differentiate between introduced invasive and noninvasive exotic species, allowing them to test only the first prediction. Given the dual roles enemies play in invasions, homogenizing invasive and noninvasive exotic species into one group could miss important information on the drivers of invasiveness, and thus provide only a conservative estimate for whether invasive species experience enemy release. Studies that do not differentiate between these two types of introduced species have found that introduced plants receive less (Agrawal et al. 2005), no difference (Agrawal and Kotanen 2003, Hawkes 2007, Chun et al. 2010), or more (Ashton and Lerdau 2008, Stricker and Stiling 2014) enemy damage compared to natives. These same patterns are found in studies looking at enemy abundance or the performance consequences of enemy damage (reviewed in Colautti et al. 2004). For example, seed pathogens and predators have similar effects on the fecundity of native and introduced species (Blaney and Kotanen 2001a, b, 2002).

A recent systematic review of the ERH literature found that there is as much evidence for ERH as there is against it (Heger and Jeschke 2014), and studies that find support for ERH tend to include just one pair of native and introduced congeners, while large multi-species experiments tend to find no difference in enemy effects between native and introduced species (Colautti et al. 2004). A meta-analysis by Chun and collaborators (2010) found that introduced plants in general receive similar amounts of damage as native species and their performance was reduced to a greater degree than was natives'. This lack of evidence for ERH may be due to combining invasive and noninvasive exotic species in analyses.

Studies that partition introduced species into invasive and noninvasive exotics are more rare (Liu and Stiling 2006) and find mixed support for ERH as well (e.g., Cappuccino and Carpenter 2005, Carpenter and Cappuccino 2005, Parker et al. 2006, Liu et al. 2007, Parker and Gilbert 2007, Jogesh et al. 2008, Dawson et al. 2014). In a study of native, noninvasive exotic, and invasive *Eugenia* species, native species did in fact receive higher damage levels than invasives, supporting Prediction 1 (Liu et al. 2007; see also Dietz et al. 2004 and Liu and Stiling 2006). The same study found no support for Prediction 2: invasive and noninvasive exotic *Eugenia* species received similar amounts of damage. Other studies support Prediction 2, finding that invasive species received less enemy damage than noninvasive exotic species, or that introduced species that are more invasive tend to receive less herbivore damage or disease (Mitchell and Power 2003, Cappuccino and Carpenter 2005, Carpenter and Cappuccino 2005). These studies reveal that the relationship between enemy pressures and invasiveness is complex and variable across species, study systems, and time (e.g., Agrawal and Kotanen 2003, Agrawal et al. 2005).

Dynamic invasions

An extension of the ERH is that the effects of enemy release may be dynamic over the course of invasion as enemies accumulate in the introduced range. As an introduced species spends more time in its introduced range, expanding into new habitats and occupying a greater area, its likelihood of encountering an enemy that can attack it increases, potentially leading to increased damage with increased residence time and geographic spread. While enemy release may facilitate colonization and establishment during the early stages of an invasion, these benefits could be lost over time as introduced species acquire enemies (Elton 1958, Mitchell et al. 2006, 2010).

Species can accumulate enemies in their introduced range in three ways: (1) as invaders expand their range, they increase their probability of encountering an enemy in the introduced range that can attack them, (2) new introductions may bring enemies from the species' native range from which they had previously escaped, and (3) evolutionary changes or plasticity in native enemies or the introduced species may result in enemies being able to exploit an introduced species as a novel resource (Gossner et al. 2009). Therefore, the magnitude of enemy release is predicted to decrease over time and with range expansion into new habitats (Hawkes 2007, Mitchell et al. 2010).

Studies on both crops and undomesticated species find that introduced species accumulate enemies over time and with increasing geographic spread in the introduced range (Strong et al. 1977, Hawkes 2007). In a study of 124 plant species introduced to North America from Europe, Mitchell and collaborators (2010) found that pathogen richness increased with species' time since introduction and geographic range. Other work has found no relation between time since introduction and damage from enemies (Carpenter and Cappuccino 2005).

Despite the widespread ecological and evolutionary processes that vary over the course of an invasion, only 40% of recent invasion literature mentions the residence times of species (Strayer et al. 2006), and even fewer factor this into their experimental design. If enemy release is dynamic, it could explain some of the contradictory findings in previous studies comparing enemy attack on noninvasive exotic, invasive, and native species (Colautti et al. 2004). Understanding whether invasive species acquire enemies over time and with range expansion will help to predict the long-term effects of biological invasions (Mitchell et al. 2006, Strayer et al. 2006). These distinctions underscore the need for multi-species experiments to test the generality and persistence of enemy release.

Here, we address this need by testing the dynamic nature of enemy release, while differentiating between damage received by invasive and noninvasive introduced species. We conducted multi-year field experiments using 61 plant species from multiple families, three provenances (native, noninvasive exotic, invasive), and with a variety of introduction dates and areas of geographic spread. The objectives of our study are to test the major predictions of the ERH (listed above), and determine how damage from insect herbivores and mammalian browsers changes over the course of invasion. We address two questions: (1) Do invasive, noninvasive exotic, and native species experience different amounts of damage from enemies? (2) Is enemy release lost with increased residence time and geographic spread in the introduced range? We predict that if ERH contributes to invasiveness, invasive plants should receive less damage from insect herbivores and mammalian browsers, compared to native and noninvasive exotic plants. Further, if introduced species lose the benefits of enemy release over time and with increased geographic spread in the introduced range, we predict that noninvasive exotic and invasive plants with earlier introduction dates and larger regional distributions will experience increased insect herbivory and browsing damage.

METHODS

Study species

We planted 61 plant species into an old field community in Michigan, near the W. K. Kellogg Biological Station (42°24′ N, 85°23′ W; Appendix A: Table A1). Species were categorized as native, noninvasive exotic, or invasive ($n = 25$, 25, and 11 species, respectively). We defined native species as those naturally occurring in Michigan, prior to widespread European settlement. Invasive and noninvasive exotic species were both introduced to Michigan from outside the United States, either accidentally or intentionally by humans, according to herbarium and historical records (Reznicek et al. 2011). While noninvasive exotic species assimilated into the native community with little effect, invasive plants aggressively colonized natural areas, threatening biodiversity and human interests.

Invasiveness for this study was determined by inclusion on one or more of the following local invasive species lists, as of June 2014 (Table A1): (1) Michigan Natural Features Inventory (Borland et al. 2009), (2) listed by Czarapata (2005) as "major invader of natural areas" and not categorized as needing disturbance to establish, (3) Wild Type Plants (*available online*),[4] and (4) the Michigan Seed Law (Act 329 of 1965; Legislative Council, State of Michigan 1965). Inclusion on these lists means the species have been categorized as invasive within the midwestern United States based on reports from land managers, inclusion on government invasive species lists, or published documentation of their impacts on native plant and animal communities. Final decisions on status were made in consult with local land managers. We acknowledge that the classification of "invasive" is not an absolute; it can depend on many biotic and abiotic factors (i.e., depends on context). For invasive species found on only one list, we conducted a second analysis of our data listing them as noninvasive exotic; this analysis did not alter the main findings of the paper so we only report the analysis with them listed as invasive.

We chose species based on the following criteria: First, to test for the generalizability of the ERH, we used a species mix that represented a wide range of phylogenetic diversity, residence times (number of years in Michigan), and geographic spread (number of counties occupied; Ahern et al. 2010). Second, we included only herbaceous species to control for life form. Third, we used species already reported in herbarium records for Kalamazoo County (Reznicek et al. 2011) and commonly found in old field or grassland habitats to ensure that experimental plants grew in conditions similar to where they typically occur and also to make certain that we did not introduce species into parts of Michigan where they were not previously found. Finally, we preferentially chose species for which we could obtain seeds from nearby populations, either from personal field collections or orders from local growers, although some species were obtained from a broader geographic region (Table A1).

Experimental design

We planted two common garden field experiments: the first running from June through November 2011 and the second from May 2012 through September 2014. For Experiment 1 in 2011, we germinated seedlings of 30 species from six plant families (13 native, 11 noninvasive exotic, and 6 invasive; Table A1) in greenhouses at the Kellogg Biological Station. We then transplanted two to three replicate seedlings of each species into randomly assigned locations within a 10×10 planting grid located within each of nine field plots ($N = 540$ seedlings). These nine field plots represented the control plots of a large manipulative field experiment. Field plots were 2×2 m

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[4] http://www.wildtypeplants.com/invasive.html

in size, with 2 m separating each plot. Species were planted within a grid of 100 cells within each plot, and were separated from the nearest experimental seedling by 20 cm. From 11 October to 3 November, we measured damage from insect herbivores as the proportion of leaf area removed on 10 leaves per plant, selected as every third leaf starting at the top of the plant, and damage from mammalian browsers as the proportion of aboveground vegetation removed by browsing damage, calculated as the proportion of stems with browsing damage for all plant families except the Poaceae. For the Poaceae, browsing was calculated as the proportion of tillers with browsing damage. If the individual was fully browsed down to the soil surface, we recorded this as 100% browsed. E. H. Schultheis collected all damage data to ensure estimates of aboveground vegetation removal were consistent.

In 2012, we established Experiment 2, which included 50 species from three plant families (20 native, 20 noninvasive exotic, and 10 invasive; Table A1). We transplanted two replicate seedlings of every species into randomly assigned locations within each of five field plots ($N = 500$ seedlings). These five field plots represent the control plots of a large common garden experiment manipulating invertebrate, mammalian, and disease to study their fitness effects on native, noninvasive exotic, and invasive plants. Plots were 2×2 m in size, with 2 m separating each of the 40 plots. Within each plot, species were located within a grid of 100 cells and were separated from the nearest experimental seedling by 20 cm. From 10 September to 4 October in 2012 and 26 August to 12 September in 2013, we estimated insect herbivore damage and mammalian browsing damage as in Experiment 1. Annuals were harvested at the end of the 2012 growing season and are not present in the 2013 census. In Experiment 2, we focused on the plant families Asteraceae, Fabaceae, and Poaceae, which represent three of the four plant families with the most invasive species in Michigan (Ahern et al. 2010). Additionally, these families vary widely in chemical and structural traits, which could play a large role in herbivore defense strategies (Agrawal 2007).

Both experiments were planted in the same old field in Hickory Corners, Michigan, USA. Old field habitats are common in the area and are formed when abandoned agricultural areas convert back to unmanaged land. These communities consist of a wide diversity of both native and introduced plant and animal species. Based on field observations and trapping experiments, the dominant mammalian browsers in this community were *Peromyscus maniculatus bairdii*, *Tamias striatus*, *Spermophilus tridecemlineatus*, *Sylvilagus floridanus*, and *Odocoileus virginianus* (P. Howell, *unpublished data*). These mammals are native to the area (Baker 1983), with *O. virginianus* existing at a moderate to high density of ~30 individuals per square mile (MDNR 2010). Detailed sampling of the insect community was performed in nearby prairie habitats (Robertson et al.

2011), however we were unable to find records that identified insect herbivores down to species, precluding our ability to assign them native or introduced status. It is likely that the community consists of a mix of native and introduced insect herbivores, which differ in their effects on introduced plants (Parker et al. 2006).

Residence time and spread data

To study the dynamic nature of enemy release, we determined the residence time and geographic spread for our invasive and noninvasive exotic species. We defined spread as the number of counties occupied by a species, according to presence in herbarium records. We defined residence time as the number of years a species has occurred in Michigan, and calculated it as the year from the first herbarium specimen or historical record of introduction, subtracted from 2014. The method of using herbarium records to define spread and residence time of species is well established (citations within Ahern et al. 2010), but not without bias, including differential accessibility of field sites and variable sampling efforts over time. Therefore, residence time may actually indicate dates when an introduced species became apparent and occurred at high enough densities to be sampled, especially for species not intentionally introduced and for which we have no historical record of introduction.

We collected Michigan spread data from a published data set, constructed from herbarium and historical records compiled in the Michigan Flora (Reznicek et al. 2011) and updated with recent herbarium records from the University of Michigan Herbarium (Ann Arbor, Michigan; Ahern et al. 2010). Spread data at a regional and broader geographic scale was collected from the USDA PLANTS database, which records county level occurrence data for plant species (*available online*).[5] The USDA assigns county-level occurrence by the presence of herbarium records and the scientific literature, similar to our data set for Michigan. From these data sets we recorded (1) the number of counties invaded in Michigan (local scale), (2) the number of counties invaded in the five nearest states surrounding our study site (Michigan, Wisconsin, Illinois, Indiana, and Ohio; regional scale), and (3) the number of counties invaded in the United States (broad geographic scale).

Phylogenetic reconstruction

To control for phylogenetic nonindependence in our study, we accounted for phylogenetic relatedness in all ANOVA analyses. Nucleotide sequences for matK, rbcL, and ITS were retrieved from NCBI Genbank for each species (accessed February 2015) (Appendix A: Table A1). If a species had no accession for a gene, a sequence from a closely related taxon was chosen, if available. Gene sequences were aligned using the MUSCLE algorithm in Geneious v6.1.8 (Kearse et al.

[5] http://plants.usda.gov/

2012). The ends of sequences were trimmed from each gene, and the three genes were concatenated using phyutility (Smith and Dunn 2008). We determined the optimal model of molecular evolution for the alignment using the Akaike information criterion (AIC), Bayesian information criterion (BIC), and Performance Based Selection (DT) using jModelTest2 v2.1.7 (Darriba et al. 2012). All three methods selected the General Time Reversible (GTR) model, with rate heterogeneity including invariable sites (I) and the rate of evolution at other sites as a gamma distribution (GTR + I + Γ), as the optimal model. Maximum likelihood (ML) analysis with 100 bootstrap replicates was implemented with the high performance computing version of RAxML v8.1.17 (Stamatakis 2014). We included a partition file for ML analysis to account for gene regions in the concatenated alignment. To assess phylogenetic structure for insect herbivory and mammalian browsing across the study species, we calculated Blomberg's K (Blomberg et al. 2003) separately for each year of the study, following methods found in Swenson (2014) and using the phytools package in R (v0.4-21; Revell 2012). Blomberg's K is a measure of whether a trait shows more or less phylogenetic divergence than expected by a null model of Brownian motion.

Statistical analysis

We performed all analyses in R (R Core Team 2015; version 3.0.2). Due to shared ancestry, traits in related species cannot always be viewed as being independent. We therefore incorporated comparative methods with linear models to determine whether invasive, noninvasive exotic, or native species differ in herbivore damage. We performed phylogenetic generalized least squares (PGLS) with Brownian motion and Ornstein-Uhlenbeck (OU) models of trait evolution (Garland et al. 1993, Martins and Hansen 1997), with subsequent AIC model selection. PGLS was implemented by incorporating the constructed phylogeny into the covariance structure using the ape package (v. 3.1-4; Paradis 2012), after which the linear models were fit using the gls function in the nlme package in R (v. 3.1-119; Pinheiro et al. 2015). Proportion of leaf area removed and proportion of stems (or tillers) browsed were included as separate response variables, and plant status (native, noninvasive exotic, or invasive) was included as a fixed predictor variable. Because species is our unit of replication for questions on status, we averaged individuals within a species within a year. Analyses on herbivory and browsing were conducted on within-year species averages; separate analyses were run for each year of data because species composition varied. To determine whether there is a relationship between the damage a species received from insect herbivores and that received from mammalian browsers, we performed a regression using the lm function in R. Species were excluded from some analyses due to high mortality in the field (Appendix A: Table A1, grayed out boxes), likely due to limited rainfall and water availability at the time of

planting, competition from the background community, and enemy damage. Post-hoc tests were used to evaluate differences between treatment combinations when the main effect of status was significant ($P \leq 0.05$), and were implemented with a Holm multiple comparisons correction using the phylANOVA function in the phytools package in R. An additional analysis, including plant family in our models in place of phylogenetic structure, can be found in Appendix B.

To determine whether enemy damage changes with increased residence time or spread, we performed nonlinear ANCOVAs using the glm function in R (R Core Team 2015; v.3.1.1). We included a logit link transformation in the generalized linear model to accommodate the nonlinear associations with county spread and time variables (Bolker 2008). We did not incorporate phylogeny into these models. Current phylogenetic methods that can incorporate nonlinear relationships (such as independent contrasts) can reduce statistical power, and ignoring nonlinearity can affect biological inferences (Quader et al. 2004). Additionally, alternative techniques such as PGLS assume linear relationships and could not be used for our data.

Only invasive and noninvasive exotic species were included in spread and residence time analyses. In our data set, an introduced species' range size is a function of its residence time in the introduced range, meaning that generally when given more time, an introduced species will continue to expand its range (Ahern et al. 2010). Because of the high degree of correlation between time and spread ($r = 0.70$, $P < 0.001$), and between our different measures of spread (Michigan and five-state spread, $r = 0.86$, $P < 0.001$; Michigan and U.S. spread, $r = 0.72$, $P < 0.001$), these predictor variables could not be tested simultaneously in one ANCOVA model (Underwood 1997, Miller and Chapman 2001). Therefore, when discussing how residence time and spread relate to herbivory and browsing damage, we cannot differentiate between their effects, though we can still explore the relationships between these variables and enemy damage (Miller and Chapman 2001). Here, we explore the effects of these variables separately, testing their individual influences in different models (Underwood 1997), and then discuss their effects making clear that either residence time or spread could be driving the observed patterns. To test whether enemy damage increases with residence time, proportion of leaf area removed and proportion of stems (or tillers) browsed were included as response variables; plant status, residence time, and their interaction were included as fixed factors. We tested the same model for each of our spread measures, substituting spread for time as a predictor variable. Model fit and hypothesis testing were conducted using likelihood ratio tests, and significance was assessed from the χ^2 distribution. Post-hoc contrasts were used to evaluate whether the slopes for invasive or noninvasive exotic species were significantly different from zero when a
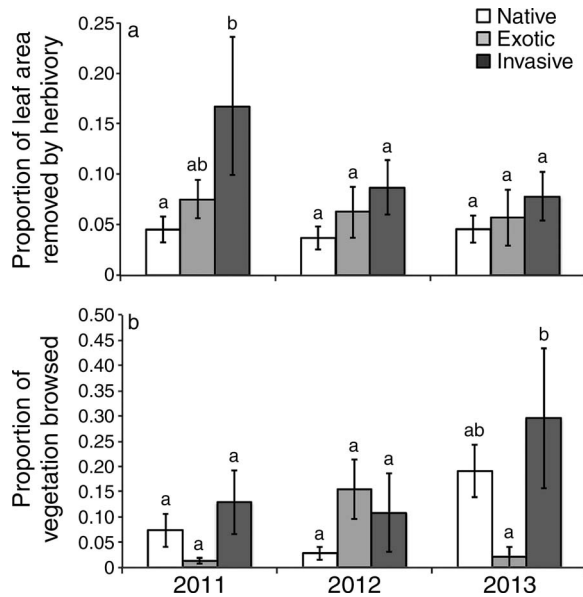
FIG. 1. Three years of (a) insect herbivore and (b) mammal browser damage data on native (white bars), noninvasive exotic (gray bars), and invasive (black bars) plants. Bars indicate mean ± SE. Means with different letters are significantly different ($P \leq 0.05$) based on post-hoc contrasts.

status by time, or status by spread, interaction was significant ($P \leq 0.05$).

RESULTS

In our system, we found no evidence that invasive species receive reduced enemy damage, compared to native and noninvasive exotic species. Enemy damage from insect herbivores and mammalian browsers tended to be higher on invasive species, compared to native and noninvasive exotic species (Fig. 1, Appendix A: Table A2). In 2011, invasive species received significantly more damage from insect herbivores than natives, and noninvasive exotics received intermediate amounts of damage (Fig. 1a; 2011, $t_{2,27} = 2.20$, $P = 0.04$). Though not significant, this trend remained consistent through 2012 and 2013 (Fig. 1a; 2012, $t_{2,43} = 0.24$, $P = 0.81$; 2013, $t_{2,31} = 1.20$, $P = 0.24$). Notably, out of the top 10 species with the most insect herbivore damage, six were invasive and three are noninvasive exotic. Only one of the top 10 species with the most insect damage was native (Fig. 2).

Browsing was variable across years, but again we find no evidence consistent with the ERH (Fig. 1b, Appendix A: Table A2). In all years, native, noninvasive exotic, and invasive species did not differ significantly in browsing, but our post hoc contrasts revealed differences between noninvasive exotic and invasive species in 2013. In 2011 and 2013, invasives and natives generally received the most browsing damage (Fig. 1b; 2011, $t_{2,27} = -0.16$, $P = 0.56$; 2013, $t_{2,31} = 0.28$, $P = 0.78$). In 2012, invasive and noninvasive exotic species tended to receive more browsing damage than natives (2012, $t_{2,43} = 0.96$, $P = 0.34$). Of the 10 species with the most browsing

damage, three were invasive, four were noninvasive exotic, and three were native. About half of species received little or no damage from mammalian browsers (Fig. 2). There was no relationship between the damage a species received from insect herbivores and that received from mammalian browsers ($R^2 = 0.01$, $F_{1,31} = 0.31$, $P = 0.58$).

The phylogeny created for PGLS analyses was well resolved with high bootstrap support at the nodes and expected grouping by genus and family (Appendix A: Fig. A1). All of our values for Blomberg's K are < 1 (Appendix A: Table A2), indicating that leaf damage and stem browsing in close relatives were more divergent than expected across the phylogeny (Blomberg et al. 2003) and provides additional evidence that the lack of control for phylogeny in our ANCOVA analyses likely does not bias results.

Enemy damage was dynamic, depending on residence time and areas of spread in the introduced range (Figs. 3 and 4, Appendix A: Table A3), and these patterns were consistent across multiple geographic scales. With increased residence time, noninvasive exotic species experienced increased insect herbivore damage (Fig. 3a; $\chi^2 = 2.57$, $P = 0.02$), but this pattern was not observed for invasive species (Fig. 3a; status × time interaction, $\chi^2 = 1.76$, $P < 0.001$). Introduced species with longer residence times tended to experience less mammalian browsing, although this trend was marginally nonsignificant (Fig. 3b; $\chi^2 = 9.82$, $P = 0.06$). With increasing area occupied in Michigan (spread), noninvasive exotic species experienced greater insect herbivory (Fig. 4a; $\chi^2 = 2.04$, $P < 0.001$), and both invasive and noninvasive exotics experienced greater insect herbivory with increasing area occupied at larger spatial scales. (Fig. 4b and c; five states $\chi^2 = 1.74$, $P < 0.001$; U.S. $\chi^2 = 2.16$, $P = 0.001$). Noninvasive exotic species experienced reduced mammalian browsing with increasing spread at all three scales and, at larger scales, invasive species experienced increased mammalian browsing with increasing spread (Fig. 4 d–f, status × county interaction at all three scales; Michigan $\chi^2 = 7.83$, $P = 0.009$; five states $\chi^2 = 5.43$, $P < 0.001$; U.S. $\chi^2 = 5.86$, $P < 0.001$).

DISCUSSION

We found no evidence consistent with ERH contributing to invasiveness in this system. We detected few significant differences in damage between native, invasive, and noninvasive exotic species, although invasives tended to receive more damage from insect herbivores than did native or noninvasive exotic plant species across all study years (Fig. 1a). Browsing damage did not differ based on status, however native and invasive plants tended to get more browsing damage than did noninvasive exotics, not supporting either ERH prediction (Fig. 1b). Our results are consistent with other experiments using the common garden approach. For example, in a study of 12 temperate vine species, native and invasive vines experienced more foliar damage from
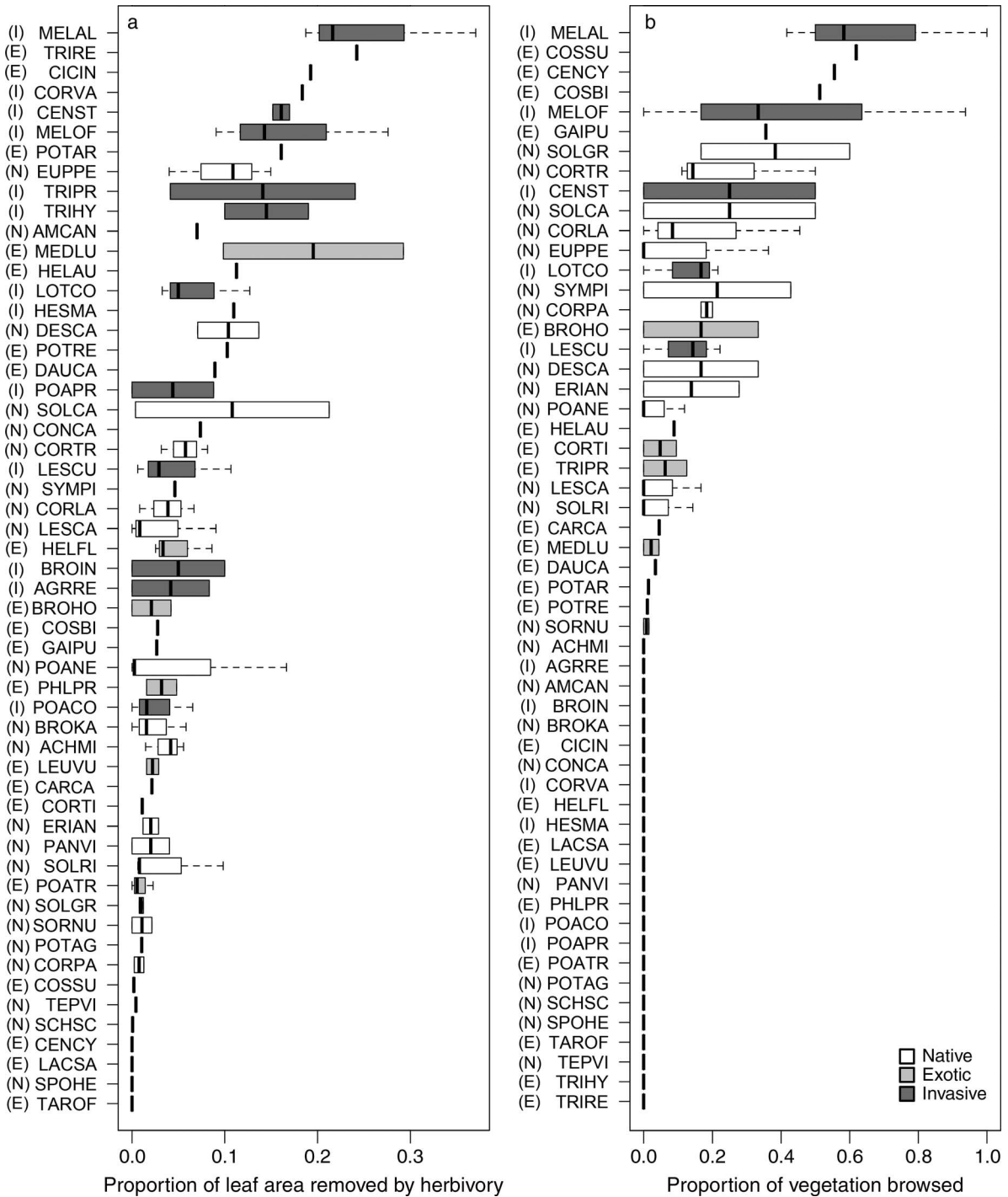
FIG. 2.   Boxplots of the median (black line), first and third quartiles (box), maximum, and minimum for (a) insect herbivory and (b) mammalian browsing for each species. Native species (N) are shown in white, noninvasive exotic species (E) in light gray, and invasive species (I) in dark gray. Species with one year of data, or the same amount of damage in all years, have boxplots only showing the median without quartiles. Species are organized in descending order by mean. Species names are spelled out in Appendix A: Table A1.
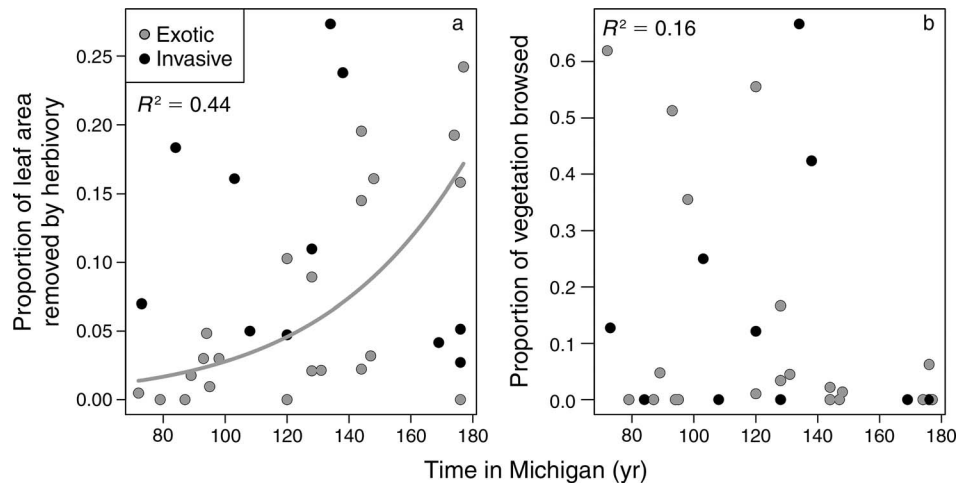
FIG. 3. (a) Insect herbivore and (b) mammalian browser damage on noninvasive exotic (gray points) and invasive (black points) plants with increasing residence time in Michigan. Analysis was performed on species averages across the three study years; each point represents one species. The gray regression line indicates insect herbivory increases with residence time for noninvasive exotic species, but not invasive species.

insect and mammal herbivores than noninvasive exotics, not supporting ERH predictions (Ashton and Lerdau 2008). Similarly, invasive *Eugenia uniflora* sustained more insect herbivore damage than congeneric native and noninvasive exotic species in a common garden experiment, also not supporting Predictions 1 and 2 (Stricker and Stiling 2014). In a study using 18 clover species, introduced and native species experienced similar amounts of disease, and the most invasive introduced species experienced the most disease (Parker and Gilbert 2007).

Further, we found that invasions are dynamic and enemy release from insect herbivores is lost over time for noninvasive exotic species, and with increasing spread at all scales for both invasive and noninvasive introduced species (Figs. 3a and 4a–c). Our herbivory results on the dynamic nature of invasions are consistent with other studies that have found that enemy release is lost with increased residence time (Siemann et al. 2006, Hawkes 2007, Diez et al. 2010; but see Carpenter and Cappuccino 2005) and spread (Mitchell and Power 2003, Diez et al. 2010) in the introduced range. While there was no relationship between residence time and browsing (Fig. 3b), we found that the most widespread noninvasive exotic species actually received the least amount of browsing, contrary to our predictions (Fig. 4d-f). Because we are not able to determine the direction of causality, browsers may in fact be driving the pattern in spread, acting as a filter and determining which species can spread furthest in the landscape. In contrast, invasive species with the largest ranges experienced higher amounts of browsing damage (Fig. 4e and f), indicating that these two types of introduced plants might interact differently with mammalian browsers, although this result should be interpreted cautiously given that two

species in a single genus (*Melilotus officinalis* and *M. albus*) drive the observed patterns for invasives.

Due to the tight correlation between time and spread, we are unable to determine which variable is driving the patterns observed. Additionally, because we are unable to manipulate these two variables, other unmeasured correlated variables could be acting in our system. Previous analyses on our Michigan data set of residence time and spread have found that the average introduced species will be present in 50% of counties after 160 years, with only the most invasive species spreading more quickly (Ahern et al. 2010). Given sufficient time, 10–20% of introduced plants will be listed as invasive, indicating that invasiveness may be a function of residence time in the introduced range (Ahern et al. 2010).

In our study, we find consistent patterns across all three years of data collection, despite slight variations in experimental species composition (Appendix A: Table A1). Enemy pressures can vary greatly across years and growing seasons (Agrawal and Kotanen 2003, Agrawal et al. 2005, Parker and Gilbert 2007). For example, in the first year of a common garden experiment, Agrawal and Kotanen (2003) found that introduced plants experienced more herbivory than did natives, similar to the results of our own study. They collected a second year of data on the same common garden and found that introduced plants now received less herbivory, supporting the ERH (Agrawal et al. 2005). They hypothesized that variable herbivore communities could drive these yearly differences, as well as ontogenetic changes in study plants and a potentially delayed response of the herbivore community to the establishment of their experiment. Thus, in their system, time periods where native species receive high amounts of enemy attack, but introduced species receive little damage, may provide an opportunity window for
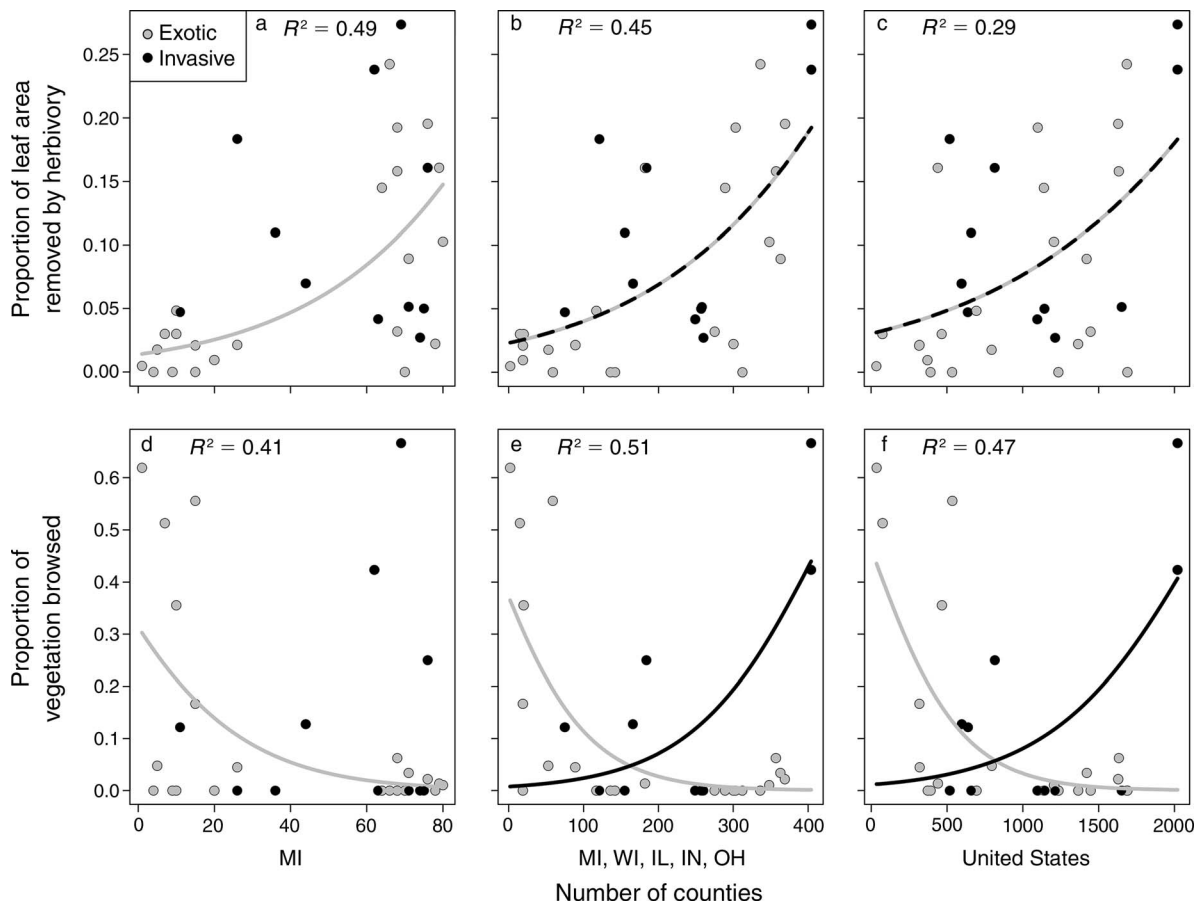
F_{IG.} 4. (a–c) Insect herbivore and (d–f) mammal browser damage on noninvasive exotic (gray points) and invasive (black points) plants with increasing spread. Spread measures for counties (a and d) within Michigan, (b and e) spread within Michigan (MI), Wisconsin (WI), Illinois (IL), Indiana (IN), and Ohio (OH), and (c and f) spread within the United States. Analysis was performed on species averages across the three study years; each point represents one species. Regression lines show significant relationships ($P \leq 0.05$). A dashed black and gray regression line indicates insect herbivory increases with spread, but no difference between noninvasive exotic and invasive species. Black and gray lines indicate patterns only significant for invasive and noninvasive exotic species, respectively.

introduced plants to dominate the system. In our experiment, no opportunity windows were apparent; the consistency of our results across three years provides strong support against ERH and suggests that enemy release windows, where invasive species experience reduced damage for a particular growing season, may be relatively infrequent in this system.

Several mechanisms could explain higher enemy damage to invasives than noninvasive exotics or natives. First, fast growing species tend to allocate less to defense, resulting in higher amounts of herbivore damage than slow growing species (Cebrian and Duarte 1994, Endara and Coley 2011), and invasive species may have faster growth rates than noninvasive exotic and native plant species (van Kleunen et al. 2010). Second, a lack of a shared coevolutionary history between introduced species and enemies in their introduced ranges could lead to higher amounts of damage because introduced species may lack defenses against these

enemies, unlike native plants with coevolved defenses (increased susceptibility hypothesis; Hokkanen and Pimentel 1989, Colautti et al. 2004, Verhoeven et al. 2009). Consistent with this hypothesis, herbivore feeding trials on aquatic (Parker and Hay 2005, Morrison and Hay 2011) and terrestrial (Parker and Hay 2005) plants have shown that native herbivores preferentially consume introduced plants over natives, and the defensive chemistry of invasive plants serves as no more of a deterrent to herbivores than does the defensive chemistry of natives (Lind and Parker 2010). Third, invasive species may have higher local population densities than native or noninvasive exotic species (e.g., Herrera et al. 2011), which could potentially increase the abundance of enemies feeding on these species or make invasive plants more apparent to insect herbivores and mammalian browsers (Feeny 1976). This final hypothesis is unlikely in our system. In our common gardens, all species were planted at equal densities, and although some experi-

mental species also naturally occurred at our experimental site, we found that herbivory ($r = 0.19$, $P = 0.42$) and browsing ($r = 0.003$, $P = 0.99$) damage were not correlated with species abundance at our site (percent cover estimated at 1% intervals for each species based on visual observation of 100 20×20 cm cells nested within 2×2 m experimental plots).

The question remains, if invasive plants tend to receive the most enemy damage, how is it that they are still invasive? There now exist over two dozen hypotheses attempting to explain invasiveness (Catford et al. 2009), and it is clear that no single hypothesis can explain the diversity of invasion strategies employed by today's invaders (Gurevitch et al. 2011, Lau and Schultheis 2015). Invasiveness could be driven, not by enemy release, but instead by performance and defense strategy traits of invasive species. In this study, we have identified differences in enemy damage between native, invasive, and noninvasive exotic species, and in future studies we will determine whether this damage translates into different effects on performance. Invasive species may lie on one end of a trade-off between an individual's ability to resist damage and ability to maintain performance when damaged (i.e., tolerance; Strauss and Agrawal 1999). Though invasive species in our system received the most insect herbivore damage, if they are also more tolerant, then their performance (growth, survival, fecundity) may be less affected by this damage compared to noninvasive exotics and natives. Contradictory to this hypothesis, a meta-analysis found introduced species to be *less* tolerant to damage (Chun et al. 2010). In a different meta-analysis, Parker and colleagues (2006) classified introduced species along a spectrum of invasiveness and determined that herbivores had similar effects on the performance of both noninvasive exotic and invasive species.

Alternatively, release from enemies not tested in our system, such as disease or belowground enemies, could contribute to invasion success. Mitchell and Power (2003) demonstrated that plant species that experienced release from fungal and viral pathogens were more widely invasive than those that did not. Similarly, invasive plants experienced lesser effects from belowground enemies than rare, native plants (Klironomos 2002). In contrast, a meta-analysis by Levine and collaborators (2004) found herbivores (as well as competition and diversity in the native community) provided resistance to invasion, while fungal pathogens did not (Levine et al. 2004), indicating that some enemies may contribute more to ERH than others (Levine et al. 2004).

Though we find that ERH, mediated through aboveground herbivores, was not a common pattern across the species tested in our study location, some invasive and noninvasive exotic species did receive low amounts of enemy damage (Fig. 2), indicating that the success of these species may be driven by enemy release. During at least one study year, the invasive Poaceae species *Bromus inermis* (2012), *Poa compressa* (2013), and *Poa pratensis* (2013) experienced no damage from either insect herbivores or mammalian browsers. These species could be candidates for further study to assess whether enemy release contributes to increased fitness over native competitors.

CONCLUSION

The Enemy Release Hypothesis (ERH) remains among the most popular hypotheses explaining the successes and failures in introduced species, despite mixed support. A review on the ERH found that 36% of studies support it, while 43% do not (Heger and Jeschke 2014, see also Colautti et al. 2004). Meta-analyses and reviews on enemy richness and damage for introduced and native species find results both for (Liu and Stiling 2006, Hawkes 2007) and against the ERH (Chun et al. 2010).

Our study helps to identify some of the sources of variation in previous ERH studies, namely distinguishing between invasive and noninvasive exotic species and considering the dynamic interplay between an introduced species and their enemies over decadal timescales. Our findings indicate that invasive species generally receive more damage from enemies, compared to native and noninvasive exotic species, not supporting key predictions arising from the ERH. Therefore, we conclude that enemy release is not a general mechanism associated with invasiveness in our system, although enemy release could apply to specific cases of invasion and early on in the invasion process.

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