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FROM POPULATION SOURCES TO SIEVES: THE MATRIX ALTERS HOST–PARASITOID SOURCE–SINK STRUCTURE

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Abstract. Field experiments that examine the impact of immigration, emigration, or landscape structure (e.g., the composition of the matrix) on the source–sink dynamics of fragmented populations are scarce. Here, planthoppers (*Prokelisia crocea*) and egg parasitoids (*Anagrus columbi*) were released among host-plant patches that varied in structural (caged, isolated, or in a network of other patches) and functional (mudflat matrix that impedes dispersal vs. brome-grass matrix that facilitates dispersal) connectivity. Planthoppers and parasitoids on caged patches exhibited density-dependent growth rates, achieved high equilibrium densities, and rarely went extinct. Therefore, experimental cordgrass patches were classified as population sources. Because access to immigrants did not result in elevated population densities, source populations were not also pseudosinks, i.e., patches whose densities occur above carrying capacity due to high immigration. Planthoppers and parasitoids in open patches in mudflat had dynamics similar to those in caged patches, but went extinct in 4–5 generations in open patches in brome. Brome-embedded patches leaked emigrants at a rate that exceeded the gains from reproduction and immigration; populations of this sort are known as population sieves. For species whose suitable patches are becoming smaller and more isolated as a result of increased habitat fragmentation, emigration losses are likely to become paramount, a condition favoring the formation of population sieves. An increase in the proportion of patches that are sieves is predicted to destabilize regional population dynamics.

Key words: Anagrus columbi; egg parasitoid; emigration; extinction; host–parasitoid interactions; matrix; metapopulation; planthopper; Prokelisia crocea; *pseudosink; sieve; source–sink structure.*

INTRODUCTION

The population structures of organisms living in fragmented habitats are often cast in terms of metapopulations or source–sink systems (for reviews see Hanski 1999, Kawecki 2004). Whereas classic metapopulation theory assumes that variation in patch quality is trivial and local extinction is mainly stochastic, source–sink theory assumes intrinsic heterogeneity in patch quality and that low-quality patches (i.e., sinks) deterministically go extinct in the absence of immigration (Dias 1996). The classification of populations as sources, sinks, or variations thereof (e.g., pseudosinks and sieves), depends on the relative magnitudes of the birth, immigration, death, and emigration (*BIDE*) rates. Local populations in which $B > D$ are self-sustaining source populations that contribute propagules ($E > I$) to neighboring populations (Pulliam 1988). Patches in which the reverse is true ($B < D$, $E < I$) are known as sinks and can only persist through the rescue effect (Brown and Kodric-Brown 1977). Pseudosinks are inherently self-sustaining populations (in the absence of *I* and *E*) with densities maintained above the carrying capacity by relatively high *I* (Watkinson and Sutherland

1995, Boughton 2000). Strong density dependence at these elevated densities renders $B < D$, giving the false impression that the population is a sink. Finally, sieve populations are also sources, but $E > B - D$ (Thomas and Kunin 1999). As with sinks, sieves persist via the rescue effect.

Source–sink dynamics have been studied extensively by theoretical ecologists. The relative abundance of source and sink habitats can affect the size, growth rate, and persistence of metapopulations (Holt 1985, Doebeli 1995, Kawecki 2004). From a conservation standpoint, long term and predictable source populations (i.e., reservoirs) are thought critical to the persistence of threatened or endangered species (Ehrlich and Murphy 1987, Tscharntke 1992). Even sink habitats can contribute to regional population dynamics by providing stepping stones that facilitate dispersal between source habitats (Laurance 1991) and by helping to rescue source populations from extinction (Gyllenberg et al. 1997, Crone et al. 2001, Delibes et al. 2001, Murphy 2001). Conceivably, a metapopulation consisting entirely of sink populations may persist if dispersal among independently fluctuating local populations enhances the growth rate of the metapopulation (Hanski 1999). For interacting species such as a predator and its prey, the addition of sink habitat can stabilize an otherwise unstable or neutrally stable model (Holt 1985,

McLaughlin and Roughgarden 1991, Holt and Hassell 1993). In general, sink habitat in these models acts as a buffer, absorbing excess individuals from source habitats, and preventing the population from overshooting its equilibrium and subsequently crashing to extinction (i.e., overcompensating density dependence).

Population sieves are not well documented empirically, nor have they been given much consideration by theoreticians (but see Thomas and Kunin 1999). However, sieve patches may be integral to global persistence by providing stepping stones between sources (as with sink patches) that organisms may use as a refuge or as a site for feeding and reproduction. Also, sieves may serve as an important source of propagules for the colonization of vacant patches or the rescue of declining populations. If sieves are common, regional rates of movement may be high, leading to increased synchrony in densities among patches. According to metapopulation theory, asynchronous local dynamics are necessary for persistence at the regional level (Harrison and Taylor 1997, Ims and Yoccoz 1997, Hanski 1999).

Despite the rich literature characterizing the structure of natural populations, few experimental studies have assessed the relative contributions of *BIDE* to local population growth (Diffendorfer 1998, Thomas and Kunin 1999, Rosenheim 2001, Kawecki 2004, Runge et al. 2006). In most instances, populations that exhibit positive or negative growth are assumed to be sources and sinks, respectively. An example where observational studies can lead to erroneous conclusion is detailed by Thomas et al. (1996). In their study with the checkerspot butterfly *Euphydria editha*, observational data suggested that populations in forest clearings were sources and populations on rocky outcrops were potentially sinks. However, a summer frost eliminated populations in the clearings, providing a natural experiment with which to evaluate the structure of outcrop populations. True sinks are predicted to go extinct in the absence of immigration from source populations, but this was not observed with the outcrop populations. In fact, Thomas et al. concluded that outcrop populations were pseudosinks because they persisted at lower densities than before the loss of clearcut populations. Elucidation of the true structure of local populations requires a fortuitous natural experiment such as that observed by Thomas et al. (1996), or the manipulation of *BIDE* rates (Watkinson and Sutherland 1995, Rosenheim 2001, Kawecki 2004, Runge et al. 2006). There is also a need for studies that explore how landscape-level factors affect population source–sink structure. For example, there is a considerable body of evidence that indicates matrix composition (i.e., the habitat between patches) strongly influences I and E, and therefore the functional connectivity among habitat patches (reviewed in Haynes and Cronin 2004). Therefore, a matrix that facilitates dispersal could cause source patches to function as

pseudosinks or sieves, or make sinks appear as sources (owing to a strong rescue effect).

Finally, there are relatively few empirical data on predator and prey source–sink dynamics that can be used to evaluate theoretical models (but see e.g., Amezcua and Holyoak 2000, Caudill 2003, Donahue et al. 2003, reviewed in Cronin and Reeve 2005). Predators and prey may have very different source–sink population structures because of differences in *BIDE* or their responses to the same landscape structure. For example, of the studies that have examined the movement of a host and its parasitoid, 88% indicate a significant difference in dispersal ability (rate or range of dispersal) between the two species (70% of the time, the host was more dispersive than the parasitoid; Cronin and Reeve 2005). Limited dispersal ability may preclude the occurrence of pseudosinks and sieves that are contingent upon high I or E, respectively. In addition, theory and empirical data suggest that predators are more sensitive to habitat fragmentation/loss than their prey, in terms of extinction risk (e.g., Pimm 1991, Holt 1996, Davies et al. 2000, Thies et al. 2003). It is conceivable that this differential response may arise because habitat patch quality is lower for the predator than the prey, e.g., because the availability of herbivorous prey may be lower than the availability of suitable host plant material in the same patch (Holt 1996, Cronin 2004). Much remains to be explored regarding the effects of habitat fragmentation/loss or changes in landscape structure on the source–sink structure of predators and their prey.

Here, I experimentally determined the source–sink structures of local populations of the prairie planthopper, *Prokelisia crocea* Van Duzee (Hemiptera: Delphacidae), and its egg parasitoid, *Anagrus columbi* Perkins (Hymenoptera: Mymaridae), and how changes in matrix composition can affect their population structures. Host-plant patches that were identical in size, shape, and plant quality were made to vary in structural (caged, isolated, or in a network of other patches) and functional (mudflat matrix that impedes dispersal vs. non-host grass matrix that facilitates dispersal) connectivity. The experimental design allowed for the determination of the relative contributions of I, E, and $B - D$ to the source–sink structure (e.g., source, sink, pseudosink, and sieve) of planthopper and parasitoid populations under different landscape conditions. I conclude by exploring how changes in source–sink structure, owing to increased habitat fragmentation or changes in landscape composition, can affect host and parasitoid population dynamics.

Planthopper–parasitoid biology and spatial ecology

The spatial ecology of *P. crocea* and *A. columbi* is among the best known for a host–parasitoid system. The host plant of *P. crocea*, prairie cordgrass (*Spartina pectinata*; Poaceae), grows as discrete patches (0.01–40 000 m²) in hydric grasslands of the North American
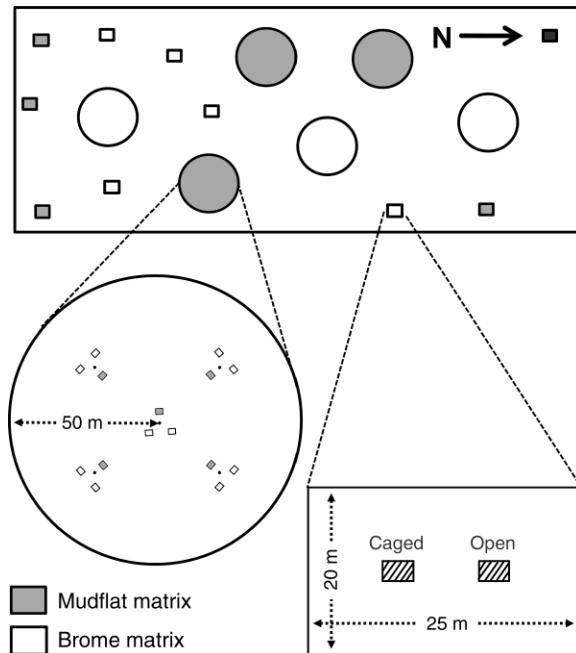
Fig. 1. Map of study site consisting of six cordgrass patch networks and 10 isolation plots embedded in either a brome or an experimentally created mudflat matrix (equal number per matrix type). The background matrix for the entire 32-ha field plot was brome; i.e., brome networks and brome isolation plots were unmanipulated controls. All experimental networks and isolation plots were separated by ≥100 m. Experimental cordgrass patches were 0.66 m². An isolation plot consisted of one caged and one uncaged patch spaced 5 m apart (from midpoint to midpoint; denoted as hatched rectangles). Each 50 m radius network consisted of 15 patches, divided into five clusters of three. Patches within a cluster were 5 m apart. Distance from the midpoint of the central cluster to the midpoint of the other four clusters was 30 m. Shaded patches in the network represented target patches used in density surveys.

Great Plains (Cronin 2003a). In northeastern North Dakota where this study was conducted, the matrix habitat within which cordgrass patches are embedded consists of three distinct types: (1) mudflat, (2) a mixture of native grasses (primarily *Andropogon scoparius* Michx., *A. gerardii* Vitman, and *Agropyron smithii* Rydb.), and (3) the exotic grass, smooth brome (*Bromus inermis* Leyss) (Haynes and Cronin 2003).

P. crocea is the dominant herbivore of prairie cordgrass (Cronin 2003a, b, c). It is monophagous and exhibits two distinct generations per year in the Great Plains (Cronin 2003a). Overwintering first instar nymphs emerge from beneath dead vegetation in May, feed on the phloem of cordgrass leaves, and mature into adults in June. Eggs are laid beneath the leaf surface. By mid-August, the second generation of planthopper adults reaches peak density. *A. columbi* is a facultative specialist of *P. crocea* eggs at my field site and singularly causes the highest rate of mortality of the planthopper (Cronin 2003b, c, Cronin et al. 2004). Patch-level rates of parasitism range from zero to 100% and average 21%

(Cronin 2003b, 2004). Parasitism of *P. crocea* eggs is spatially and temporally density independent (Cronin 2003c). However, parasitism was strongly aggregated among hosts within cordgrass patches (Cronin 2003c), which is theoretically stabilizing for the host–parasitoid interaction (Pacala et al. 1990, Hassell et al. 1991, Ives 1992). *A. columbi* also has two generations per year, with adult densities coinciding with the occurrence of planthopper eggs.

Local populations of the planthopper and parasitoid are extinction prone, 23% and 51% go extinct per generation, respectively (Cronin 2004). For the planthopper, extinction risk increased with a decrease in patch size and an increase in the proportion of smooth brome in the area surrounding the patch. Parasitism of planthopper eggs had no effect on planthopper extinction risk. For *A. columbi*, extinction risk was dependent on factors that spanned three trophic levels; risk of extinction increased with an increase in plant density and a decrease in host or parasitoid density. The regional dynamics of the host and parasitoid have been classified as the mainland–island metapopulation type because extinctions have never been observed in the few very large cordgrass patches (Cronin 2003a, b, 2004). A common misconception is that a mainland–island structure is indicative of source–sink populations, but the high extinction risk for small populations may or may not belie a negative population growth rate (Hanski 1999).

The effects of landscape structure on the movement and dynamics of local populations of the planthopper and parasitoid were examined in a large-scale experiment by Cronin and Haynes (2004). In that study, replicate networks of 15 cordgrass patches were embedded in one of two matrix types, brome or mudflat (Fig. 1; see *Methods* for details). Patches were organized into five clusters ranging from 30 to 60 m apart. Within a cluster, patches were spaced 5 m apart. Based on the release of fluorescent-marked planthoppers, we found that the proportion of individuals dispersing through brome to another patch within the same cluster (5 m away) was 4% per generation and to a patch within a different cluster 30 m away was <1% per generation. Parasitoids exhibited the same pattern but the rate was lower than for its host: 0.8% per generation at 5 m and 0.2% per generation at 30 m. Relative to a brome matrix, dispersal rates in a mudflat matrix were three and 11 times lower for the planthopper and parasitoid, respectively. At a distance of 100 m, inter-patch dispersal rates are predicted to be negligible for all species and matrix types (<0.001%).

Until this study, we had no data to discern whether local populations were sources, sinks, pseudosinks, or sieves. Based on the finding that planthopper and parasitoid population extinction risks were much lower in a mudflat than a brome matrix (Cronin 2004, Cronin and Haynes 2004), we hypothesized that populations in the former matrix were sources and the latter matrix

were sinks (Cronin and Haynes 2004). However, as described earlier, we lacked the required experiments that examined how populations grow in response to a reduction or elimination of I and E (via isolation or caging). The study I describe in the *Methods* expands on the design and data from Cronin and Haynes (2004) by including contemporaneous data on planthopper and parasitoid densities from caged and isolated patches, and by extending the study period from three to five generations. The increased time frame was necessary to reveal the equilibrial states for local planthopper and parasitoid populations.

METHODS

The experiment to evaluate the importance of I, E, and matrix composition to local population dynamics of the planthopper and parasitoid was conducted in a 32-ha field dominated by smooth brome and lacking any native cordgrass (Grand Forks County, North Dakota, USA; Cronin and Haynes 2004). In May, 2002, cordgrass was excavated from a nearby prairie. Because planthoppers and parasitoid overwinter in the thatch, I expected that the cordgrass clumps would harbor low densities of each species (see Cronin and Haynes 2004). Cordgrass clumps were planted flush to the ground in 0.7×0.9 m patches (355 ± 7 stems/patch, mean $\pm$ SE, $n = 110$). An aluminum barrier was inserted into the ground along the perimeter of each patch to limit the spread of cordgrass and encroachment of brome. Through regular fertilization and watering, variation in patch nutritional quality was minimized among treatments. The size of cordgrass patches used in this study was $\geq 22\%$ of the patches found in nearby prairies (Cronin 2003*a*).

The experimental cordgrass patches were subjected to three types of treatments: isolation (isolated or situated in a network of other patches), matrix composition (mudflat or brome), and caging (open or caged; see Plate 1). For the isolation treatment, 10 pairs of patches (1 caged, 1 uncaged) were positioned at least 100 m from any other cordgrass (isolated patches; see Fig. 1). Another subset of patches was embedded in a network of cordgrass patches. Each network ($n = 6$) consisted of 15 experimentally created cordgrass patches divided into five clusters of three patches (Fig. 1). Patches within a cluster were spaced 5 m apart and clusters were separated by at least 20 m. One patch from each cluster was used for the population analyses (target patch), the other patches served as sources of propagules.

In addition to manipulating structural connectivity through geographic isolation, I also altered the functional connectivity among patches by manipulating matrix composition (Cronin and Haynes 2004). The isolation plots and patch networks were established in either unmanipulated brome habitat or in experimentally created mudflats (assigned at random). Mudflats were created and maintained by spraying herbicide (Glyphomax Plus; Dow AgroSciences, Indianapolis,

Indiana, USA) and plowing under the dead vegetation. The 10 isolated plots and six patch networks were divided equally between the brome and mudflat treatment. An aerial photograph of the study site can be found in Cronin and Haynes (2004).

Finally, the caging treatment consisted of a polyvinyl-chloride frame ($1.0 \times 1.0 \times 1.0$ m), enclosed by fine mosquito netting and anchored to the ground (see Plate 1). Cages were erected in mid-May, prior to spring emergence of planthopper nymphs, and remained in place until late September each year. From September to May, these insects are in sedentary winter-diapause stages. Cages reduced light levels by 18%, but otherwise had no impact on temperature and relative humidity at 25 cm above ground (temperature, $t = 1.20$, df $= 18$, $P = 0.12$; humidity, $t = 1.01$, df $= 18$, $P = 0.16$), stems per square meter ($t = 0.31$, df $= 36$, $P = 0.76$), ramet height ($t = 1.02$, df $= 36$, $P = 0.16$) or percentage tissue nitrogen ($t = 0.65$, df $= 48$, $P = 0.52$) (15 months following treatment; see Cronin and Haynes [2004] for description of techniques). Thus, it is likely that the primary effect of caging would be the inhibition of planthopper and parasitoid I and E.

The above experimental design resulted in five distinct treatments: caged ($n = 10$), open-brome-isolated ($n = 5$), open-mudflat-isolated ($n = 5$), open-brome-network ($n = 3$), open-mudflat-network ($n = 3$). Based on the mark–release experiment by Cronin and Haynes (2004; see *Introduction*), the experimental cordgrass patches should have the following rankings with regard to functional connectivity for both the planthopper and parasitoid: caged (no I or E) < open-isolated (mudflat or brome; no I, normal E) < open-mudflat-network (low I and E) < open-brome-network (high I and E).

One month after establishment of cordgrass patches, 500 recently eclosed adult planthoppers (the ambient sex ratio at the time of capture was ~4:1 [females : males]) were released into each target patch (for the three patches in a network cluster, only one received insects). This represents an intermediate density for naturally occurring patches (Cronin 2003*a*, Cronin et al. 2004). Parasitoid sources were derived from individuals that were present as overwintering adults in the thatch of the excavated cordgrass.

For five generations (2002-II–2004-II), I determined the incidence and density of each species per cordgrass patch. Each census was initiated after 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 (as cast chorions) and parasitism (as circular exit holes) but no live insects. Six 10×25 cm sampling frames were placed haphazardly within each patch, and from within each frame I counted the number of cordgrass stems and collected as many infested leaves as could be found per patch, up to a maximum of 20. When no infested leaves were found in the sampling frames, the remainder of the patch was searched intensively to unambiguously

TABLE 1. Characteristics and criteria used to categorize experimental cordgrass patches as sources, sinks, pseudosinks, or sieves.

Structure type	BIDE characteristics	Criteria
Source	$B > D$, $E > I$	Mean densities in caged patches increase over time ($B > D$) or achieve a nonzero steady state ($B \approx D$).
Sink	$B < D$, $E < I$	Populations in caged patches go extinct.†
Pseudosink	$B < D$, $E < I$; $B \geq D$ when density is low or E and I prevented	Open-isolated patches have a significantly lower density than open-network patches (open-mudflat-isolated patches vs. open-mudflat-network patches; or open-brome-isolated patches vs. open-brome-network patches), but caged populations are inherent sources ($B \geq D$).‡
Sieve	$E > B - D$	Populations open to emigration steadily decline or go extinct, but caged populations are inherent sources.

Note: BIDE characteristics are: B, birth; I, immigration; D, death; and E, emigration.
† A trend toward declining densities would make determination of sink populations ambiguous.
‡ B, D, and E for isolated and network patches are assumed to be equivalent for a given density and matrix type. Thus, differences in density are expected to be driven by I alone.

ascertain patch occupancy. Leaves were dissected to determine the number of unparasitized and parasitized hosts per leaf.

The criteria used to determine whether experimental patches functioned as sources, sinks, pseudosinks, or sieves are outlined in Table 1. Local populations of planthoppers or parasitoids were classified as inherent sources if caged populations increased over time or achieved a nonzero steady state. If, on the other hand, populations went extinct, they were classified as sinks. All else being equal, pseudosinks should have elevated densities relative to sources, owing to high immigration. For local populations to be pseudosinks, the criteria for a source population had to be met. In addition, densities had to increase with increasing proximity to immigrant sources, i.e., densities in network patches were higher on average than densities in isolated patches (for a given matrix type). As stated in the *Introduction* (see also Cronin and Haynes 2004), patches isolated by 5 m (network patches) were expected to receive >4000 times more immigrants than patches isolated by 100 m (isolated patches). Compounded over five generations, this difference in I should have been sufficient to generate measurably higher densities in network vs. isolated patches. Finally, local populations were classified as sieves if caged populations persisted (i.e., they are inherent sources) and open populations (brome or mudflat) declined in density over time or went extinct.

Differences in mean density (ln-transformed) among all five patch treatments (caged, open-brome-isolated, open-mudflat-isolated, open-brome-network, open-mudflat-network) and over time (five generations) were analyzed with repeated-measures ANOVA (separate tests for planthoppers and parasitoids; SYSTAT 2004). To avoid the possibility of nonindependence in densities among the five target patches per brome and mudflat network, I averaged those densities each generation (therefore, $n = 3$ networks for these patch treatments). The same approach was used for all subsequent statistical tests. Differences between patch treatments were assessed with the same repeated-measures ANOVA model, but with the inclusion of only the two patch treatments in question. To guard against inflated Type I

errors, I used a Bonferroni-corrected level of α. Specifically, of the 10 possible pairwise comparisons, I was only interested in the differences in density between caged and open-network patches (brome and mudflat tested separately; sieve test, in part), open-brome-network and open-mudflat-network (test of matrix effect), and open-isolated and open-network patches (brome and mudflat tested separately; pseudosink test, in part). Therefore, I set α at 0.01 for these five pairwise tests.

Density dependence in population growth rate among patches ($R_0 = N_{t+1}/N_t$; where N is the number of individuals per stem) should be evident in source, and especially pseudosink populations whose densities are expected to reside near, or even above (in the case of pseudosinks), carrying capacity. The relationship between N_t and R_0 was assessed with ANCOVA (SYSTAT 2004). Patch treatment was the fixed main effect, density was the covariate, and separate tests were performed in each generation for each species. Density (+0.01) and R_0 were ln-transformed prior to analysis. These tests are nonindependent owing to possible temporal autocorrelation in densities within a patch. However, the frequent occurrence of extinctions precluded a continuous time series of data for every patch. Tests were Bonferroni-corrected and I emphasized patterns that were pervasive over time.

In the above experimental design, it was intended that cordgrass patches be of similar quality, in terms of nutritional state, biomass, and risk of predation, so that differences in planthopper and parasitoid density among treatments could be assumed to be due to the established differences in I and E. Aluminum barriers around patches and fertilization of plots were meant to minimize some of these differences among patches. However, the caging, isolation, and matrix treatments could have altered patch quality in a way that might impact I and E. To verify that patches in different treatments were of similar quality, I measured spider density (the dominant predators of *P. crocea*; Cronin et al. 2004), an index of biomass (cordgrass stems per square meter) and nutritional quality of the leaves (percentage tissue nitrogen) for each patch (see Appendix A). Based on

analyses of these data (see Appendix A), I confirmed that the different patch treatments were similar with regard to biomass, nutritional quality, and top-down effects from predators.

RESULTS

By the end of the first generation of study (2002-II), all patches were occupied by planthopper eggs and parasitoid larvae. The nontarget patches in the network (which did not receive supplemental insects) had densities that were initially 28–34% lower on average than the densities in target patches (see Appendix B). In subsequent generations, the densities in nontarget patches were at least as high as those in the target patches; thus, those patches represented a significant source of immigrants for my target patches.

Planthopper density per patch varied considerably with respect to patch treatment and time (time, $F_{3,63} =$ 45.7, $P < 0.001$; treatment, $F_{4,21} = 11.53$, $P < 0.001$; the last generation was omitted from the analysis because of zero variance in the brome treatment; Fig. 2A). Most notably, the caged and open-mudflat patches had high relatively constant densities following 2002-II, but planthoppers in all of the open-brome patches declined in density over time and ultimately went extinct by the fifth generation. These different trends resulted in a strong treatment × time interaction ($F_{12,63} = 2.38$, $P = 0.013$). Caged populations consistently had the highest density of planthoppers (18.8 ± 6.8 planthoppers per stem after 2002-II, mean ± SE), about six times higher than the density in open patches in mudflat ($F_{1,11} = 11.17$, $P = 0.007$). Based on the criteria outlined in Table 1, local planthopper populations on experimental 0.66-m^2 cordgrass patches were inherent sources. Isolation of patches did not result in lower planthopper densities relative to non-isolated patches, as would be expected if patches acted as pseudosinks. Population densities in the network vs. isolated patches, within matrix type, were quite similar (mudflat, $F_{1,6} = 0.03$, $P = 0.887$; brome, $F_{1,6} = 0.13$, $P = 0.74$; Fig. 2A). The fact that all open patches had lower planthopper densities than the caged patches (see Fig. 2A) indicates that emigration losses must have exceeded immigration gains. In the case of the open-brome patches, E was so great that extinction occurred in all cases, i.e., those patches were population sieves for the planthoppers.

The local population structure for *A. columbi* mirrored that of its host. Parasitoid densities differed significantly among treatments and over time (time, $F_{2,32} = 64.1$, $P < 0.001$; treatment, $F_{4,16} = 5.48$, $P = 0.006$; last two generations omitted because of zero variance in the brome treatment; Fig. 2B). In contrast to my findings with the host, I detected no significant time × treatment interaction term with the parasitoid (time × treatment, $F_{8,32} = 0.30$, $P = 0.96$). Caged parasitoids settled onto a relatively constant population size in one generation, and had a density from that point forth of 0.78 ± 0.20 juveniles per stem (mean ± SE, indicative of an inherent
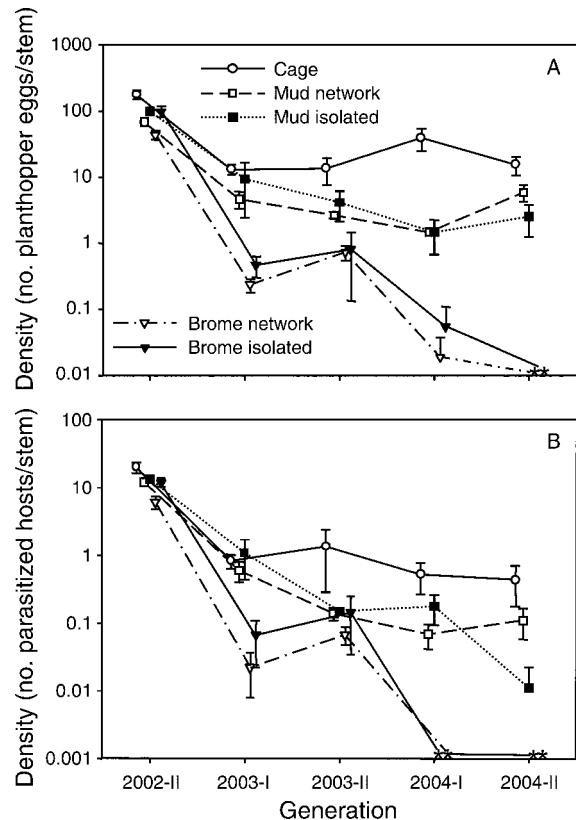

FIG. 2. Change in (A) planthopper and (B) parasitoid density (no. per stem per patch, mean ± SE) over time in experimental cordgrass patches from five different patch treatments. The stars indicate zero mean population density. For clarity, symbols depicting means per generation and treatment have been staggered slightly along the abscissa; note the y-axis log scale. Generations are labeled by year and whether it is the first (I) or second (II) generation of the year.

source population). Mean density in open-mudflat-network patches also leveled off by the fourth generation, but was 3.3 times lower than the mean density of cages ($F_{1,10} = 8.14$, $P = 0.017$; a marginally significant result based on a critical level of $\alpha = 0.01$). Local populations did not appear to be pseudosinks; there was no difference between open-isolated and open-network patches in either matrix (mudflat, $F_{1,6} = 0.39$, $P = 0.56$; brome, $F_{1,4} = 2.26$, $P = 0.21$). In the open-brome patches, the decline of parasitoid populations to extinction within four generations (Fig. 2B) supports the expectation of sieve populations.

In two of four generations for the planthopper and two of three generations for the parasitoid, there was a highly significant decrease in R_0 with increasing density (Fig. 3, Appendix C). Overall, density explained ~31% ± 13% and 37% ± 14% of the variation in R_0 for the planthopper and parasitoid, respectively (100 × SS_{Dens}/SS_{Tot}; first generation excluded). Despite the strong differences in density among patch treatments (Fig. 2), patch treatment and the treatment–density
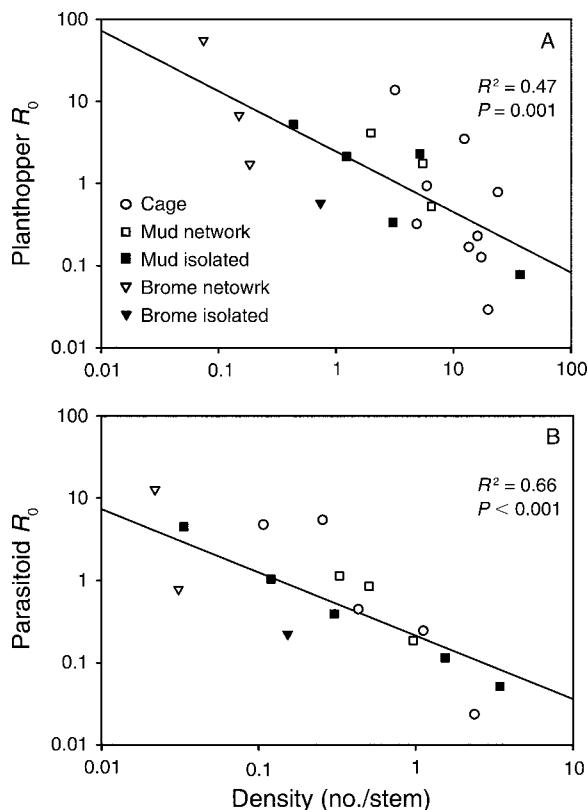
FIG. 3. Relationship between density and population growth rate R_0 for the (A) planthopper and (B) parasitoid in generation 2003-I. Line fit and statistics (R^2 and P value) were determined by least-squares regression for all patch treatments combined. Prior to the analyses, density (+0.01) and R_0 were ln-transformed. Note the log–log scale.

interaction had little effect on R_0. Thus, insects in caged patches, for which density dependence only operated on B and D, had the same response to density as insects in open patches in which density dependence could act on any of the *BIDE* rates.

DISCUSSION

This study greatly changed my earlier perceptions regarding planthopper and parasitoid population structure in which persistent populations in mudflat matrix and extinction prone populations in brome matrix were hypothesized to be sources and sinks, respectively (see Cronin and Haynes 2004). As it turns out, all populations in experimental patches, regardless of matrix type, were determined to be inherent sources. When local populations were closed to I and E (i.e., in caged patches), their densities appeared to reach a nonzero equilibrium in the latter generations. I found no evidence that open planthopper and parasitoid populations with access to immigrants from a larger network of patches (e.g., open-network patches) had higher densities than populations with virtually no access to

immigrants; source populations were not acting as pseudosinks when they occurred as part of a metapopulation (see Watkinson and Sutherland 1995, Boughton 2000). The likely explanation for why high immigration did not lead to increased densities in the network patches is strong density dependence in both R_0 and E (Fig. 3, see also Cronin 2003a). The additions to the population through immigration were likely compensated for by a decrease in reproduction or an increase in mortality or emigration. Despite the challenges associated with detecting pseudosinks (Watkinson and Sutherland 1995), evidence of pseudosinks has been reported for a variety of organisms including checkerspot butterflies (Thomas et al. 1996), lacewings (Rosenheim 2001), and Eastern Kingbirds (Murphy 2001).

This study provides the first experimental evidence to suggest that source populations can be changed into extinction-prone sieves by altering matrix composition. When the matrix was mudflat, local populations of planthoppers and parasitoids in open patches functioned as sources, but when the matrix was comprised of the introduced grass smooth brome, emigration losses became so high that extinction was inevitable (i.e., they were population sieves; Thomas and Kunin 1999). For both insect species, densities over time were significantly lower in open-mudflat patches than caged patches, suggesting that equilibrial densities in open patches were reduced by emigration.

Sieve dynamics for brome-embedded patches, where $E > I$, are likely to be robust with regard to considerable increases in the abundance of patches per network. Even when patches were only 3 m apart and twice as numerous as in this study (a 5.5-fold increase in patch number/m^2), Haynes and Cronin (2003) found that I was 10 times lower than E for the planthopper. The parasitoid had an even greater discrepancy between I and E for an isolation distance of 3 m (Cronin 2003b; J. T. Cronin, *unpublished data*).

Cronin and Reeve (2005) and Reeve and Cronin (*unpublished manuscript* and *unpublished data*) developed a landscape-level spatial population model for this planthopper and parasitoid system that reveals the potential extent of source–sieve dynamics for patches of varying size. The model was parameterized with data on intra- and inter-patch movement behavior, responses to patch-matrix boundaries, and the *BIDE* rates. We found that for the planthopper, patches embedded in brome needed to be about twice the size of my experimental patches (1.3 m^2) to convert them from sieves to sources. Even though patches ≤ 1.3 m^2 are small, they do constitute almost 30% of all patches in my field sites. At present, we do not have sufficient data on *A. columbi*'s movement behavior to predict the minimum patch size necessary to support a viable parasitoid population. However, in contrast to the planthopper, persistence of *A. columbi* populations is not related to patch size, but is most strongly dependent on host density (Cronin 2004).

PLATE 1. Photographs of different experimental treatments designed to alter the structural and functional connectivity of cordgrass patches: (A) Aerial view of an experimentally created mudflat containing a network of 15 cordgrass patches; (B) open-isolated (in circle) and caged cordgrass patches in an experimental mudflat; and (C) cluster of three cordgrass patches in a mudflat network. Photo credits: J. T. Cronin.

Small cordgrass patches in brome are sieves because brome–cordgrass boundaries are highly permeable to the movement of planthoppers and parasitoids (Cronin 2003b, Haynes and Cronin 2003, 2006). Both species at these boundaries are as likely to leave as turn back into the patch. In contrast, mudflat poses a strong barrier to movement, and the majority of insects at the boundary turn back into the patch. This likely leads to the buildup of insects within mudflat-bounded patches. A growing list of studies suggests that the composition of the adjacent matrix can significantly influence boundary behavior and inter-patch movement rates of animals (Jonsen and Taylor 2000, Cronin 2003b, Schooley and Wiens 2003, reviewed in Haynes and Cronin 2004, Haynes and Cronin 2006). Given the importance of the matrix to *BIDE* rates, we might expect that matrix composition will often affect source–sink dynamics (i.e., by causing source patches to function as pseudosinks or sieves).

The seemingly maladaptive response of the planthopper and parasitoid to brome-embedded patches (high rates of emigration from suitable host-plant patches) may be a transient response to a relatively recent change in the landscape matrix. The association between smooth brome and the planthopper and parasitoid is at most 130 years old (Hitchcock 1963). In addition,

only in the past decade have we seen brome become a dominant plant species at my field sites in northeastern North Dakota (F. P. Dillemuth, E. Rietschier, and J. T. Cronin, *unpublished data*). It is possible the *P. crocea* and *A. columbi* have not had sufficient time to evolve an appropriate dispersal response to the relatively novel brome matrix. On theoretical grounds, the evolution of dispersal rate is predicted in response to changing landscape structure (e.g., Gandon and Rousset 1999, Heino and Hanski 2000, Hanski et al. 2004). Consequently, sieve dynamics may eventually give way to source dynamics for planthoppers and parasitoids in brome-embedded patches.

The field experiment provided strong evidence for density dependence in some components of *BIDE* for the planthopper and parasitoid. A negative relationship between density and R_0 in caged patches indicates that B and/or D were density dependent. For the planthopper, previous experimental studies revealed strong density dependence in E but not in I (Cronin 2003a; J. T. Cronin, *unpublished data*). Therefore, in open patches, density dependence in planthopper B, D, or E may be operating. For the parasitoid, strong density dependence in per capita egg-laying rates (B) has been reported (Cronin 2003c), but to date, no studies have explored the relationship between parasitoid density and I, D, or E.

The absence of a patch treatment–density interaction effect on planthopper and parasitoid R_0 suggests that the reduction in R_0 as density increased was equivalent across all treatments. Therefore, when emigration is prevented (as in the cages), a compensatory decrease in B or increase in D should result. For other examples of compensatory density-dependent responses see Moe et al. (2002) and Moon and Stiling (2002). The across-treatment decline in densities of planthoppers and parasitoids between the first and second generation (Fig. 2) was likely due to strong density dependence in various BIDE rates when densities were artificially elevated (at the start of the experiment).

Implications for population structure and dynamics

This study suggests that classical source–sink dynamics (Pulliam 1988), in which $B - D$ is greater than zero for sources and less than zero for sinks, do not fit the population structures of this host and parasitoid or a number of other fragmented populations (reviewed in Thomas and Kunin 1999). However, a system of relative sources and sinks could arise, even when the quality of patches does not vary, if dispersal among patches is asymmetric (Kawecki 2004). If the dispersal rate from patch 1 to patch 2 is greater than the dispersal rate from 2 to 1, there would be a net flow of individuals from 1 (relative source) to 2 (relative sink). For a given density, relatively large cordgrass patches (>1.3 m^2) in brome are net exporters of planthoppers and parasitoids relative to patches in mudflat (Cronin 2003b, Haynes and Cronin 2003). Therefore, patches in brome can be considered relative sources and patches in mudflat relative sinks. From this perspective, the effect of matrix composition on source–sink structure is the opposite of the hypothesized structure proposed in Cronin and Haynes (2004). Relative sources and sinks are implicit in most structured or spatially explicit metapopulation models (reviewed in Etienne et al. 2004, Ovaskainen and Hanski 2004). Source–sink structure, at least in the relative sense, is probably evident in most subdivided populations (reviewed in Pulliam 1996, Stacey et al. 1997, Hanski 1999, Kawecki 2004).

The relative abundance of source and sink patches can affect the growth rate, size, and persistence of single-species metapopulations (Doak 1995, Gyllenberg et al. 1997, Hanski 1999, Kawecki 2004). Source–sink structure can also have significant consequences for predator–prey interactions. Models (e.g., Holt 1985, McLaughlin and Roughgarden 1991, Holt and Hassell 1993) and empirical studies (e.g., Amezcua and Holyoak 2000, Donahue et al. 2003) suggest that the addition of a sink for the prey can increase persistence or stabilize unstable predator–prey interactions. Also, Namba et al. (1999) found that more predator sinks favor prey and fewer predator sinks are beneficial to the predator. In my system, sources for planthoppers tend to be sources for parasitoids. Therefore, a change in landscape structure that leads to an increase or decrease in sources

or sinks for the planthopper, will likely result in a corresponding change for the parasitoid. J. D. Reeve and I are currently developing a landscape-level model (see Cronin and Reeve 2005) to explore source–sink structure and the regional dynamics of host and parasitoid populations in real landscapes.

Worldwide, many, if not most, native populations are at serious risk to the loss or fragmentation of suitable habitat, and the invasion of exotic species (Wilcox and Murphy 1985, Drake et al. 1989, Saunders et al. 1991, Debinski and Holt 2000). Under these circumstances, habitat patches would become not only smaller (which tends to increase E; e.g., Kareiva 1985, Andreassen and Ims 2001), but also more isolated (reducing I; reviewed in Hanski 1999). Overall, this would tend to make patches harder to find and easier to lose (Kareiva 1985, Turchin 1986), conditions that favor sieve dynamics. I would suggest that the continued loss and fragmentation of habitat would promote the transition of local populations from sources to sieves. A change in matrix composition (e.g., through the invasion of exotic plant species such as smooth brome), may delay or hasten this transition, depending on its impact on species movement. An increase in the proportion of local populations that are sieves should increase the average rate of emigration across the metapopulation and reduce population densities at the local and regional levels (Doak 1995, Delibes et al. 2001, Donahue et al. 2003). Whether it has to do with small population size in general, or the increase in spatial synchrony among patches owing to higher dispersal rates, we would expect patch occupancy rates to decline and the risk of regional extinction to increase (Harrison and Taylor 1997, Ims and Yoccoz 1997, Hanski 1999). The continued loss or fragmentation of habitats, or spread of invasive plants, could lead to patches passing from population sources to sieves to sinks (i.e., population inversions; Doak 1995, Pulliam 1996, Polis et al. 1997, Boughton 1999). In the future, it would be very beneficial to focus our research efforts toward quantifying changes in population structure as the species' habitat deteriorates (see Biedermann 2004, 2005).

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APPENDIX A

Methods and analyses for the effects of patch treatment on spider abundance, stem density, and percentage tissue nitrogen (*Ecological Archives* E088-184-A1).

APPENDIX B

Densities of planthoppers and parasitoids in nontarget patches in the cordgrass networks. These individuals represent the primary source of colonists for the target patches (*Ecological Archives* E088-184-A2).

APPENDIX C

Results from separate ANCOVA tests to determine the factors influencing planthopper and parasitoid growth rate (R_0) among experimental cordgrass patches (*Ecological Archives* E088-184-A3).