POPULATION ECOLOGY

James T. Cronin

Host-parasitoid extinction and colonization in a fragmented prairie landscape

Abstract Few field studies of natural populations have examined the factors influencing local extinctions and colonization of empty habitat patches for a prey species and its predator. In this study, I carried out a census of planthopper (*Prokelisia crocea*; Hemiptera: Delphacidae) and egg parasitoid (*Anagrus columbi*; Hymenoptera: Mymaridae) incidence and densities in 147 host-plant patches (*Spartina pectinata*; Poaceae) over seven planthopper generations in a tall-grass prairie landscape. For both species, the likelihood of going extinct in a patch was related to a number of patch-specific variables: density, temporal variability in density, proportion of hosts parasitized (planthopper only), host-plant density, patch size, patch isolation, and composition of the surrounding matrix. Colonization likelihood was related only to the physical attributes of the patch. There was high patch turnover in this prairie landscape. On average, planthoppers went extinct in 23% of the patches and *A. columbi* went extinct in 51% of the patches in each generation. For the planthopper, extinction likelihood increased with a decrease in patch size and the proportion of the matrix composed of mudflat. Parasitism of eggs had no effect on the extinction likelihood of local *P. crocea* populations, suggesting that *A. columbi* may not play a major role in the patch dynamics of its host. The likelihood of extinction for *A. columbi* was dependent on factors that spanned three trophic levels. An increase in plant density, decrease in host density and decrease in parasitoid density all increased the likelihood of *A. columbi* extinction within a patch. The dependency on multiple trophic levels may explain the higher extinction risk for the parasitoid than its host. *A. columbi* extinction was also affected by the matrix habitat surrounding the patch—the effect was the opposite of that for *P. crocea*. Finally, vacant patches were colonized at rates of 53% and 34% per generation for the planthopper and parasitoid, respectively. For both species, colonization probabilities decreased with an increase in patch isolation. High host densities in a patch also favored high rates of colonization by *A. columbi*. I discuss how anthropogenic changes to the prairie landscape can affect the metapopulation dynamics and persistence time of this host-parasitoid interaction.

Keywords *Anagrus columbi* · Landscape matrix · Metapopulation · *Prokelisia crocea* · Spatial correlation

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Introduction

In metapopulation theory, regional persistence of a population is made possible because of a stochastic balance between extinctions of local populations and colonization of empty habitat patches (see Levins 1969; Hanski 1999). Determining the factors influencing local extinction and colonization events is of critical importance to understanding the regional dynamics of populations, as well as developing sound conservation and wildlife management plans. Empirically, a high risk of extinction has most often been associated with small population size or area of a habitat patch (e.g., Schoener and Spiller 1987; Pimm et al. 1988; Carlson and Edenhamn 2000). Extinctions are also more likely to occur for local populations whose densities fluctuate greatly over time (e.g., Pimm et al. 1988; Boulinier et al. 1998; Vucetich et al. 2000; Fagan et al. 2001; but see Schoener and Spiller 1992). For those patches that have gone extinct, colonization is greatly enhanced by being in close proximity to other patches with extant populations (Hanski 1999; Boyett et al. 2000). Turnover rates have also been shown to be affected by a wide diversity of other environmental and demographic factors, including weather conditions (Hanski et al. 1994; Hanski 1999; Schoener et al. 2001), host plant species (Van Nouhuys and Hanski 1999; Hanski and Singer 2001), parasitism (Lei and Hanski 1997; Weisser 2000), and inbreeding depression

(Saccheri et al. 1998; Nieminen et al. 2001). To some extent, extinction and colonization events also are likely to be spatially correlated, owing to spatial correlations in environmental factors (Harrison and Quinn 1989; Palmqvist and Lundberg 1998; Hanski 1999).

Metapopulation studies are most often represented by single point-in-time samples and the underlying probabilities of colonization and extinction are inferred from the patterns of patch occupancy (Pfister 1998; Hanski 1999). Relatively few studies have the spatio-temporal data to quantify the relationship between environmental, demographic and landscape variables and turnover probabilities (but see e.g., Kindvall 1996; Pfister 1998; Hanski 1999). Moreover, metapopulation studies tend to focus on individual species (reviewed in Hanski 1999); much less information is available for a predator and its prey (e.g., Huffaker 1958; Lei and Hanski 1997; Van Nouhuys and Hanski 1999, 2002; Amarasekare 2000; Weisser 2000; Van Nouhuys and Tay 2001). Prey extinction risk may be predator dependent, and vice versa (e.g., Lei and Hanski 1997; Van Nouhuys and Hanski 1999; Weisser 2000). Predators and prey also are likely to differ in many respects with regard to the factors influencing local population turnover. Because predators often tend to be more dispersive than their prey (Holt 1996), colonization success may be less affected by changes in patch isolation for the former than latter species. Turnover in herbivorous prey patches may depend strongly on host plant quality or the frequency of preferred plant species (Kuussaari et al. 1996; Hanski and Singer 2001), whereas predator turnover may or may not be affected by the base trophic level (Van Nouhuys and Hanski 1999). Finally, species at higher trophic levels may be more prone to extinction than those at lower trophic levels because of their lower densities, higher variability in population size, narrower and more fragmented distribution of resources, and/or dependence on lower trophic levels (Pimm and Lawton 1977; Diamond 1984; Pimm 1991; Kruess and Tscharntke 1994; Holt 1996; Davies et al. 2000; Purvis et al. 2000; Thies et al. 2003). Accurate predictions regarding predator-prey local and regional dynamics will require an understanding of how patch-level extinction and colonization in predators and their prey are affected by the same factors in nature.

In this study, I examined the role of various patch attributes in the likelihood of patch extinction and colonization of a specialist planthopper (*Prokelisia crocea* Van Duzee; Hemiptera: Delphacidae) and its egg parasitoid (*Anagrus columbi* Perkins; Hymenoptera: Mymaridae). The planthopper's host, prairie cordgrass (*Spartina pectinata*; Poaceae), is an extremely patchily distributed native grass of the Great Plains (Cronin 2003a). In a census spanning five generations and up to 147 cordgrass patches, I (Cronin 2003a) found that extinction rates for "island patches" were negatively correlated, and colonization rates positively correlated with patch size. Isolation effects on planthopper population turnover were ambiguous. Nothing to date has been reported on *A. columbi* turnover among patches. In the present study, I used census data reported in Cronin (2003a), but now expanded to seven generations, to explore whether planthopper and parasitoid density, temporal variability in density, proportion of hosts parasitized (planthopper only), host-plant density, patch size, patch isolation, and composition of the surrounding matrix were correlated with the likelihood of planthopper and parasitoid patch extinction and colonization. Finally, because it can reduce the effective number of patches in a metapopulation and therefore influence regional persistence (Harrison and Quinn 1989; Palmqvist and Lundberg 1998; Hanski 1999), the presence of spatial correlations in local extinction and colonization events was also examined. In light of this information on host-parasitoid turnover, I discuss how anthropogenic changes to the prairie landscape may affect the metapopulation dynamics and persistence time of this interaction.

Materials and methods

Natural history

In the North American Great Plains, prairie cordgrass patches are numerous and closely interspersed; maximum isolation from nearest neighbors is typically <46 m (Cronin 2003a, 2003b, 2003c). Within the prairie landscape, cordgrass patches are embedded in one of three matrix types: (1) mudflats, (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) (see Haynes and Cronin 2003).

Numerically, the most common herbivore of prairie cordgrass is *P. crocea* (Holder and Wilson 1992, Cronin 2003a, 2003b, 2003c, Haynes and Cronin 2003). *P. crocea* is monophagous (Holder and Wilson 1992) and exhibits two distinct generations per year in the northern Great Plains (Cronin 2003a). Planthoppers overwinter as first instar nymphs, reach peak adult densities in early June, and then lay eggs beneath the adaxial surface of cordgrass leaves. A second generation follows, with adults peaking in early August. Adults represent the primary dispersive stage, with >90% of males and females being macropterous (Cronin 2003a).

P. crocea has two parasitoids, *A. columbi* and an undescribed nymphal-adult parasitoid in the family Dryinidae (Cronin 2003b, 2003c). *A. columbi* parasitism rates per cordgrass patch range from zero to 100% and average 21% (Cronin 2003a). In comparison, the dryinid occurs at consistently low levels (1.3% mean parasitism rate). I focused this study only on the numerically dominant parasitoid, *A. columbi*. Within the prairies where this research was conducted, *A. columbi* 's only host is *P. crocea* (Cronin 2003b). The behavior and life history of this egg parasitoid are quite similar to that of the congener *Anagrus sophiae*, a parasitoid of the salt-marsh planthoppers *Prokelisia marginata* and *P. dolus* (Cronin and Strong 1993a, 1993b, 1996, 1999). Predators are also a very important source of planthopper mortality, particularly the suite of spiders that are present in cordgrass patches (>21 species; Cronin et al., in press). The effects of the spider assemblage on planthopper mortality, dispersal and spatial distributions is addressed in a separate paper (Cronin et al., in press).

For both the planthopper and parasitoid, even small patches (<0.75 m^2) can support a viable population for multiple generations, provided that the patch is closed to migration (e.g., caged; J. T. Cronin, unpublished data). Open patches, however, are subject to much movement and turnover by these two species. Based on a series of experiments, dispersal in the planthopper is primarily affected by patch size: small patches have higher rates of emigration and lower rates of immigration than large patches (Cronin 2003a). Isolation is more important than patch size in affecting parasitoid movement rates (Cronin 2003b). Both species are similarly affected

by the matrix habitat within which patches are embedded (Cronin, 2003c; Haynes and Cronin 2003). Emigration and immigration rates were highest for patches embedded in brome and lowest for patches embedded in mudflats.

Census procedure

Censuses of *P. crocea* and *A. columbi* densities were carried out for seven generations from 1999 to 2002 from cordgrass patches located within a single prairie fragment (site 104), a 65-ha area adjacent to Kelly's Slough National Wildlife Refuge in northeastern North Dakota (47.94184 N, 97.31036 W). The number of patches included in the census increased over time from 25 in the first generation, to 105 in the second generation, and finally to 147 in the fourth to the seventh generations inclusive. Patches were not a random sample of the ≈1900 patches present in the prairie fragment, but instead were chosen to represent a wide range of patch sizes and isolation distances. 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 25 cm×25-cm sampling frame was haphazardly placed at three locations and from within each frame we counted the number of cordgrass stems and collected a maximum of ten infested leaves. The intent of this sampling procedure was to minimally alter planthopper and parasitoid densities over time. If no infested leaves were found, the remainder of the patch was searched intensively 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 remaining planthopper egg chorions).

The size and isolation of each patch was determined every summer from a combination of digital photographs and differential GPS measurements. Patches ranged in size from 0.1 to 126.7 m^2, and averaged (± SE) 7.4±1.2 m^2 (Cronin 2003a). Because cordgrass patches were so numerous at site 104, nearest-neighbor distances were short, ranging from 1 m (the minimum distance allowable for inclusion in this study) to 46 m (mean of 5.7±0.4 m). Patch isolation was based on the linear distance to, and size of the nearest neighbor in each of four quadrats (Hanski 1994; Hanski and Kuussaari 1995). The index of isolation (*I*) is:

$$I = 1\sum_{i}^{4} A_i e^{-D_i} \tag{1}$$

where A_i and D_i are the area of (m^2) and distance to the nearest patch in the ith quadrat, respectively. Larger values of *I* indicate greater patch isolation. There is a high correlation between *I* and an isolation index using the equation above and based on all cordgrass patches within a 50-m buffer around a focal patch (Cronin 2003a). The matrix within which a patch was embedded was quantified by measuring the proportion of ground cover within a 3-m buffer strip surrounding the patch that consisted of mudflat (bare ground). Previous studies have shown that *P. crocea* and *A. columbi* immigration and emigration are most strongly affected by the amount of mudflat within just a couple of meters of the patch (Cronin, 2003c; Haynes and Cronin 2003; J. T. Cronin, unpublished data). Moilanen and Hanski (1998) used a similar approach to quantifying the matrix for the Glanville fritillary.

P. crocea turnover among patches

A planthopper extinction event was deemed to have occurred if a patch was occupied during generation *t*−1 and subsequently vacant at *t*; whereas a colonization event took place if the patch was vacant at *t*−1 and occupied at *t*. I used logistic regression (Hosmer and Lemeshow 2000) to determine the effect of ln planthopper egg density (*t*−1), proportion of eggs parasitized by *A. columbi* (*t*−1), host plant density (stems/m^2), ln patch size, ln isolation, proportion mudflat and planthopper generation (*n*=5) on the likelihood of planthopper extinction per patch at generation *t*. Prior to the analysis, the binomial dependent variable, whether or not the planthoppers in a patch went extinct at *t*, was logit-transformed [*ln* (*p*/1−*p*); where *p* = probability that the patch went extinct at *t*). The significance level for each independent variable was determined with a *G*-test (Hosmer and Lemeshow 2000). I also report McFadden's Rho-squared (ρ^2), which is comparable to the coefficient of determination (R^2) used in least-squares regression (Hosmer and Lemeshow 2000). By removing variables one-by-one from the analysis and examining changes in ρ^2 it was possible to determine the relative importance of each factor in explaining the variability in extinction risk.

I also examined whether the risk of extinction for a patch was related to the variation in planthopper egg densities within a patch over time [based on the coefficient of variation (CV); McArdle et al. 1990; Kindvall 1996]. Here, I define extinction risk as the proportion of generations in a time series (for a single patch) in which a patch that was occupied by planthoppers went extinct the following generation. The CV in planthopper egg density (CV$_H$) was based on time-series sequences in which no extinction events took place; thus, excluding zeros that might bias estimates of CV toward higher values (see also Schoener and Spiller 1992; Kindvall 1996). Also, because I was interested in predicting the occurrence of extinctions at the patch level, it was inappropriate to include the extinction event in the analysis. The minimum length of the time series for the computation of the CV was 3. Due to a lack of normality in the distribution of extinction risk, a Spearman's rank correlation was used to assess the association between these two variables. Lastly, I assessed whether there were significant correlations between CV$_H$ and the following variables: planthopper density, cordgrass density, patch size, patch isolation and proportion mudflat (using the means among generations for each variable). Bonferroni-corrected *P*-values are reported for these multiple correlations (Sokal and Rohlf 1995).

The factors influencing planthopper colonization of vacant cordgrass patches one generation later were evaluated using logistic regression. All variables except host and parasitoid density were included in the model.

A common assumption of metapopulation theory is that there is no spatial correlation in the occurrence of extinction or colonization events (Harrison and Quinn 1989; Hanski 1999). To determine if either of these turnover processes were spatially correlated, I computed the inter-patch distance between the centroids of all pairs of patches. Given an extinction in a patch at generation *t*, I tested whether the likelihood of an extinction in another patch (also at *t*) was dependent upon the distance between those patch pairs. Logistic regression was used in which distance between patch pairs and generation were the independent variables and whether or not the neighboring patch also suffered an extinction was the binomial dependent variable. A similar procedure was used to determine if colonization of patch pairs in the same generation was spatially dependent.

A. columbi turnover among patches

The same procedures were used to evaluate the factors that influenced *A. columbi* extinction and colonization at site 104. The effect of ln parasitoid density at *t*−1, ln host egg density at *t*, host plant density at *t*, ln patch size, ln isolation, proportion mudflat and generation on the likelihood that *A. columbi* would go extinct in a patch was assessed with logistic regression. Here, only patches were used that had an extant host population at *t*; thus, *A. columbi* extinctions were not a simple consequence of host extinctions. Parasitoid extinction risk (proportion of generations in which an *A. columbi*-occupied patch went extinct the following generation) and its relationship to the CV in parasitoid density (parasitized hosts/leaf/patch; CV$_P$) was assessed with a Spearman's rank correlation

Table 1 *Prokelisia crocea* extinction and colonization events over six generations at site 104

Generation	Patches in census	Extinction events		Colonization events	
		No. extant at $t-1$	No. extinct at t (% in parentheses)	No. extinct at $t-1$	No. colonized at t (% in parentheses)
1999-II	25	-	-	-	-
2000-I	105	25	0 (0)	0	-
2000-II	105	87	15 (17.2)	18	6 (33.3)
2001-I	146	90	38 (43.7)	15	5 (33.3)
2001-II	146	72	16 (21.3)	68	50 (73.5)
2002-I	146	112	24 (21.4)	21	11 (52.4)
2002-II	146	110	14 (12.7)	25	18 (72.0)

(extinction risk was not normally distributed). I also examined the relationship between CV_P and mean parasitoid density (averaged over the time series), CV_H, and the other patch variables. Finally, a logistic regression was also used to evaluate whether the likelihood of a patch being colonized one generation later (at generation t) was influenced by the abundance of host eggs at t, generation, or any of the other patch attributes (excluding parasitoid density).

The procedure used to determine whether *A. columbi* extinction and colonization events were spatially correlated was identical to that used for the planthopper. As before, I excluded from the analyses all patches that were not occupied by host eggs.

Results

P. crocea turnover among patches

Planthopper turnover among patches at site 104 was high. Each generation, planthoppers went extinct in 23.3±5.4% (mean ± SE) of the patches that were occupied by this species in the previous generation (Table 1). Of those patches in which an extinction occurred, 52.9±8.8% were colonized one generation later by planthoppers. After two and three generations, 82.1±6.5% and 88.3±5.1% of those vacant patches were colonized, respectively. Planthopper generation, patch size and matrix composition significantly influenced the likelihood of a patch extinction event (Table 2). The likelihood of extinction (proportion of patches with planthoppers that went extinct the next generation) declined from >0.40 in patches <0.5 m^2 to ≈0.10 in patches >25 m^2 (Fig. 1A). Of more novelty, I found that patch-level extinctions were significantly less likely to occur as the proportion of the matrix that was

mudflat increased (Fig. 1B). No other variables were significantly correlated with extinction risk. Overall, the logistic regression model explained an average of 46% of the variation in planthopper patch extinctions per generation (based on McFadden's ρ^2). Generation contributed the most to the variation in planthopper extinction likelihood (explaining 22.1% of the variation), followed by patch size (16.4%) and the proportion mudflat (5.0%).

The risk of extinction for a patch (averaged across generations) was strongly correlated with the CV_H [Spearman's rank correlation (R_S) = 0.55, n=53, P <0.001; Fig. 2]. There was also a significant negative correlation between CV_H and patch size (R=−0.37, P<0.001), but not with mean planthopper density, mean cordgrass density, patch isolation or the proportion of the matrix composed of mudflat (for all tests, R≤0.20, P≥0.14). To determine if CV_H influenced extinction risk independent of patch size, I first obtained the residuals from a regression analysis of CV_H on ln patch size. I then determined the correlation between extinction risk and these residual values of CV_H (which were now independent of patch size). Following this procedure, I still found a positive correlation between CV_H (residuals) and extinction risk (R_S=0.47, P<0.001). The reverse was also true: after factoring out the effects of temporal variability in density, there was still a significant negative relationship between patch size and extinction risk (R_S=−0.24, P=0.026).

Patch isolation was the most important factor influencing planthopper colonization (Table 3). As the I for a patch increased, the likelihood of a patch being colonized

Table 2 The effect of different patch attributes and planthopper generation on the likelihood that planthoppers went extinct in a patch at generation t. Data were analyzed using logistic regression and McFadden's ρ^2 for the overall model was 0.46

Dependent variables	G-statistic	df	P	% Variation explained
Ln planthopper egg density[a]	0.86	1	0.354	<1%
Parasitism by *A. columbi*[a]	1.15	1	0.283	<1%
Host plant density	0.24	1	0.622	<1%
Ln patch size	25.47	1	<0.001	16.4%
Ln patch isolation	3.45	1	0.063	1.2%
Proportion mudflat	11.22	1	0.001	5.0%
Generation	36.04	4	<0.001	22.1%

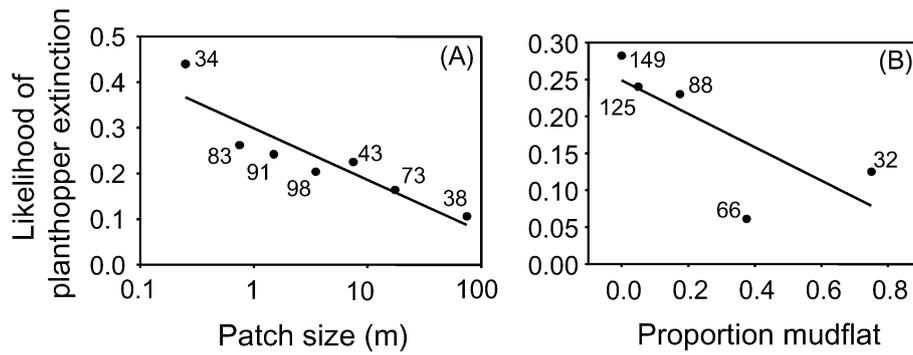[a]Measured at generation $t-1$; all other variables measured at generation t

Fig. 1 The effect of **A** patch size and **B** proportion of the surrounding matrix that was mudflat on the likelihood of planthopper extinction (the proportion of patches in which planthoppers went extinct between generations $t-1$ and t). Patch sizes and proportions mudflat were divided into discrete categories (patch size: ≤ 0.5 m^2, 0.5–1 m^2, 1–2 m^2, 2–5 m^2, 5–10 m^2, 10–25 m^2 and >25 m^2; proportion mudflat: 0.0, 0–0.1, 0.1–0.25, 0.25–0.5, 0.5–1.0). The midpoint of each category is reported on the x-axes and *numbers associated with each point* indicate the total patches per category. Data were pooled from five planthopper generations. *Lines* were fit by least-squares regression and statistical analyses are reported in Table 2
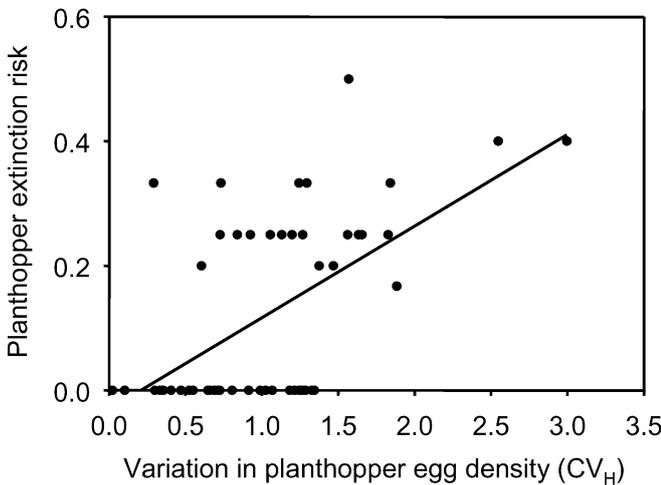

Fig. 2 The relationship between planthopper extinction risk (proportion of generations in which an extant patch went extinct between generations $t-1$ and t) and coefficient of variation in planthopper egg density among generations (CV$_H$) per patch. Each point represents a single cordgrass patch monitored for at least six planthopper generations. *Line* was fit by least-squares regression
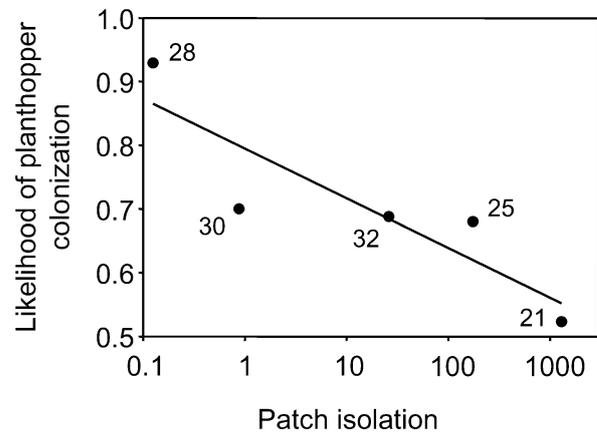

Fig. 3 Patch isolation (higher index values indicate greater isolation from nearest neighbors) and planthopper colonization likelihood (proportion of vacant patches that was colonized by planthoppers one generation later). The isolation index was divided into discrete categories and the midpoint of each reported on the x-axis. Data were pooled from five generations and the *number of patches per category* are reported adjacent to symbols. Statistical analysis is reported in Table 3

declined (Fig. 3). Patch size, cordgrass density, matrix composition and generation had no significant effect on the colonization of cordgrass patches by the planthopper (Table 3).

Table 3 The influence of host-plant density, patch size, isolation, matrix composition (proportion of the surrounding habitat that was bare mud) and generation on the likelihood that a patch was colonized by planthoppers one generation after it went extinct (based on logistic-regression analysis). McFadden's ρ^2 for the overall model was 0.31

Dependent variable	G-statistic	df	P	% Variation explained
Host plant density	0.24	1	0.624	<1%
Ln patch size	3.13	1	0.077	4.3%
Ln patch isolation	11.69	1	<0.001	23.5%
Proportion mudflat	0.80	1	0.372	1%
Generation	1.64	2	0.442	2.0%

I found no evidence to suggest that planthopper extinction or colonization events were spatially dependent. Given that planthoppers in a patch went extinct in generation t, the likelihood that planthoppers in neighboring patches also went extinct at t was independent of the distance between those patches (G=0.56, df=1, P=0.453). Similarly, for any given pair of vacant cordgrass patches, the likelihood of both of them being colonized by planthoppers in the same generation was independent of the distance between those patches (G = 1.79, df=1, P=0.180).

A. columbi turnover among patches

A. columbi went extinct in 51.6±13.9% of the patches each generation (based on those patches that were occupied by this species in the previous generation; Table 4). However, excluding cases in which extinctions

Table 4 *Anagrus columbi* extinction and colonization events over six generations at site 104

Generation	Extinction events			Colonization events	
	No. extant at $t-1$	Total extinctions at t (% in parentheses)	Extinctions at t when hosts present (% in parentheses) [a]	No. vacant at $t-1$	No. colonized at t (% in parentheses) [a]
2000-I	25	7 (28.0)	3 (14.3)	–	–
2000-II	75	10 (13.3)	4 (6.1)	10	6 (60.0)
2001-I	78	43 (55.1)	9 (20.5)	8	3 (37.5)
2001-II	40	30 (75.0)	23 (69.7)	24	2 (8.3)
2002-I	15	13 (86.7)	11 (84.6)	67	2 (3.0)
2002-II	4	0 (0)	0 (0)	116	68 (58.6)

[a] Based only on patches that had a viable local host population at t

were brought about by a host extinction, the proportion of patches in which *A. columbi* went extinct was 39.0±16.1% per generation. On average, the likelihood of extinction for the parasitoid was 1.7 times higher than the likelihood for its host, although the difference was not significant ($t = 0.95$, $df=8$, $P =0.372$). Patches in which *A. columbi* went extinct but the host did not were colonized by *A. columbi* at a rate of 33.5±12.1% (Table 4), 59.8±18.3% and 79.7 ±10.6% one, two and three generations later, respectively. The colonization rate of *A. columbi* was 37% greater than that of its host (one generation post extinction), but the difference was not significant ($t = 1.30$, $df=8$, $P=0.230$).

The likelihood of *A. columbi* extinction (proportion of patches in which *A. columbi* went extinct each generation) increased significantly with an increase in cordgrass stem density and the proportion of the matrix that was mudflat, and with a decrease in its own density or that of its host (Table 5; Fig. 4). In addition, *A. columbi* extinction likelihood varied significantly over the five-generation census period (Table 5). Host density contributed the most to explaining the variation in *A. columbi* extinction likelihood (explaining 23% of the variation), followed by generation (14%), stem density (8%), parasitoid density at $t-1$ (3%), and proportion mudflat (3%). Overall, the logistic-regression model explained 51% of the variation in *A. columbi* extinction likelihood. Finally, the risk of *A. columbi* extinction for a patch (averaged across generations) was not significantly correlated with variation in parasitoid density (CV_P) ($R_S=-0.13$, $n=36$, $P=0.449$). The CV_P was positively correlated with mean parasitoid

density per patch ($R = 0.37$, $P < 0.001$), negatively correlated with patch size ($R = 0.39$, $P=0.020$) and uncorrelated with CV_H, cordgrass plant density, the proportion of the matrix composed of mud or patch isolation (for all tests, $R \leq 0.21$, $P \geq 0.20$). Contrary to expectations, variability in parasitoid densities per patch was not significantly greater than the variability in planthopper densities (CV_H, 1.04±0.08 and CV_P, 0.97 ±0.06; based on analysis of covariance with patch size as a covariate, $F_{1,89}=0.32$, $P=0.56$).

A patch in which *A. columbi* went extinct was significantly more likely to be colonized by *A. columbi* one generation later if the patch had an abundance of hosts (G-test; $G=39.62$, $df=1$, $P < 0.001$; Fig. 5A), or if the patch was in close proximity to neighboring cordgrass ($G = 5.15$, $df=1$, $P=0.023$; Fig. 5B). Cordgrass density, patch size or the proportion mudflat had no effect on colonization likelihood (Table 6). Generation, host density and isolation explained 23%, 14% and 5% of the variation in the likelihood of colonization, respectively, and ρ^2 for the overall model was 0.46.

Pairs of cordgrass patches occupied by *A. columbi* were significantly more likely to go extinct in the same generation when they were close together than when they were far apart ($G=8.41$, $df=1$, $P=0.004$). The relationship between inter-patch distance (divided into discrete categories) and the proportion of patch pairs in which *A. columbi* went extinct in both patches at generations t is presented in Fig. 6A. Relative to the regional extinction rate (44% per generation, excluding

Table 5 Logistic regression analysis for the effect of different patch variables and parasitoid generation on the likelihood of *A. columbi* extinction in generation t. Only patches with a viable host population were included in the analysis. McFadden's ρ^2 for the overall model was 0.51

Dependent variables	G-statistic	df	P	% Variation explained
Ln parasitoid density ($t-1$) [a]	4.35	1	0.035	3.6%
Ln host egg density	24.97	1	<0.001	23.2%
Cordgrass plant density	8.13	1	0.004	8.1%
Ln patch size	1.43	1	0.232	<1%
Ln patch isolation	0.78	1	0.377	<1%
Proportion mudflat	3.78	1	0.052	3.1%
Generation	19.14	4	<0.001	13.7%

[a] Obtained from generation $t-1$; whereas all other variables determined at generation t

Fig. 4 Relationship between *Anagrus columbi* extinction likelihood (the proportion of patches in which *A. columbi* went extinct between generations $t-1$ and t) and **A** parasitoid density (number per stem at $t-1$), **B** host density (number per stem at t), **C** cordgrass density (stems/m^2), and **D** the proportion of the surrounding matrix that was mudflat. Each independent variable was divided into discrete categories and the midpoint of each reported on the *x*-axis (*number of patches per category* is reported adjacent to each symbol). Data were pooled from five generations, *lines* were fit by least-squares regression, and statistical analyses are reported in Table 5
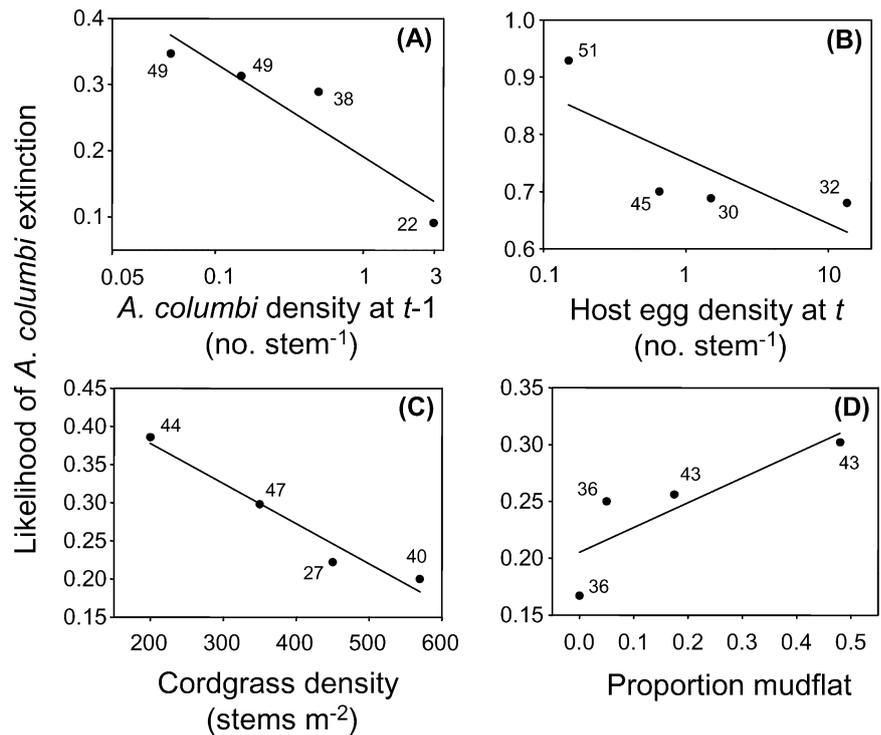
patches in which hosts went extinct; Table 4), patches ≤25 m apart were 1.5 times more likely to have *A. columbi* go extinct at the same time ($\chi^2=8.2$, $df=1$, $P=0.004$; Fig. 6A). As distance between patch pairs increased, the likelihood that *A. columbi* went extinct in both patches in the same generation declined. In fact, at an inter-patch distance of 200–400 m, the likelihood of extinction was significantly below the regional average ($\chi^2=5.5$, $df=1$, $P=0.019$; Fig. 6A). Finally, the probability that two patches would be colonized in the same generation by *A. columbi* was also spatially dependent ($G=9.22$, $df=1$, $P=0.002$), but there were no obvious trends in the data (Fig. 6B).

Discussion

P. crocea turnover among patches

Among the patch attributes considered in this study, patch size was the most significant predictor of planthopper extinction likelihood (see also Cronin 2003a). Small patches were particularly prone to planthopper extinction, a pattern predicted by theory (MacArthur and Wilson 1967; Hanski 1999) and well supported empirically (e.g., Schoener and Spiller 1987; Carlson and Edenhamn 2000; Van Nouhuys and Tay 2001). Interestingly, planthopper egg density, which is generally correlated with patch size (Cronin 2003a), did not affect planthopper extinction likelihood (independently of patch size). Several factors may explain the overriding importance of patch size on planthopper extinction likelihood. First, small patches favor high planthopper emigration rates (Cronin 2003a; see also Kareiva 1985; Kuussaari et al. 1996). Second, as

Fig. 5 *A. columbi* colonization likelihood (proportion of vacant patches that was colonized by the parasitoid one generation later) and its relationship to **A** host density (numbers per stem) and **B** patch isolation. Host density and isolation were divided into discrete categories and the midpoint of each reported on the *x*-axis. Data were pooled from five generations and the *number of patches per category* are reported adjacent to symbols. Statistical analysis is reported in Table 6
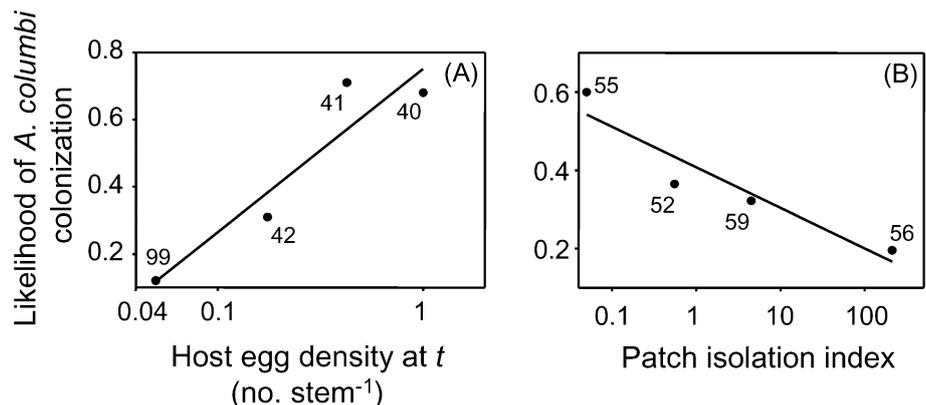
Table 6 Factors influencing the likelihood that a patch was colonized by *A. columbi* one generation after it went extinct. Logistic-regression analysis was performed using only patches occupied by host eggs. McFadden's ρ^2 for the overall model was 0.46

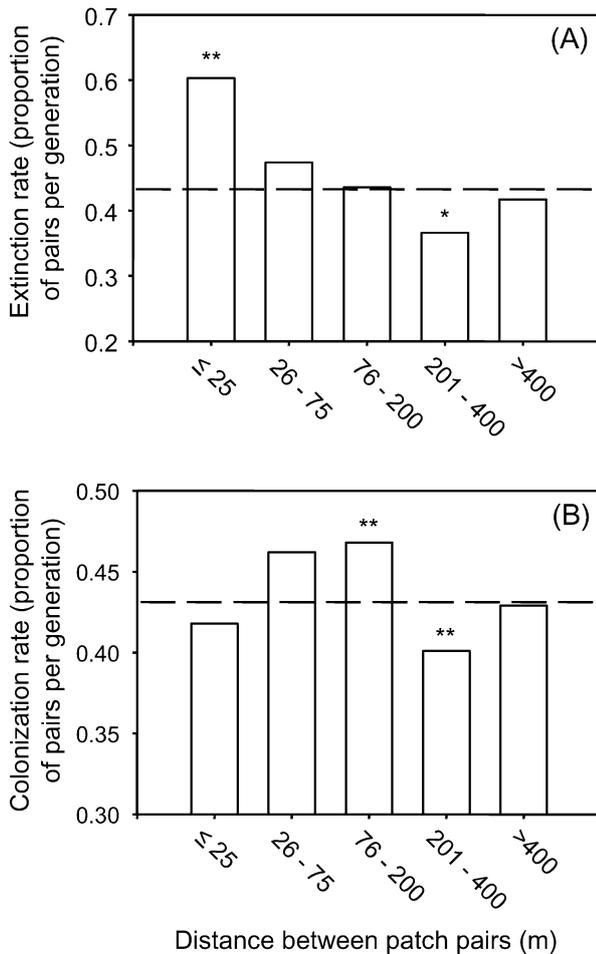| Dependent variables	G-statistic	df	P	% Variation explained
Ln host egg density	21.17	1	<0.001	13.7%
Cordgrass plant density	0.73	1	0.391	<1%
Ln patch size	1.35	1	0.245	<1%
Ln patch isolation	10.93	1	0.001	5.2%
Proportion mudflat	0.05	1	0.990	<1%
Generation	36.57	4	<0.001	22.6%

Fig. 6 For *A. columbi*, the probability that pairs of patches will either **A** both suffer parasitoid extinctions or **B** both be colonized during the same generation with respect to the proximity between patches. The *dashed reference lines* indicate the regional extinction and colonization rate for site 104, respectively. *$0.05 \geq P \geq 0.01$, ** $P<0.01$, in turnover rates between a distance class and the regional rate (based on χ^2-test)

crocea in tall-grass prairie fragments as a mainland-island metapopulation (see Cronin 2003a).

Although planthopper egg density per se did not affect the likelihood of a planthopper patch extinction, variability in local egg densities (CV_H) was positively correlated with extinction risk. It has been a long-standing viewpoint among ecologists that populations subject to large fluctuations in density are at greater risk to extinction than populations whose densities are more constant over time (e.g., MacArthur 1972; Diamond 1984; Pimm et al. 1988; Boulinier et al. 1998; Vucetich et al. 2000). However, in theory, both positive and negative relationships between population variability and extinction risk are possible (e.g., Schoener and Spiller 1992; Tracy and George 1992). For example, if population density and variability are positively correlated, then it is also likely that extinction risk will decrease with increasing variability (Schoener and Spiller 1992). For *P. crocea*, the positive correlation between CV_H and extinction risk was independent of the density of planthoppers per patch, patch size and several other landscape features. Experimental cordgrass patches, identical in all respects (size, shape, isolation, host-plant quality, and initial planthopper and parasitoid densities), also exhibited a positive correlation between CV_H and planthopper extinction risk and no correlation between CV_H and planthopper density (J. T. Cronin, unpublished data). These results suggest that features of the landscape are not responsible for the variability-extinction risk correlation in the planthopper.

In this study, I found that the composition of the matrix surrounding a patch also influenced planthopper extinction likelihood. Here, the greater the proportion of mudflat surrounding a patch, the less likely planthoppers in the patch would go extinct. The lower extinction likelihood for planthoppers in mudflat-embedded patch is not likely due to a scarcity of predators in those patches. Spiders, which as a group are the dominant predators of planthoppers, are as numerous and species rich in mudflat-embedded patches as they are in brome-embedded patches (Cronin et al., in press). The most likely explanation for the matrix effect on planthopper extinction likelihood is that patches embedded in a predominantly mudflat matrix have reduced planthopper emigration losses relative to brome-embedded patches (Haynes and Cronin 2003). Planthoppers are reluctant to cross the cordgrass-mudflat boundary (i.e., the patch edge is hard; sensu Stamps et al. 1987) whereas they readily cross a non-host grass-cordgrass boundary (i.e., the patch edge is soft). As a consequence, egg densities (a strong correlate

patch size decreases, the density of generalist spider predators increases (Cronin et al., in press). Spiders not only consume planthoppers but also promote higher rates of planthopper emigration as their density increases. As a result, smaller patches have difficulty sustaining viable planthopper populations (i.e., small patches are population sinks). Large patches, especially those over 1 ha in size remain continually occupied by the planthopper and serve as population sources (Cronin 2003a). Based on these findings, I have classified the population structure of *P.*

of adult densities; Cronin 2003a, 2003c) tend to increase with the proportion of the matrix that is mudflat (Haynes and Cronin 2003). There is also a corresponding non-significant trend toward reduced temporal variability in planthopper density as mudflat becomes more prevalent in the matrix; thus, potentially contributing to reduced planthopper extinction risk for patches in this matrix type. To date, a number of studies have found that matrix composition affects movement and patch occupancy (e.g., Kuussaari et al. 1996; Roland et al. 2000; Haynes and Cronin 2003), but to my knowledge none has found a link between matrix composition and the risk of local extinction.

Parasitism by *A. columbi* had no significant effect on the likelihood of planthopper patch extinction. Over the course of this census, parasitism within a patch very rarely reached 100% (<0.2% of patches) and averaged only 16.4% (see also Cronin 2003b). Whereas a number of *Anagrus* species play an important role in the suppression of agricultural pests (e.g., Meyerdirk and Moratorio 1987; Fowler et al. 1991; Williams and Martinson 2000), *Anagrus*-driven extinctions of hosts at the level of natural patches has not been reported. However, there are several studies with insect parasitoids that have linked local host extinctions with increasing rates of parasitism. Examples include parasitism of the Glanville fritillary by the braconid *Cotesia melitaearum* (Lei and Hanski 1997; but see Van Nouhuys and Tay 2001) and parasitism of aphids by the aphidiid *Lysiphlebus hirticornis* (Weisser 2000).

A planthopper extinction only had a short-term effect on the occupancy of a patch. On average, over 50% of the vacant patches were colonized by planthoppers the next generation and almost 90% after just two generations. High colonization rates can be attributed to the strong dispersal capabilities of the predominantly macropterous *P. crocea* adults, coupled with the generally short distances between patches and their nearest neighbors (Cronin 2003a). However, I did find strong evidence that planthopper colonization rates decreased significantly with increasing patch isolation. At the scale of the prairie landscape, *P. crocea* does appear to be dispersal limited (see also Hanski 1999; Boyett et al. 2000; Doak 2000).

A. columbi turnover among patches

An average of 52% of the patches occupied by *A. columbi* went extinct the following generation. About one-fourth of those extinction events can be attributed to the extinction of the host. After removing those cases of host extinction from the analysis, *A. columbi* had a likelihood of extinction that was 1.7 times higher than that of its host (39% versus 23% per generation; although the difference was not significant). These data support the idea that higher trophic levels are at greater risk of extinction than lower trophic levels (Pimm and Lawton 1977; Diamond 1984; Pimm 1991; Kruess and Tscharntke 1994; Holt 1996). Several reasons may explain this pattern in my system. First, *A. columbi* has an average density that is one-fifth that of its host (planthopper eggs), and its extinction risk does increase as its density decreases (see also Holt 1996). Second, *A. columbi* is a local specialist in these prairies and its extinction risk is significantly dependent on not only the density of its host, but also the density of the host plant. Dependency on two trophic levels (in addition to its own) may elevate *A. columbi*'s overall extinction risk (see also Schoener 1989; Holt 1996; Komonen et al. 2000). In the few other available studies on this subject, parasitoid extinction risk does seem to be tied to the abundance of its host (Lei and Hanski 1997, 1998; Van Nouhuys and Hanski 1999). Interestingly, within-patch variability in the density of host eggs (CV_H) was not related to the risk of parasitoid extinction, nor was variability in parasitoid density per patch (CV_P) higher than the variability in host density per patch (contrary to expectations; see e.g., Kruess and Tscharntke 1994). Finally, because only an average of 77% of the cordgrass patches are occupied by *P. crocea* at any one time (Cronin 2003a), *A. columbi* experiences a more fragmented landscape than its host. A number of studies have shown that predators and parasitoids are more sensitive to habitat fragmentation than their prey (e.g., Komonen et al. 2000; Kruess and Tscharntke 1994; Thies et al. 2003). Any or all of the above factors may conspire to make *A. columbi* more extinction prone than its host.

Cordgrass-stem density and the proportion of the matrix that was mudflat had unexpected effects on the likelihood of extinction of *A. columbi* at the patch level. Although planthopper turnover was independent of the density of its host plant, extinction likelihood for *A. columbi* increased significantly with an increase in stem density. I suggest that this represents a foraging constraint on the parasitoid. Studies with both *A. columbi* and a closely related species, *A. sophiae*, have revealed that these parasitoids do not detect hosts through long-range chemoreception (Cronin and Strong 1993a; Cronin 2003b). Instead, parasitoids appear to detect hosts only after landing upon a cordgrass leaf (through antennal contact with host oviposition damage). If detection requires proximal contact, higher stem densities may limit the efficacy of host location. Host plant effects on parasitoid extinction risk were also found by Van Nouhuys and Hanski (1999). In that study, extinction risk of *C. melitaearum* decreased with an increase in the fraction of host caterpillars on the plant, *Veronica spicata*. Reports of plant-parasitoid interactions are numerous (e.g., Gomez and Zamora 1994; Lill et al. 2002), but generally have not focused on their patch-dynamic consequences.

The increased likelihood of *A. columbi* extinction with an increase in the proportion of the matrix composed of mudflat was unexpected because it was the opposite of that found for the planthopper. Densities of *A. columbi* per patch tend to increase with an increase in the proportion of the surrounding matrix that is mudflat, but the colonization rate for patches embedded in pure mudflat is 6 times less than the colonization rate for patches in pure brome (Cronin, 2003c). Without the benefit of a strong rescue effect (Brown and Kodric-Brown 1977), *A. columbi* in

mudflat-embedded patches may be more extinction prone. The population-dynamic consequences of the matrix effect on planthopper and parasitoid extinction risk will be addressed below.

The likelihood that *A. columbi* will colonize a vacant cordgrass patch was most strongly influenced by the abundance of host eggs; more hosts meant a higher colonization rate. As I had found for the planthopper, the likelihood of patch colonization by *A. columbi* decreased with increasing patch isolation but was unaffected by the size of the patch. This response to the geography of a patch fits well with my previous experimental findings regarding the dispersal behavior of *A. columbi*. The number of immigrants arriving to de-faunated cordgrass patches (determined from sticky-trap captures) declined exponentially with an increase in isolation and was independent of patch size (Cronin 2003b). At the scale of a prairie fragment (65 ha), *A. columbi* is significantly more dispersal limited than *P. crocea* (Cronin 2003a, 2003b).

Metapopulation dynamics

Because the causes of planthopper and parasitoid turnover in patches are not the same, the regional population dynamics of each species may differ, and be affected differentially by anthropogenic changes to the landscape. One important difference between the planthopper and parasitoid is that extinctions are spatially correlated only in the latter species. At least for patch pairs within 25 m of each other, the probability that the *A. columbi* populations will both go extinct in the same generation is significantly higher than the regional average for pairs of patches. The consequence of this spatial correlation is that the effective number of independent patches for *A. columbi* is less than the actual number observed within the prairie. Because cordgrass patches occur within close proximity of each other (Cronin 2003a), the effective number may be far less than the observed number of patches. All else being equal (e.g., patch density, area, and isolation), a reduction in the number of independent patches is expected to reduce the regional persistence time of a population (Harrison and Quinn 1989; Palmqvist and Lundberg 1998; Hanski 1999). Thus, at the level of the whole prairie, *A. columbi* may be at much greater risk of extinction than *P. crocea*.

Spatially correlated *A. columbi* extinctions are likely to be driven by environmental or demographic factors that are themselves spatially correlated (see Harrison and Quinn 1989; Palmqvist and Lundberg 1998; Hanski 1999). Of the factors known to affect *A. columbi* extinctions, matrix composition is very strongly correlated in space (J. T. Cronin, unpublished data). The prairie landscape is a mosaic of regions dominated by one of the three matrix types (mudflat, native grasses, brome). Patches together in the same depression (mudflats are associated with low elevation areas), should all have similarly low rates of *A. columbi* immigration (see above). The restricted mobility of *A. columbi* relative to *P. crocea*, particularly within a mudflat (Cronin 2003b, 2003c), may explain why extinction rates are spatially correlated in the former and not the latter species. Stem densities are also significantly spatially correlated, but not host density (Cronin 2003a).

Finally, data on the factors that influence population turnover can be very useful in developing predictions regarding how anthropogenic changes to the landscape might affect the patch dynamics of the planthopper and parasitoid. One anthropogenic factor that has become a problem for ecosystems worldwide is the invasion and spread of exotic plants such as smooth brome (Drake et al. 1989; D'Antonio and Vitousek 1992). Brome has become established in the Great Plains of the United States and Canada by invading disturbed prairie (D'Antonio and Vitousek 1992), and through repeated introductions to prevent soil erosion and provide animal graze (Wilson 1989; Larson et al. 2001). In my prairie sites, not only is brome becoming a dominant matrix type, but it also appears to be infiltrating normally pure cordgrass patches and displacing patches altogether (J. T. Cronin, unpublished data). As a consequence of brome invasion, cordgrass patches are becoming fewer in number, farther apart and comprise lower stem densities (J. T. Cronin, unpublished data). For *P. crocea*, increased patch isolation is expected to reduce the likelihood of patch colonization by this species, but this effect is likely to be countered by the substantially higher dispersal rates for *P. crocea* in brome compared to any other matrix type (Haynes and Cronin 2003). More importantly, the rate of *P. crocea* extinction at the patch level will likely increase because its extinction likelihood rises with a decrease in the proportion of the surrounding matrix that is mudflat. Also, because brome favors high planthopper connectivity among cordgrass patches (Haynes and Cronin 2003), planthopper population densities among patches are likely to become spatially synchronous. In total, fewer patches, coupled with higher extinction rates and synchronous spatial dynamics is a recipe for a high probability of regional extinction (reviewed in Hanski 1999). In comparison, *A. columbi*'s response to these anthropogenic changes to the prairie is expected to be quite different. Both a decrease in stem densities and an increased dominance of brome in the matrix should favor reduced *A. columbi* extinction rates. Whether these reductions in extinction risk would compensate for the reduction in *A. columbi* colonization success associated with more isolated patches is unclear. What is clear, however, is that the invasion of brome into the tall-grass prairie is likely to drastically alter the spatial and temporal dynamics of these two species.

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