

AN INVASIVE PLANT PROMOTES UNSTABLE HOST–PARASITOID PATCH DYNAMICS

JAMES T. CRONIN¹ AND KYLE J. HAYNES

Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803-1715 USA

Abstract. In theory, the rate of interpatch dispersal significantly influences the population dynamics of predators and their prey, yet there are relatively few field experiments that provide a strong link between these two processes. In tallgrass prairies of North America, the planthopper, *Prokelisia crocea*, and its specialist parasitoid, *Anagrus columbi*, exist among discrete host-plant patches (prairie cordgrass, *Spartina pectinata*). In many areas, the matrix, or habitat between patches, has become dominated by the invasive exotic grass, smooth brome (*Bromus inermis*). We performed a landscape-level field study in which replicate cordgrass networks (identical in number, size, quality, and distribution of cordgrass patches) were embedded in a matrix composed of either mudflat (a native matrix habitat) or smooth brome. Mark–recapture experiments with the planthopper and parasitoid revealed that the rate of movement among cordgrass patches for both species was 3–11 times higher in smooth brome than in mudflat. Within three generations, planthopper and parasitoid densities per patch were on average ~50% lower and spatially 50–87% more variable for patches embedded in a brome as compared to a mudflat matrix. A brome-dominated landscape also promoted extinction rates per patch that were 4–5 times higher than the rates per patch in native mudflat habitat. The effect was more acute for the parasitoid. We suggest that the differences in population dynamics between networks of patches in brome and those in mudflat were driven by underlying differences in interpatch dispersal (i.e., patch connectivity). To our knowledge, this is the first experimental study to reveal that matrix composition, in particular, the presence of an invasive plant species, affects the spatial and temporal dynamics of an herbivore and its natural enemy.

Key words: *Anagrus columbi*; *Bromus inermis*; connectivity; emigration; extinction; host–parasitoid interactions; immigration; matrix; *Prokelisia crocea*; tallgrass prairie.

INTRODUCTION

The most significant threats to population persistence and biodiversity are the loss and fragmentation of habitats, and the invasion and spread of exotic species (Wilcox and Murphy 1985, Drake et al. 1989, Saunders et al. 1991, Debinski and Holt 2000). For herbivores of native plant species, exotic plants may occupy much of the habitat between their host-plant patches (i.e., the matrix). A growing body of evidence suggests that the composition of the matrix can significantly affect interpatch movement rates of herbivores (Roland et al. 2000, Ricketts 2001, Goodwin and Fahrig 2002, Haynes and Cronin 2003) and their natural enemies (Cronin 2003a), and that these changes in movement rates can theoretically affect population dynamics and persistence (e.g., Reeve 1988, Comins et al. 1992, Vandermeer and Carvajal 2001). A plausible, but undocumented, way in which exotic plant species might affect native faunas is via their effects on connectivity among native habitat patches.

Connectivity is considered critical to the regional persistence of populations residing in subdivided habitat patches (Holyoak and Lawler 1996, Harrison and

Taylor 1997, Ims and Yacoz 1997, Hanski 1999, Thomas and Kunin 1999). If there is too little connectivity among patches, patches should exhibit independent fluctuations in densities and have a low probability of being rescued from extinction or re-colonized following an extinction event. Alternatively, if connectivity among patches is too high, patches are likely to have lower mean densities (if high emigration losses cannot be compensated for by immigration or density-dependent reproduction), increased spatial synchrony in densities, and a relatively high risk of extinction for the whole ensemble of patches. Invasive plant species may greatly affect connectivity by displacing native vegetation and either altering patch geography (size or isolation) and/or affecting matrix resistance to animal movement. Despite the significance of dispersal to the local and regional dynamics of populations, relatively few field studies have provided a strong link between the two, particularly with regard to predators and their prey (but see, e.g., Huffaker 1958, Kareiva 1987, Dempster et al. 1995; recently reviewed in Bowne and Bowers 2004). Furthermore, no experimental studies to date have documented the effects of invasive, non-native plant species on predator–prey dispersal and population dynamics within spatially subdivided landscapes.

Manuscript received 11 February 2004; revised 5 April 2004; accepted 14 April 2004. Corresponding Editor: N. Cappuccino.

¹ E-mail: jcronin@lsu.edu

In the North American Great Plains, patchily distributed prairie cordgrass (*Spartina pectinata* Link; Poaceae) hosts an obligate specialist planthopper (*Prokelisia crocea* Van Duzee; Hemiptera: Delphacidae) and its stenophagous egg parasitoid (*Anagrus columbi* Perkins; Hymenoptera: Mymaridae) (Cronin 2003a, b, c). These insects exhibit mainland-island metapopulation dynamics among host-plant patches within a prairie landscape. Local population extinctions followed by the colonization of cordgrass patches are a common occurrence among the many small patches (<50 m²) but have never been reported for the few large patches (>3 ha) in a prairie landscape (Cronin 2003a, b, 2004). The matrix habitat within which the cordgrass patches are embedded has a significant impact on planthopper and parasitoid interpatch movement rates, at least at distances of <5 m (Cronin 2003a, Haynes and Cronin 2003). Planthoppers and parasitoids dispersing through a matrix composed of the invasive, non-native grass smooth brome (*Bromus inermis*) (D'Antonio and Vitousek 1992, Larson et al. 2001) colonized cordgrass patches at a rate that was 5–6 times higher than the rate for individuals traversing a native matrix habitat (mudflat) (Cronin 2003a, Haynes and Cronin 2003). In this study, we created replicate cordgrass networks (identical in number, size, quality, and distribution of cordgrass patches) embedded in a matrix composed of either mudflat (experimentally created) or smooth brome. *P. crocea* and *A. columbi* populations were established within each network and their movement among cordgrass patches in each matrix type quantified with mark-recapture experiments. In addition, we examined how the two matrix types influenced local patch dynamics (density, spatial variability in density among patches, and extinction rates) of the planthopper and parasitoid over three generations. We show that by significantly increasing patch connectivity, the brome as compared to the mudflat matrix promoted very unstable host and parasitoid patch dynamics.

METHODS

Study system

Prairie cordgrass is a native species of North American grasslands and in northeast North Dakota exists as numerous discrete patches ranging in size from 0.1 m to 4 ha (Hitchcock 1963, Cronin 2003b). The maximum isolation of a cordgrass patch from its nearest neighbor is only ~46 m (Cronin 2003b). The matrix within which these patches are embedded can be classified into three main types: (1) periodically flooded mudflats sometimes dominated by saltwort (*Salicornia rubra* Nels.); (2) mixtures of predominantly native grasses (primarily foxtail barley *Hordeum jubatum* L., western wheatgrass *Agropyron smithii* Rydb., and little bluestem *Andropogon scoparius* Michx.); and (3) monospecific stands of smooth brome (Cronin 2003a, Haynes and Cronin 2003). Brome has become estab-

lished by invading disturbed prairie and through repeated introductions for soil erosion control and animal graze (D'Antonio and Vitousek 1992, Larson et al. 2001, Haynes and Cronin 2003).

The planthopper, *Prokelisia crocea*, is the dominant herbivore of prairie cordgrass (Holder and Wilson 1992, Cronin 2003b). In North Dakota, first instar nymphs emerge from their overwintering sites (senescent leaves from the previous year) in late May, reach peak adult densities in mid June, and then lay eggs beneath the adaxial surface of cordgrass leaves. Adults from this second generation reach a peak in early August. One of the most important natural enemies of the planthopper is the egg parasitoid *Anagrus columbi* (Cronin 2003a, c; see Plate 1). Parasitism rates per cordgrass patch range from 0 to 100%, with an average of 21% (Cronin 2003c). In our study area, the parasitoid's only host is *P. crocea*. *A. columbi* also has two generations per year, with adult densities coinciding with the occurrence of planthopper eggs.

Experimental design

The experiment was conducted in a 32-ha field dominated by smooth brome and lacking any native cordgrass (Grand Forks County, North Dakota, USA). In June 2002, replicate cordgrass networks were established in either unmanipulated brome habitat or in experimentally created mudflats (assigned at random). Mudflats were created by spraying areas of brome with Glyphomax Plus herbicide (Dow AgroSciences LLC, Indianapolis, Indiana, USA), and then plowing under the dead vegetation. The experimental mudflats were re-treated with herbicides (excluding cordgrass patches) and plowed twice per summer, always at times when planthoppers and parasitoids were in sedentary stages (i.e., eggs or early instar larvae). This procedure was very effective at maintaining a relatively vegetation-free matrix habitat (any existing vegetation was considerably shorter in stature than that found in the brome matrix). Three replicate networks were established in each matrix type. Replicates were separated by at least 150 m, a distance very rarely traversed by *P. crocea* or *A. columbi* (Cronin 2003b, c, Haynes and Cronin 2003).

Each network consisted of 15 cordgrass patches (0.7 × 0.9 m) divided into five clusters of three patches (Fig. 1). Patches within a cluster were spaced 5 m apart, and the midpoint of the central cluster was 30 m from the midpoint of each of the four surrounding clusters. At a distance of just a few meters between a source and target patch, the rates of dispersal for *P. crocea* and *A. columbi* are <10% (Cronin 2003b, c, Haynes and Cronin 2003). Moreover, previous small-scale studies (Cronin 2003b, c, Haynes 2004) suggested that the dispersal rate for both species should decay approximately exponentially with distance from a source patch. Therefore, the scale of this study was potentially large enough, and interpatch dispersal low enough (see

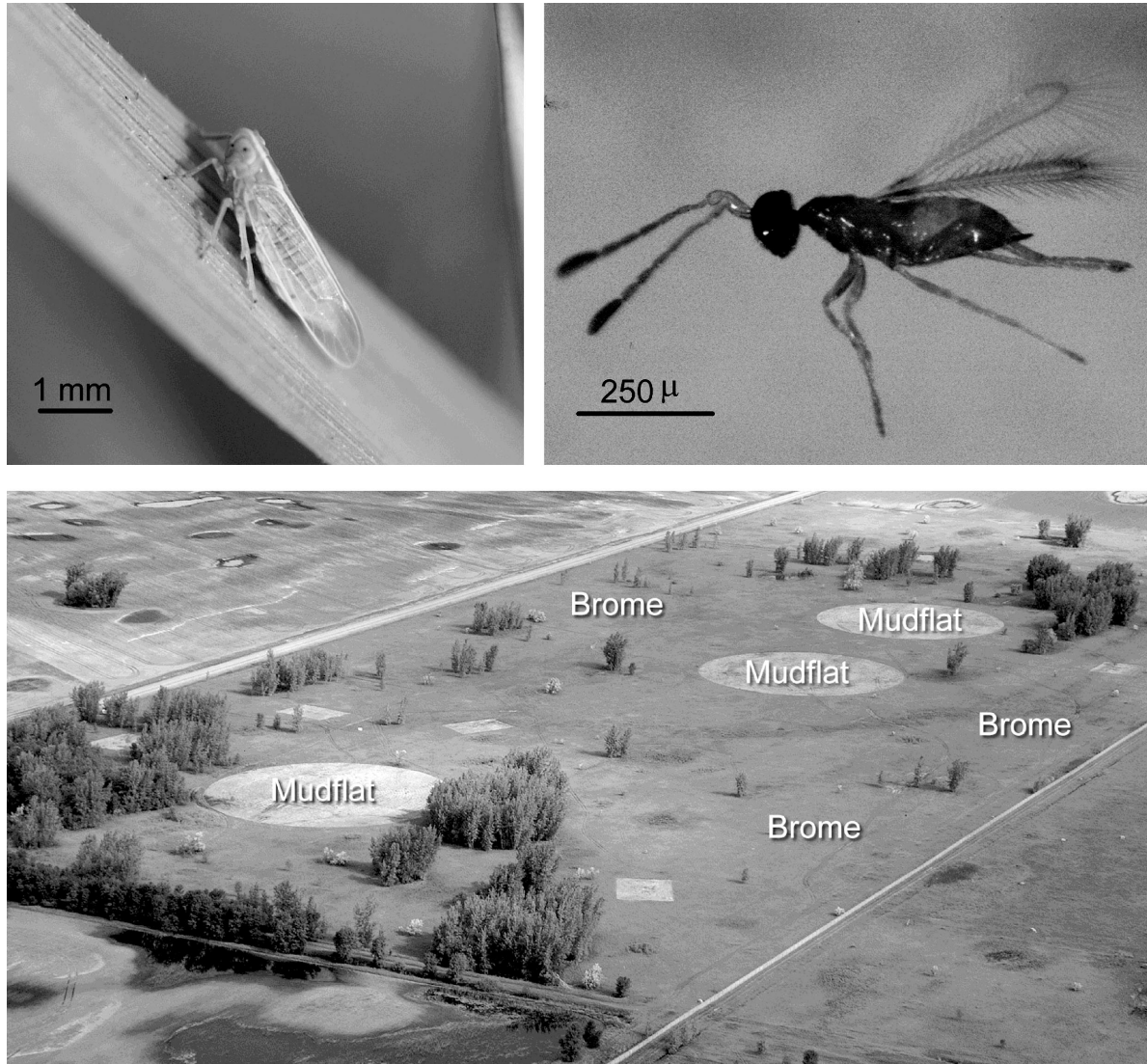


PLATE 1. (Top left) Female *Prokelisia crocea* and (top right) female *Anagrus columbi*. (Bottom) Experimental study site consisting of replicate cordgrass networks embedded in either a brome or experimental mudflat matrix. For scale, mudflat replicates have a diameter of 100 m. Photo credit: J. T. Cronin.

Hastings 1993, Bowne and Bowers 2004), for asynchronous local patch dynamics to occur. In this paper, we focused more generally on the local patch dynamics of the system, and deferred consideration of the regional (e.g., metapopulation) dynamics to a later paper (J. T. Cronin, *unpublished data*).

The cordgrass for this experiment was excavated in clumps from a nearby prairie in May 2002 and planted flush to the ground. A 25-cm aluminum barrier was inserted into the ground along the perimeter of each patch to limit the outward spread of cordgrass and the encroachment of brome. Cordgrass patches of this size are equal to, or larger than, 22% of the patches found in nearby prairie landscapes (Cronin 2003b) and possess an average (mean \pm 1 SE) of 355 ± 7 cordgrass stems. At the time cordgrass patches were created,

planthoppers and parasitoids were still in their overwintering sites, either within the dead vegetation or beneath the soil surface (Cronin 2003b, c). Because source plants were purposely obtained from an area with very low planthopper densities the previous year (<1 per 50 stems, based on sweep net samples), we expected that the densities of both species initially would be low in our experimental networks. Also, because the excavated clumps of cordgrass were distributed randomly among experimental networks, it was very unlikely that any initial bias in insect distributions occurred between matrix types. Through regular fertilization (Osmocote Outdoor and Indoor Slow Release Plant Food; Scotts, Maryville, Ohio, USA), and watering of patches, variation in patch nutritional quality was minimized between matrix treatments.

To determine if the microclimate within patches was dependent on matrix type, we placed a single Hobo Pro data logger (Onset Computer Corporation, Pocasset, Massachusetts, USA) into the center of one cordgrass patch per replicate network ($n = 6$). The data logger was positioned 25 cm above ground, approximately one half of the mean height of the cordgrass, and recorded temperature and humidity at hourly intervals from 1 to 21 August 2002 (coinciding with peak activity of adult planthoppers in the second generation). From each patch, the daily mean, minimum, and maximum temperature and humidity were determined. We then averaged these values among the three replicates per matrix type for a total of 21 daily temperature and humidity readings (mean, minimum, and maximum). Separate paired t tests were used to determine if patches in brome and mudflat differed with respect to each weather-related variable. An additional set of Hobo data loggers were simultaneously deployed within the matrix itself, one in each of the replicate brome and mudflat networks. Data loggers were placed near the center of each network, but at least 5 m from the cordgrass patches. We used a similar procedure to evaluate whether temperature and humidity levels differed in each of the two matrix habitats.

Host and parasitoid dispersal

One month after the transplantation of cordgrass, we performed a release of planthoppers into the cordgrass networks. Five hundred recently eclosed adult planthoppers, at a ratio of ~ 12 females to one male (corresponding to ambient proportions), were released into five patches per network (Fig. 1). This corresponds to ~ 1.4 planthoppers per stem; an intermediate density for naturally occurring patches (Cronin 2003b, Cronin et al. 2004). Planthoppers were marked with fluorescent powder (Dayglo Corporation, Cleveland, Ohio, USA), using a different color in each patch. The mark is detectable for ~ 2 wk and has no apparent effect on planthopper survival or dispersal (Cronin 2003b). For 7 d following the release, all cordgrass patches were inspected daily for the presence of marked individuals. While searching for planthoppers in the brome landscapes, observers reduced trampling of vegetation by stepping in their footprints and avoiding the creation of direct pathways between patches. The cumulative number of marked planthoppers detected per patch at 5 m, 20–40 m, and 50–60 m from the release patch was recorded as a proportion of the total numbers of planthoppers marked (500). Because marked planthoppers were observed in patches other than their patch of origin, the proportion of marked individuals that were sighted represents a true measure of immigration success or connectivity between patches at a given distance.

Parasitoid dispersal through brome and mudflat was determined from established populations in the third generation (2003-II). In August 2003, three cordgrass

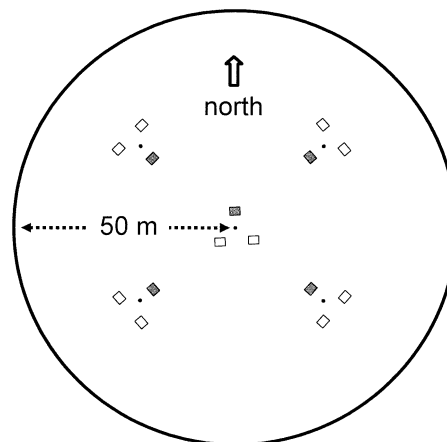


FIG. 1. Diagram of an experimental cordgrass network. Each network consisted of 15 cordgrass patches (small boxes; 0.66 m² in area), divided into five clusters of three. Patches within a cluster were 5 m apart. The distance from the midpoint of the central cluster to the midpoint of the other four clusters was 30 m. Each network was embedded in either a brome matrix ($n = 3$) or an experimentally created mudflat matrix (ploughed brome; $n = 3$). Shaded patches represent those in which marked planthoppers were released. Parasitoids were marked in three of the shaded patches (center, north-east, and southwest clusters).

patches per replicate network (see Fig. 1) were dusted with a different color of fluorescent powder (using a hand-cranked dust blower). The powder was reapplied as needed to ensure a thin dry coating on the plants for most of the duration of the study. As parasitoids emerged from host eggs and walked about the leaves, they became self-marked (see also Corbett and Rosenheim 1996). Dispersing parasitoids were then captured on yellow sticky traps (8×13 cm Dayglo Saturn yellow index cards coated with Tanglefoot; Tanglefoot Company, Grand Rapids, Michigan, USA) attached to the tops of 0.5-m tall polyvinyl chloride (PVC) poles (Cronin 2003a, c). The traps were positioned around each dusted patch at distances of 0.5 m ($n = 2$ traps), 1.0 m ($n = 4$), 2.5 m ($n = 6$), and 5.0 m ($n = 8$). At each distance, traps were spaced evenly apart. Therefore, it was possible for an emigrant parasitoid to be captured on sticky traps 5 m from its patch of origin, or at traps positioned around one of the other two dusted patches, a distance of 20–50 m away. The traps were deployed for the duration of the parasitoid emergence period (3 wk), after which time the traps were examined with a dissecting microscope ($25\times$) for *A. columbi* marked with one of the three colors (usually no more than a few particles of dust were present, and colors were easily distinguishable). Based on laboratory trials, virtually 100% of the parasitoids emerging and dispersing away from fluorescent-marked leaves carried the marker (J. T. Cronin, unpublished data). Trap captures were divided into distance categories that corresponded to those for the planthopper. The cumulative number captured per trap at each distance was ex-

pressed as a proportion of the total numbers of parasitoids marked (emerging) from within a patch (determined from the patch census at 2003-II; see *Methods: Local patch dynamics*). For the parasitoid, trap captures are positively correlated with the rate of immigration to cordgrass patches at the same distance (Cronin 2003c; J. T. Cronin, *unpublished data*), and thus the proportion captured on traps is a good surrogate measure of patch connectivity.

For both the planthopper and parasitoid, differences in the proportion of marked insects that were sighted or captured (square-root transformed) between matrix types were evaluated with Profile ANOVA (Tabachnick and Fidell 2000). Here, profile ANOVA is a multivariate test (comparable to a repeated-measures ANOVA) that allows for the trap distances associated with each dusted patch to be non-independent (traps share a common source patch and are potentially correlated in *A. columbi* captures). Matrix type was the main effect and trap distance was the non-independent factor (see also Cronin 2003a, c).

Local patch dynamics

For three generations following the creation of the replicate cordgrass networks (three per matrix), we determined the incidence and density of each species per cordgrass patch. Each census was initiated after the planthopper eggs had hatched and parasitoid adults emerged, mid July or late August. At these times, planthopper-infested leaves possessed a complete record of *P. crocea* eggs laid and parasitism, but no live insects. For each patch, a 10 × 25 cm sampling frame was randomly placed at six locations (three at the edge and three in the interior of the patch), and from within each frame we counted the number of cordgrass stems and leaves bearing planthopper oviposition scars. A maximum of 10 oviposition-damaged leaves were collected from the patch edge and interior. If no infested leaves were found, the remainder of the patch was thoroughly searched to ascertain patch occupancy. Leaves were dissected to determine the number of unparasitized and parasitized hosts per leaf (easily determined from the shape of the exit hole in the egg chorions). These leaves contained only traces of the occurrence of the two species (i.e., cast chorions and emergence holes), so their collection did not affect densities per patch (Cronin 2003a, b, c). From these leaves, we determined the density per stem of planthoppers (eggs) and parasitoids (emerged adults).

For each species and replicate cordgrass network, we also computed the extinction rate (proportion of patches occupied in generation t that were subsequently vacant in generation $t + 1$), colonization rate (proportion of vacant patches at t that were colonized at $t + 1$), and the coefficient of variation in density among patches (cv). In the calculation of parasitoid extinction rate, we excluded patches in which the host went extinct; therefore, parasitoid extinctions were

independent of host extinctions. Similarly, if hosts were absent from the patch, we considered those patches unavailable for the colonization of parasitoids. Differences in density (ln-transformed), cv, and extinction rate between matrix types were assessed with separate repeated-measures ANOVAs. Generation ($n = 3$) was the repeated measure and the responses of the planthopper and parasitoid to the matrix were evaluated separately.

RESULTS

Planthopper and parasitoid connectivities among cordgrass patches within experimental networks were significantly higher in a non-native brome than a native mudflat matrix. On average, the proportions of marked individuals that were sighted or captured at each distance were 3.4 and 10.9 times higher in brome than in mudflat for the planthopper and parasitoid, respectively (planthopper, $F_{1,4} = 30.2$, $P = 0.005$; parasitoid, $F_{1,4} = 20.4$, $P = 0.011$; Fig. 2). For each species, there was no significant matrix–distance interaction ($P > 0.05$), suggesting that the decline in recaptures with distance was similar between matrix types.

In addition to affecting connectivity, matrix composition also had a substantial impact on the dynamic properties of planthopper and parasitoid subpopulations (existing within individual cordgrass patches) within the cordgrass patch networks. Beginning one generation after the release of insects into the experimental plots, and for two subsequent generations, patch densities of the two species were, on average, 50% lower in a brome than a mudflat matrix (planthopper, $F_{1,4} = 43.8$, $P = 0.002$; parasitoid, $F_{1,4} = 27.8$, $P = 0.006$; Fig. 3A). For both species, variability in densities per patch within the cordgrass network (based on the coefficient of variation [cv]) were initially indistinguishable between matrix types (2002-II; based on separate within-generation t tests, $P > 0.50$; Fig. 3B). However, by the second and third generations, the cvs in densities per patch were significantly higher in the brome than in the mudflat matrix (planthopper, $F_{1,4} = 15.4$, $P = 0.017$; parasitoid, $F_{1,4} = 25.4$, $P = 0.007$; Fig. 3B). Parasitoid densities in brome-embedded patches were substantially more variable than for any other matrix–species combination, and as a result, the mean cv for the parasitoid was significantly higher than the mean cv for the planthopper (repeated-measures ANOVA with matrix and species as main effects; $F_{1,9} = 25.3$, $P < 0.001$). Owing most likely to lower and more variable densities, patch populations of the planthopper and parasitoid were five times and four times more prone to extinction, respectively, when embedded in a brome than a mudflat matrix (planthopper, $F_{1,4} = 8.69$, $P = 0.042$; parasitoid, $F_{1,4} = 48.6$, $P = 0.002$; Fig. 3C). Finally, in mudflat-embedded patches, planthoppers and parasitoids had similar rates of extinction ($F_{1,4} = 0.8$, $P = 0.42$), but in brome-embedded patches, the rate of extinction for the parasitoid averaged three

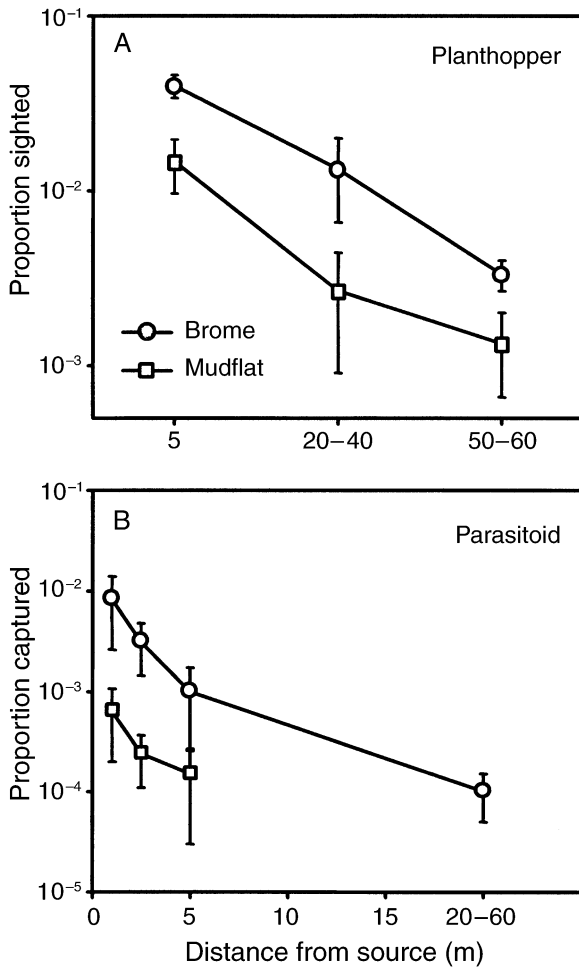


FIG. 2. Proportion (log scale) of marked planthoppers and parasitoids that were sighted or captured dispersing from their patch of origin. On average, (A) planthoppers and (B) parasitoids had significantly higher rates of dispersal in a brome matrix than a mudflat matrix ($F_{1,4} = 30.2, P = 0.005$ and $F_{1,4} = 20.4, P = 0.011$, respectively). Means ± 1 SE per patch (planthoppers) or sticky trap (parasitoids) are reported. Beyond a distance of 5 m, no marked parasitoids were captured in the mudflat.

times higher than the rate for its host (25% vs. 8%; $F_{1,4} = 25.2, P = 0.007$; Fig. 3C). Through three generations, there were insufficient data to evaluate whether planthopper and parasitoid colonization rates were matrix dependent. Most patches had viable planthopper and parasitoid populations in 2002-II, and only for the cordgrass networks in brome were there sufficient numbers of patch vacancies in 2003-I to quantify colonization rates in the following generation. Based on these limited data, planthopper and parasitoid colonization of patches in brome occurred at a rate of $66.7\% \pm 16.7\%$ and $72.2\% \pm 14.7\%$ (means ± 1 SE) per generation, respectively; a statistically indistinguishable difference ($t = 0.25, df = 4, P = 0.81$).

Finally, cordgrass patches within each matrix type did not appear to be exposed to different environmental

conditions. Daily maximum and minimum temperatures and relative humidity were indistinguishable between patches embedded in brome and mudflat ($P > 0.05$ for all tests; Table 1). However, there were small but significant differences in climatic conditions between the two matrix habitats. Experimental mudflats were, on average, 0.5°C warmer and had nighttime lows that were 1.4°C higher, than brome habitats (Table 1). Mudflats were also on average 2.2% less humid, and had daily lows that were 3.4% lower than the brome habitats (Table 1).

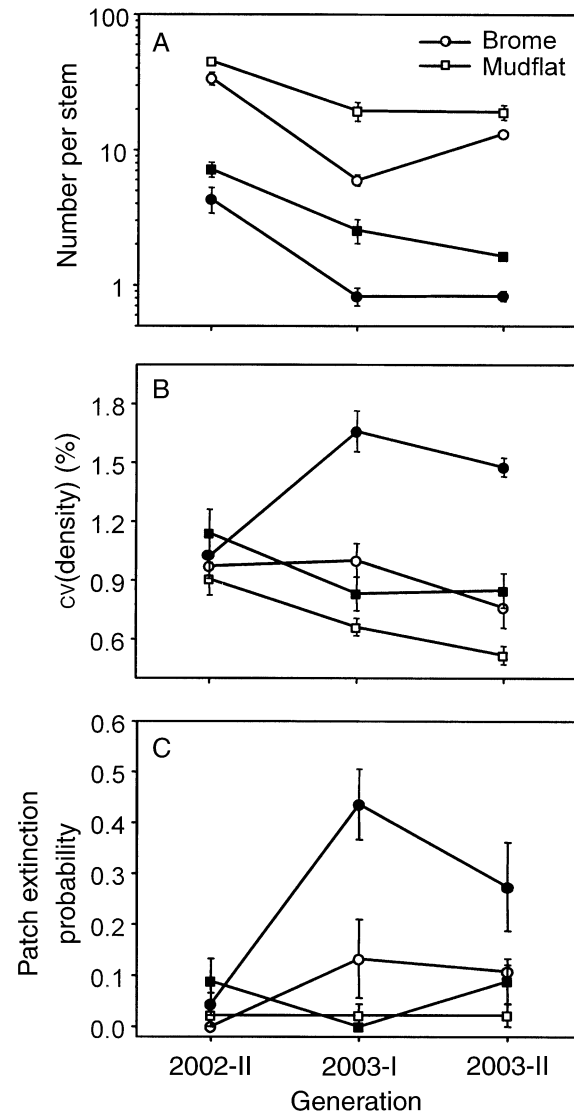


FIG. 3. (A) Density per patch (log scale), (B) coefficient of variation in density among patches (cv), and (C) the proportion of patches that went extinct per generation for the planthopper (open symbols) and parasitoid (solid symbols) in either a mudflat matrix (squares) or brome matrix (circles). Means ± 1 SE are based on three replicate cordgrass networks per matrix treatment and three consecutive generations.

TABLE 1. Temperature and humidity levels within cordgrass patches embedded in a brome or mudflat matrix, or within the matrix itself.

| Habitat type | Daily temperature (°C) | | | Daily humidity (%) | | |
|---------------------------------|------------------------|--------------|------------|--------------------|-------------|------------|
| | Mean | Minimum | Maximum | Mean | Minimum | Maximum |
| Within patch | | | | | | |
| Brome | 19.1 ± 0.7 | 10.9 ± 0.7 | 27.3 ± 0.9 | 78.5 ± 1.7 | 52.7 ± 2.8 | 98.0 ± 0.5 |
| Mudflat | 19.0 ± 0.7 | 11.0 ± 0.7 | 27.0 ± 0.9 | 79.4 ± 1.8 | 52.2 ± 2.7 | 98.8 ± 0.9 |
| <i>t</i> statistic (<i>P</i>) | 1.7 (0.11) | 0.4 (0.68) | 0.8 (0.40) | 1.8 (0.09) | 0.5 (0.59) | 1.7 (0.10) |
| Within matrix | | | | | | |
| Brome | 19.1 ± 0.7 | 11.2 ± 0.7 | 27.1 ± 0.9 | 79.5 ± 1.6 | 53.3 ± 2.7 | 98.7 ± 0.3 |
| Mudflat | 19.6 ± 0.7 | 12.6 ± 0.7 | 27.0 ± 1.0 | 77.3 ± 2.0 | 49.9 ± 3.1 | 98.0 ± 0.6 |
| <i>t</i> statistic (<i>P</i>) | 6.2 (<0.01) | 11.4 (<0.01) | 0.5 (0.62) | 4.7 (<0.01) | 3.6 (<0.01) | 1.8 (0.08) |

Notes: Daily mean, minimum, and maximum values of temperature and humidity, reported as means ± 1 SE among days, were determined for 21 d from three replicate Hobo data loggers per habitat type. Every day, an average for each of the six weather variables was obtained from the three replicates per habitat type. A paired *t* test was used to determine if the daily mean in brome (patches or matrix) differed significantly from the daily mean in mudflat (patches or matrix). A separate *t* test was performed for each of the six weather statistics, and *P* values are reported in parentheses.

DISCUSSION

At a spatial scale comparable to the maximum isolation distance between cordgrass patches (~46 m; Cronin 2003b), connectivity among patches for the planthopper and parasitoid appears to be 3–11 times higher in the non-native grass, smooth brome, than in the native matrix, mudflat. These results correspond very closely to findings from our earlier small-scale experiments with this system (Cronin 2003a, Haynes and Cronin 2003, Haynes 2004). Although in this study we did not consider the impact of the native grass matrix (predominantly consisting of foxtail barley *H. jubatum*, western wheatgrass *A. smithii*, and little bluestem *A. scoparius*) on planthopper and parasitoid movement, our previous studies indicate that connectivity among patches in a native matrix is intermediate between that of the brome and mudflat matrix (Haynes and Cronin 2003, J. T. Cronin, *unpublished data*). Our studies add to the growing body of evidence that matrix composition significantly affects interpatch movement rates (reviewed in Haynes and Cronin 2004).

For *A. columbi*, the mark–recapture experiment was performed at a time when both host and parasitoid densities were, on average, higher in mudflat- than in brome-embedded patches (Fig. 3A). Therefore, it is conceivable that the eleven-fold difference in recaptures-with-distance between the two matrix types was due to the parasitoid's response to host and/or conspecific densities in the source patch. However, several lines of evidence suggest that density was not a mitigating factor in causing the difference in dispersal between the mudflat and brome. First, the ratio of hosts to parasitoids was equally high for patches embedded in the two matrix types: 15.7 ± 0.6 for patches in brome and 16.6 ± 1.9 for patches in mudflat (Fig. 2). Second, the proportion of *A. columbi* adults in a source patch that colonized a target patch three meters away was independent of both host and parasitoid density in the source patch (matrix composition held constant; analysis based on data from Cronin 2003a). In the present

study, the greater proportion of captures at 1–5 m in the mudflat relative to the brome matrix was therefore not likely due to a density effect on dispersal. Finally, it seems unlikely that the density of hosts and parasitoids in a source patch would influence the range of dispersal of *A. columbi*: In the mudflat, no parasitoids were captured beyond a distance of 5 m, but in brome, parasitoids were captured at distances of >20 m.

To date, most matrix studies have involved naturally occurring habitat patches in which the quality of the patch (e.g., plant height, density, flowering rates, tissue nitrogen) may have been confounded with matrix composition (Haynes and Cronin 2004). For example, natural cordgrass patches in mudflat are more nitrogen rich than patches in a grass matrix (Haynes and Cronin 2003). Because patch quality is known to influence emigration (e.g., Cook and Denno 1994, Kuussaari et al. 1996, Fownes and Roland 2002) and immigration (Matter and Roland 2002), differences in patch connectivity among matrix types in many of these studies may have been driven by host patch quality, not matrix composition. In this experiment, and the one by Haynes and Cronin (2003), we controlled or attempted to minimize the differences among patches in each matrix; therefore, the matrix per se is the likely factor causing the differences in cordgrass patch connectivity.

Higher rates of dispersal through a brome, as compared to a mudflat matrix can be attributed to the response of these insects to the matrix–cordgrass edge and to their behavior in the matrix. For both species, the cordgrass–mudflat edge poses a strong barrier to emigration, whereas the cordgrass–brome edge is quite porous (Cronin 2003a, Haynes and Cronin 2003). Once in the matrix, the planthoppers and parasitoids also exhibit very different patterns of movement depending on the composition of the matrix; highly directional pathways in mudflat and circuitous pathways in brome (Cronin 2003a, Haynes and Cronin 2003, Haynes 2004). The latter movement pattern may increase patch-finding abilities and increase immigration rates

by these insects when the distribution of patches is aggregated (Baum and Grant 2001, Haynes and Cronin 2003; but see Zollner and Lima 1999); as is the case for cordgrass patches in our system (J. T. Cronin, *unpublished data*). In fact, both planthoppers and parasitoids have significantly higher probabilities of immigrating into patches embedded in brome than in mudflat (for patches isolated from a source patch by 3 m; Cronin 2003a, Haynes and Cronin 2003). In both matrix types, the likelihood of finding a new cordgrass patch appears to be very small, even when suitable patches are just a few meters away (Cronin 2003a, Haynes and Cronin 2003). Whether the low immigration rate at the spatial scale of this study is due to high mortality during dispersal, an inefficient search strategy, or some other mechanism, is presently unknown.

The effect of matrix composition on subpopulation or metapopulation dynamics has been explored theoretically in only a few studies (Gustafson and Gardner 1996, Moilanen and Hanski 1998, Cantrell and Cosner 1999, Vandermeer and Carvajal 2001). For example, Vandermeer and Carvajal (2001) demonstrated that a high-quality matrix (one that favors a high rate of colonization of empty patches) generally buffers a metapopulation against global extinction, but may promote chaotic subpopulation dynamics with a higher probability of subpopulation extinction. Under some circumstances, extinction-prone subpopulations can become persistent when matrix quality is high. Overall, Vandermeer and Carvajal's (2001) study suggests that matrix composition can have very complex and significant effects on the dynamics of fragmented populations. Empirical evaluations of the population-dynamic effects of the matrix are few (but see, e.g., Kareiva 1987, Roland and Taylor 1997, Moilanen and Hanski 1998), and until this study, limited to the correlation between matrix composition and patch incidence or density. For example, Moilanen and Hanski (1998) concluded that patch occupancy of the Glanville fritillary was mostly unrelated to the composition of the matrix. On the other hand, Cronin (2003a, 2004) and Haynes and Cronin (2003) found that patch incidences and densities, and rates of extinction of *P. crocea* and *A. columbi* were significantly matrix dependent (see also Walker et al. 2003). These survey data are consistent with the experimental data presented herein.

To our knowledge, this is the first experimental study to reveal that matrix composition, in particular, the presence of an invasive plant species, affects the spatial and temporal dynamics of an herbivore (and its natural enemy). Manipulation of the matrix composition of identical networks of cordgrass patches (in terms of quality, size, number, and dispersion of patches), significantly affected not only the connectivity among cordgrass patches, but also the spatial and temporal population dynamics of *P. crocea* and *A. columbi*. Within three generations, planthopper and parasitoid densities per patch were on average ~50% lower and

spatially 50–87% more variable for patches embedded in a brome as compared to a mudflat matrix. A brome-dominated landscape also promoted subpopulation extinction rates that were 4–5 times higher than the rates in native mudflat habitat.

We suggest that the differences in population dynamics between networks of patches in brome and those in mudflat were driven by underlying differences in patch connectivity, not by matrix-specific differences in the quality and/or microclimate of cordgrass patches. All patches were derived from the same soil source and regularly fertilized and watered. Interspecific competition with matrix plants was further reduced by the presence of an aluminum barrier inserted into the ground around the perimeter of the patch. Tissue nitrogen levels, a strong indicator of plant quality to many planthopper species (Cook and Denno 1994), were indistinguishable between patches embedded in brome and mudflat during the course of this study (J. T. Cronin, *unpublished data*). Finally, daily mean, minimum, and maximum temperatures and relative humidities were similar between cordgrass patches embedded in each matrix type ($P > 0.05$ for all tests). There were temperature and humidity differences in the matrix itself: Mudflats averaged 0.5°C warmer and 2.2% less humid than brome habitats. However, it seems unlikely that these subtle differences between matrix types could have caused such profound differences in planthopper and parasitoid population dynamics in the two landscapes.

In a landscape with high connectivity among patches, dogma suggests that an abundance of immigrants will not only reduce the variability in density among patches, but also rescue those patches from extinction (Brown and Kodric-Brown 1977, Hanski 1999). The discrepancy between our results and this theory can best be understood by considering the birth–immigration–death–emigration (BIDE) processes operating within a patch (Pulliam 1988, Watkinson and Sutherland 1995, Holyoak and Lawler 1996, Donahue et al. 2003). In the absence of immigration and emigration (e.g., a caged patch), patch populations of the planthopper and parasitoid are self-sustaining or have positive growth ($B \geq D$; J. T. Cronin, *unpublished data*). Mudflat-embedded patches also tend to be self-sustaining, but are also net exporters of individuals (i.e., source populations in which $E > I$; Cronin 2003a, Haynes and Cronin 2003). Even though I is greater for brome- than mudflat-embedded patches, brome-embedded patches have such high emigration losses that E often exceeds $B + I - D$, and the patches go extinct. Extinctions resulting from the overriding effects of high emigration are most often associated with small patches (Kareiva 1987, Andreassen and Ims 2001). As populations in brome-embedded patches decline toward lower densities, stochasticity in demographic (BIDE) processes may increase variability in population densities and further contribute to the risk of patch

extinction (Lande 1998). This study exemplifies the need for detailed experiments on the movements of organisms among habitat patches if we wish to understand the source-sink or regional dynamics of organisms (Watkinson and Sutherland 1995, Holyoak and Lawler 1996, Andreassen and Ims 2001, Cronin 2003a, b, c, Donahue et al. 2003, Bowne and Bowers 2004).

Finally, this experimental study suggests that a change in landscape structure, e.g., brought about by the invasion and spread of exotic plant species, may have a greater impact on higher rather than lower trophic levels. In a mudflat-dominated landscape, planthoppers and parasitoids had comparable rates of sub-population extinction, but in a brome-dominated landscape, parasitoid extinction rates were three times higher than for the planthopper. This result is congruent with the expectation that predators are more prone to extinction than their prey (Pimm and Lawton 1977, Diamond 1984, Pimm 1991, Kruess and Tscharrntke 1994, Holt 1996, 2002, Davies et al. 2000). In a seven-generation survey of cordgrass patches, Cronin (2004) found that *A. columbi*'s extinction rate averaged over all landscapes matrix types was 1.7 times higher than the rate for its host. Extinction rate in *A. columbi* was dependent on factors that spanned three trophic levels (plant, planthopper, and parasitoid abundance per patch), whereas planthopper extinction rate was dependent only on landscape structure (patch size and matrix composition). The dependency on multiple trophic levels may explain the overall higher extinction rate for the parasitoid than its host (see also Schoener 1989, Holt 1996, 2002, Komonen et al. 2000). There are also several possible explanations for why the brome matrix had a greater impact on *A. columbi* than *P. crocea* extinction rates. First, in brome-embedded patches, *A. columbi* densities were an order of magnitude lower than the densities of its host, making them particularly vulnerable to extinction (Cronin 2004). Second, whereas 98% of the mudflat-embedded patches were occupied by planthoppers during the latter two generations of this study, only 83% of the brome-embedded patches were occupied by this species. *A. columbi*, therefore, experienced a more fragmented landscape than its host in brome. Several studies have shown that predators and parasitoids are more sensitive to habitat fragmentation than their prey (e.g., Kruess and Tscharrntke 1994, 2000, Komonen et al. 2000, Thies et al. 2003; but see Holyoak and Lawler 1996).

Since the settlement of Europeans in North America, prairie habitat has declined in area by over 99% (Samson and Knopf 1996). Many of the remaining prairie fragments in the Great Plains have been invaded by smooth brome (Wilson and Belcher 1989, D'Antonio and Vitousek 1992, Larson et al. 2001). At our study sites in North Dakota, the matrix is composed of approximately 30% mudflat, 40% native non-host grasses, and 30% brome. Within the past five years, brome

has expanded its range within these sites (J. T. Cronin, unpublished data). Not only has brome displaced whole cordgrass patches and other native vegetation, but also it has invaded low elevation areas of mudflat (see also Blankespoor and May 1996). Given the continued spread of brome, we would anticipate increases in planthopper and parasitoid emigration and immigration rates at the site or regional level. The consequences of this appear to be instability at the patch level. We are currently exploring the consequences of brome invasion and spread at the regional level using simulation models (J. D. Reeve, J. T. Cronin, and K. J. Haynes, unpublished data).

The broad implications of this study are four fold. First, our study reveals a novel and potentially important mechanism underlying the negative effects that invasive exotic plant species can have on native faunas (Drake et al. 1989, D'Antonio and Vitousek 1992). By changing the composition of the matrix habitat within a landscape, exotic plants may alter animal movement and therefore the connectivity among existing native habitat patches. Our study adds to the growing body of empirical evidence that changes in dispersal patterns ultimately can affect the population dynamics of predators and their prey (see also, e.g., Kareiva 1987, Holyoak and Lawler 1996, van Nouhuys and Hanski 2002). Until additional studies are performed, we will not know how common such a mechanism is in disrupting the population dynamics of native species. Second, the invasion of exotic plant species, and the subsequent change in landscape structure, may be more detrimental to trophic levels higher up in the food web. Third, a change in matrix composition can significantly affect patch connectivity: a common goal in conservation programs (Rosenberg et al. 1997, Tewksbury et al. 2002, Haddad et al. 2003). It may be possible to employ a matrix that facilitates dispersal (i.e., brome), either alone, or in combination with stepping stones or corridors to enhance movement among isolated habitat fragments (Rosenberg et al. 1997, Wiens 1997, Baum et al. 2004). Finally, as a cautionary note, in striving to attain high connectivity among fragmented populations, local reproduction and immigration may become overridden by emigration leading to unstable local patch dynamics. For habitat fragments that are small, as is often the case for populations in need of conservation, fragments already may be hard to find and easy to lose for the organisms that live among them (e.g., Kareiva 1987, Turchin 1986, Kindvall 1999, Andreassen and Ims 2001). Promoting higher rates of dispersal among those fragments could tip the balance in favor of local extinction ($B + I < D + E$) if emigration rates are more strongly impacted than immigration rates. In altering the landscape to promote high connectivity among fragments, conservation biologists should consider how those changes affect emigration and immigration (see also Bowne and Bowers 2004).

ACKNOWLEDGMENTS

T. Arbour, E. Bless, J. Carlson, A. Caro, D. Cronin, F. Dillimuth, K. Legleu, C. Nelson, C. Rhodes, N. Shah, and A. Widdell assisted with various aspects of this project. J. LaDuke granted me permission to work on property owned by the University of North Dakota. K. Baum, N. Cappuccino, J. Reeve, and two anonymous reviewers provided helpful comments on previous drafts of this manuscript. This work was supported by the Louisiana State University and the National Science Foundation grants DEB-0296141 and DEB-0211359 and an REU Supplement.

LITERATURE CITED

- Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology* **82**:2911–2926.
- Baum, K. A., and W. E. Grant. 2001. Hummingbird foraging behavior in different patch types: simulation of alternate strategies. *Ecological Modelling* **137**:201–209.
- Baum, K. A., K. J. Haynes, F. P. Dilleuth, and J. T. Cronin. 2004. The matrix enhances the effectiveness of corridors and stepping stones. *Ecology* **85**:2671–2676.
- Blankespoor, G. W., and J. K. May. 1996. Alien smooth brome (*Bromus inermis* Leyss) in a tallgrass prairie remnant: seed bank, seedling establishment, and growth dynamics. *Natural Areas Journal* **16**:289–294.
- Bowne, D. R., and M. A. Bowers. 2004. Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology* **19**:1–20.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. *Ecology* **58**:445–449.
- Cantrell, R. S., and C. Cosner. 1999. Diffusion models for population dynamics incorporating individual behavior at boundaries: applications to refuge design. *Theoretical Population Biology* **55**:189–207.
- Comins, H. N., M. P. Hassell, and R. M. May. 1992. The spatial dynamics of host–parasitoid systems. *Journal of Animal Ecology* **61**:735–748.
- Cook, A. G., and R. F. Denno. 1994. Planthopper/plant interactions: feeding behavior, plant nutrition, plant defense, and host–plant specialization. Pages 114–139 in R. F. Denno, and T. J. Perfect, editors. *Planthoppers: their ecology and management*. Chapman and Hall, New York, New York, USA.
- Corbett, A., and J. A. Rosenheim. 1996. Quantifying movement of a minute parasitoid, *Anagrus epos* (Hymenoptera: Mymaridae), using fluorescent dust marking and recapture. *Biological Control* **6**:35–44.
- Cronin, J. T. 2003a. Matrix heterogeneity and planthopper–parasitoid interactions in space. *Ecology* **84**:1506–1516.
- Cronin, J. T. 2003b. Movement and spatial population structure of a prairie planthopper. *Ecology* **84**:1179–1188.
- Cronin, J. T. 2003c. Patch structure, oviposition behavior, and the distribution of parasitism risk. *Ecological Monographs* **73**:283–300.
- Cronin, J. T. 2004. Host–parasitoid extinction and colonization in a fragmented prairie landscape. *Oecologia* **139**:503–514.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63–87.
- Davies, K. E., C. R. Margules, and J. E. Lawrence. 2000. Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**:1450–1461.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* **14**:342–355.
- Dempster, J. P., D. A. Atkinson, and M. C. French. 1995. The spatial population dynamics of insects exploiting a patchy food resource. II. Movements between patches. *Oecologia* **10**:354–362.
- Diamond, J. M. 1984. 'Normal' extinctions of isolated populations. Pages 191–246 in M. H. Nitecki, editor. *Extinctions*. Chicago University Press, Chicago, Illinois, USA.
- Donahue, M. J., M. Holyoak, and C. Feng. 2003. Patterns of dispersal and dynamics among habitat patches varying in quality. *American Naturalist* **162**:302–317.
- Drake, J. A., F. DiCasteri, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmanek, and M. H. Williamson. 1989. *Biological invasions: a global perspective*. Wiley, New York, New York, USA.
- Fownes, S., and J. Roland. 2002. Effects of meadow suitability on female behaviour in the alpine butterfly *Parnassius smintheus*. *Ecological Entomology* **27**:457–466.
- Goodwin, B. J., and L. Fahrig. 2002. Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology* **80**:24–35.
- Gustafson, E. J., and R. H. Gardner. 1996. The effect of landscape heterogeneity on the probability of patch colonization. *Ecology* **77**:94–107.
- Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent, and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* **84**:609–615.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, New York, New York, USA.
- Harrison, S., and A. D. Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27–42 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Hastings, A. 1993. Complex interactions between dispersal and dynamics: lessons from coupled logistic equations. *Ecology* **72**:896–903.
- Haynes, K. J. 2004. Herbivore movement and spatial population dynamics in a heterogeneous landscape. Dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.
- Haynes, K. J., and J. T. Cronin. 2003. Matrix composition affects the spatial ecology of a prairie planthopper. *Ecology* **84**:2856–2866.
- Haynes, K. J., and J. T. Cronin. 2004. Confounding of patch quality and matrix effects in herbivore movement studies. *Landscape Ecology* **19**:119–124.
- Hitchcock, A. S. 1963. *Manual of the grasses of the United States*. Dover Publications, New York, New York, USA.
- Holder, M. W., and S. W. Wilson. 1992. Life history and descriptions of the immature stages of the planthopper *Prokelisia crocea* (Van Duzee) (Homoptera: Delphacidae). *Journal of the New York Entomological Society* **100**:491–497.
- Holt, R. D. 1996. Food webs in space: an island biogeographic perspective. Pages 313–323 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman and Hall, New York, New York, USA.
- Holt, R. D. 2002. Food webs in space: on the interplay of dynamic instability and spatial processes. *Ecological Research* **17**:261–273.
- Holyoak, M., and S. P. Lawler. 1996. Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. *Ecology* **77**:1867–1879.
- Huffaker, C. B. 1958. Experimental studies on predation: dispersion factors and predator–prey oscillations. *Hilgardia* **27**:343–383.
- Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: emigration, migration, and col-

- onization. Pages 247–265 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Kareiva, P. 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature* **326**:388–390.
- Kindvall, O. 1999. Dispersal in a metapopulation of the bush cricket, *Metrioptera bicolor* (Orthoptera Tettigoniidae). *Journal of Animal Ecology* **68**:172–185.
- Komonen, A., R. Penttilä, M. Lindgren, and I. Hanski. 2000. Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* **90**:119–126.
- Kruess, A., and T. Tschardtke. 1994. Habitat fragmentation, species loss, and biological control. *Science* **264**:1581–1584.
- Kruess, A., and T. Tschardtke. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* **122**:129–137.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65**:791–801.
- Lande, R. 1998. Anthropogenic, ecological and genetic factors in extinction and conservation. *Researches on Population Ecology* **40**:259–269.
- Larson, D. L., P. J. Anderson, and W. Newton. 2001. Alien plant invasion in mixed-grass prairie: effects of vegetation type and anthropogenic disturbance. *Ecological Applications* **11**:128–141.
- Matter, S. F., and J. Roland. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. *Ecological Entomology* **27**:308–316.
- Moilanen, A., and I. Hanski. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology* **79**:2503–2515.
- Pimm, S. L. 1991. *The balance of nature?* Chicago University Press, Chicago, Illinois, USA.
- Pimm, S. L., and J. H. Lawton. 1977. Number of trophic levels in ecological communities. *Nature* **268**:329–331.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Reeve, J. D. 1988. Environmental variability, migration, and persistence in host–parasitoid systems. *American Naturalist* **132**:810–836.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* **158**:87–99.
- Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. *Ecology* **81**:1642–1653.
- Roland, J., and P. D. Taylor. 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386**:710–713.
- Rosenberg, D. K., B. R. Noon, and E. C. Meslow. 1997. Biological corridors, form, function, and efficacy. *BioScience* **47**:677–687.
- Samson, F., and F. Knopf. 1996. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Washington, D.C., USA.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation. *Conservation Biology* **5**:18–32.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* **70**:1559–1589.
- Tabachnick, B. G., and L. S. Fidell. 2000. *Using multivariate statistics*. Allyn and Bacon, Boston, Massachusetts, USA.
- Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences of the United States of America* **99**:12923–12926.
- Thies, C., I. Steffan-Dewenter, and T. Tschardtke. 2003. Effects of landscape context on herbivore and parasitism at different spatial scales. *Oikos* **18**:18–25.
- Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. *Journal of Animal Ecology* **68**:647–657.
- Turchin, P. B. 1986. Modelling the effect of host patch size on Mexican bean beetle emigration. *Ecology* **67**:124–132.
- Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* **158**:211–220.
- van Nouhuys, S., and I. Hanski. 2002. Colonization rates and distances of a host butterfly and two specific parasitoids in a fragmented landscape. *Journal of Animal Ecology* **71**:639–650.
- Walker, R. S., A. J. Novaro, and L. C. Branch. 2003. Effects of patch attributes, barriers, and distance between patches on the distribution of a rock-dwelling rodent (*Lagidium viscacia*). *Landscape Ecology* **18**:187–194.
- Watkinson, A. R., and W. J. Sutherland. 1995. Sources, sinks and pseudo-sinks. *Journal of Animal Ecology* **64**:126–130.
- Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43–62 in I. Hanski and M. E. Gilpin, editors. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Wilcox, B. A., and D. D. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. *American Naturalist* **125**:879–887.
- Wilson, S. D., and J. W. Belcher. 1989. Plant and bird communities of native prairie and introduced Eurasian vegetation in Manitoba, Canada. *Conservation Biology* **3**:39–44.
- Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. *Ecology* **80**:1019–1030.