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Modeling the density–area relationship in a dynamic landscape: an examination for the beetle *Tetraopes tetraophthalmus* and a generalized model

Stephen F. Matter*

Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, USA

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Abstract

The relationship between local population density and habitat area is an important factor in spatial population ecology. I examined how density dependence in the growth of local insect populations and their host plant patches, combined with patch birth and death, and insect dispersal affect the density–area relationship. I constructed a simulation model to examine the relationship for an insect herbivore, *Tetraopes tetraophthalmus*, inhabiting patches of its host plant, *Asclepias syriaca*. Given the observed growth of insect populations, patch growth, dispersal of insects, and change in the number of patches within the landscape, the model predicts that *T. tetraophthalmus* density should decrease with increasing *A. syriaca* patch size. The model also predicts moderate amounts of temporal variation in the relationship. A more general insect herbivore-host plant model was also developed to extend the results. The general model shows that density dependence in patch and insect population growth rates have large effects on the density–area relationship. The density–area relationship was strongly affected by density dependence in insect growth. Increasing density dependence in insect growth caused insect density to decrease with increasing patch size. Temporal variation in the relationship was most strongly affected by density dependence in patch growth. Variation in the density–area relationship increased as density dependence in patch growth increased. The results of this study show that density–area relationships can be variable and are not necessarily a species-specific trait. Application of density–area relationships, especially in dynamic landscapes, need to be aware of and account for factors that affect the size and number of patches as well as growth and dispersal of the target populations.

Keywords: Asclepias; Density dependence; Dispersal; Individuals–area relationship; Metapopulation; Patch

1. Introduction

How population density relates to habitat size is an important consideration in the research of spatial population dynamics. Reviews of this topic, the density–area relationship (also called the individuals–area relationship; Schoener, 1986), have shown patterns of increasing, decreasing, and constant density relative to habitat area (Bowers and Matter, 1997; Bender et al., 1998; Connor et al., 2000). Despite the diversity of relationships, in general, population densities tend to increase with patch or habitat area (Connor et al., 2000; but see Gaston and Matter, 2002). The relationship between population density and habitat size underlies basic ecological theory and is pertinent to conservation issues (Haila, 1988; Andrén, 1994; Gaston et al., 1999; Connor et al., 2000; Matter, 2000;

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* Tel.: +1-513-556-9713; fax: +1-513-556-5299.
E-mail address: mattersf@email.uc.edu (S.F. Matter).

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Gaston and Matter, 2002). From a phenomenological perspective, the relationship affects population dynamics and community patterns. Within a metapopulation, increasing or decreasing population density with area results in individuals being clustered into large or small patches, respectively. This clustering changes the relative importance of different sized patches, altering predictions of metapopulation dynamics and community patterns (Matter, 2000, 2001a). Similarly, local populations of the same size, but within networks with different density–area relationships can show different dynamics (Matter, 1999). The density–area relationship has been proposed as a tool for reserve design, particularly in relation to the single large or several small (SLOSS) debate (Connor et al., 2000). The reasoning here is simple. For species that show increasing density with area, a large reserve will contain a greater abundance of individuals than any number of smaller reserves summing to the same size (Matter, 2000).

As a null expectation, density should not vary with habitat area (Haila, 1988; Bowers and Matter, 1997). Several mechanisms have been offered to explain deviations from this expectation. Root (1973) proposed that insect density should increase with increasing patch size if emigration rates are greater from small patches, and immigration rates and residence times are greater for large patches. Several studies have shown dispersal rates consistent with density patterns (Raupp and Denno, 1979; Kareiva, 1985; Bach, 1988), supporting a dispersal-based mechanism. However, behavioral models indicate that immigration rates may not be expected to increase with habitat area (Bowman et al., 2002). The enemies hypothesis predicts that predation rates are higher on small patches than on large patches producing positive density–area relationships (Denno et al., 1981; Risch, 1981). Habitat quality may vary with patch size producing increasing or decreasing density with area (Bach, 1988; Hanski, 1994; Matter, 1997). If habitat quality varies within patches such that the edges of patches are of higher or lower quality, the density–area relationship may vary with the perimeter to area ratio (Bowers et al., 1996; Bender et al., 1998; Haddad and Baum, 1999). Bowers and Matter (1997) proposed that mechanisms producing density–area relationships may depend on spatial scale. Habitat selection at small spatial scales may produce negative relationships if territorial individuals preempt non-territorial individuals from larger habitats. Positive relationships may arise at broader spatial scales through colonization-extinction dynamics. Here, small patches would support smaller populations on average due to their higher frequency of extinction. Density–area relationships may also result from methodological problems such as the mis-estimation of habitat area for edge species (Bender et al., 1998) or the inclusion of increasing amounts of non-habitat with increasing size of census areas (Smallwood and Schonewald, 1996; Gaston and Matter, 2002; Matter et al., 2003).

Despite the importance of and attention given to density–area relationships, previous research has neglected two key aspects. First, density–area relationships may show temporal variability. Most empirical relationships have been demonstrated only over a single generation, which precludes between generation effects and ignores temporal variation in the relationship (Matter, 1999). Second, most investigations have ignored any effect of variability in the landscape, which may be significant for insect herbivores inhabiting patches of their host plants.

This research investigates the magnitude of and temporal variation in the density–area relationship. I focus on herbivorous insects inhabiting patches of their host plant in a dynamic landscape. It is unclear how the relationship in a dynamic landscape compares to that for static systems, and how change in the landscape affects density–area relationships. Most models of spatial population dynamics assume that landscapes are stable (Kareiva, 1983; Pulliam, 1988; Hanski, 1994), or that variability occurs over large spatio-temporal scales (Pease et al., 1989; Bowers and Harris, 1994). Previous models investigating the density–area relationship have also assumed a stable landscape (e.g. Matter, 1999, 2000, 2001a). A great deal of our knowledge concerning density–area relationships comes from herbivorous insects where change in the size or number of habitat patches can occur rapidly, often at time scales equal to changes in insect populations (Harrison et al., 1995). Alteration in the size or number of patches may introduce variability in the density–area relationship in addition to that attributable to the target organism.

2. Methods

2.1. Tetraopes–Asclepias system

I used a simulation modeling approach to evaluate how local population growth and change in the size and number of patches affect the density–area relationship for an herbivorous beetle, *Tetraopes tetraophthalmus*, inhabiting patches of common milkweed, *Asclepias syriaca*. The model incorporates the life history of the univoltine beetle and its clonal, perennial host (see Matter, 1996, 1997, 2001b, for life history details). Adult beetles emerge at the beginning of a generation and move between patches. After dispersal, beetles reproduce to form a larval cohort. Changes in the size and number of patches occur during the insect's larval stage. Patch size is based on the number of ramets produced by each clone, thus change in the size and number of patches was modeled discretely, occurring on the same time scale as change in the insect population.

2.2. Model parameters

Several factors potentially affecting the magnitude of the density–area relationship were considered. First was the amount and pattern of dispersal with respect to patch size. Second were factors affecting the number of patches within the landscape, both their loss and creation. The third factor was the reproduction of beetles within each patch. Finally, change in the size of milkweed patches was considered.

Parameter estimates were based on mark-recapture and host plant censuses conducted at the Blandy Experimental Farm Boyce, VA, USA during 1992 and from 1995 to 1997. The proportion of the population moving between patches was taken directly from mark recapture data. Sixty-one percent of beetles observed at least twice made one or more interpatch movements. Although beetles tended to emigrate from and immigrate to smaller patches at higher rates than for larger patches, the net movement of beetles was proportional to patch size. This dispersal pattern does not affect local population density. Thus, the pattern of dispersal with respect to patch size was not incorporated into the model (see Matter, 1999 for effects in a static landscape).

To model changes in the number of patches within the landscape, I examined the birth and death rates of patches. The number of patches in the landscape followed a logistic growth model fit by non-linear regression with an upper bound (carrying capacity) of 500 patches and a growth rate of $r = 0.12 \pm 0.14$ (±asymptotic S.E., $R^2 = 0.97$). If birth and death rates were constant for 2 unobserved years (1993–1994), the probability of a patch dying was 0.05 ± 0.03 per patch per year (S.D., used throughout unless otherwise noted) and the birth rate of new patches was 0.17 ± 0.06 per patch per year. These independent estimates correspond well with the estimate of $r = 0.12$ from the logistic model ($r = \text{birth} - \text{death}$). Because the death rate of milkweed patches did not appear to be density dependent, the birth rate of patches was assumed to account for the density dependence in the change in number of patches within the landscape.

It is important to note two things concerning the change in number of patches. The first is that the overall probability of a patch dying was not related to its size. Early in the growing season, herbivory by mammals often decimates patches (Hochwender et al., 2000), and several small patches died due to herbivory. However, flooding affected both large and small patches. Thus, the size (number of ramets) of patches dying (41.0 ± 94.0) did not differ from those surviving (21.8 ± 35.7, no statistical test was performed as surviving patches are not independent). Secondly, new patches in this system are inherently small; generally, one ramet is produced from a seed.

To evaluate the effects of change in the size of patches and local (within-patch) beetle populations on the density–area relationship, it is important to consider whether these growth rates vary among patches or populations and if growth rates vary with size, i.e. is there density dependence in the growth rates? Growth rates alone have little direct effect on the density–area relationship as equal linear growth in either beetle abundance or patch size will change abundance, but will not alter density. To examine whether patch growth rates and beetle growth rates vary among populations or with size, I fit a non-linear regression: $N_{t+1} = rN_t^B$ where N is size (number of emerging beetles or ramets), r is the growth rate, t is time, and B scales with size to patch size and beetle abundance data from 1995 to 1997.

Milkweed patch growth did not vary between years (t-test; $t = 0.20$, separate variance, $\mathrm{d.f.} = 152.6$, $P = 0.84$) and was therefore estimated as the mean of both years. It should be noted that this test violates the assumption of independence, as patches could be included twice and may have individual growth rates (Matter, 2001b). The growth rate slowed as patch size increased (Fig. 1). The growth rate was estimated as $r = 2.33 \pm 0.48$ (asymptotic S.E.) and size dependence as $B = 0.90 \pm 0.04$.

The growth rate of beetle populations varied considerably between years $r = 4.26 \pm 0.38$ (1995–1996) and $r = 0.86 \pm 0.23$ (1996–1997). The growth rate also varied among populations $r = 2.17 \pm 0.62$ (estimate considering all years) and slowed with increasing population size, $B = 0.85 \pm 0.06$ (Fig. 1). That there is density dependence in the population growth rate of *T. tetraophthalmus* is in agreement with experimental results (Matter, 2001b).

The simulation for the *Tetraopes–Asclepias* system had several parameters. The dispersal rate was fixed at 0.61 leaving their natal patch and immigrating to new patches in proportion to their size. The probability of a patch dying each generation was drawn from a normal distribution with a mean of 0.05 ± 0.03. The death rate of patches was not related to patch size, or the number of patches within the system. The birth rate of patches was modeled as a logistic function with a yearly growth rate drawn from a normal distribution with a mean of 0.17 ± 0.06 and an upper bound (carrying capacity) of 500 patches. A yearly growth rate for the beetle populations was drawn from a normal distribution with a mean of 1.91 ± 0.30. This yearly growth value set a mean that varied among populations by ± 0.62. Thus, there were ‘good’ and ‘bad’ years for beetles, and always variation among local populations. Size dependence in beetle population growth was drawn from a normal distribution with a mean of 0.85 ± 0.06. Finally, the growth rate for each patch, each year was drawn from a normal distribution with a mean of 2.33 ± 0.48, and size dependence in patch growth from a normal distribution with mean of 0.90 ± 0.04.

The timing of when density measurements are made during the life cycle can have substantial effects on the density–area relationship (Matter, 1999). Therefore, the density–area relationship was measured before dispersal, emphasizing between-generation effects, and after dispersal emphasizing within-generation and colonization effects. For each generation, the density–area relationship was calculated as the mean

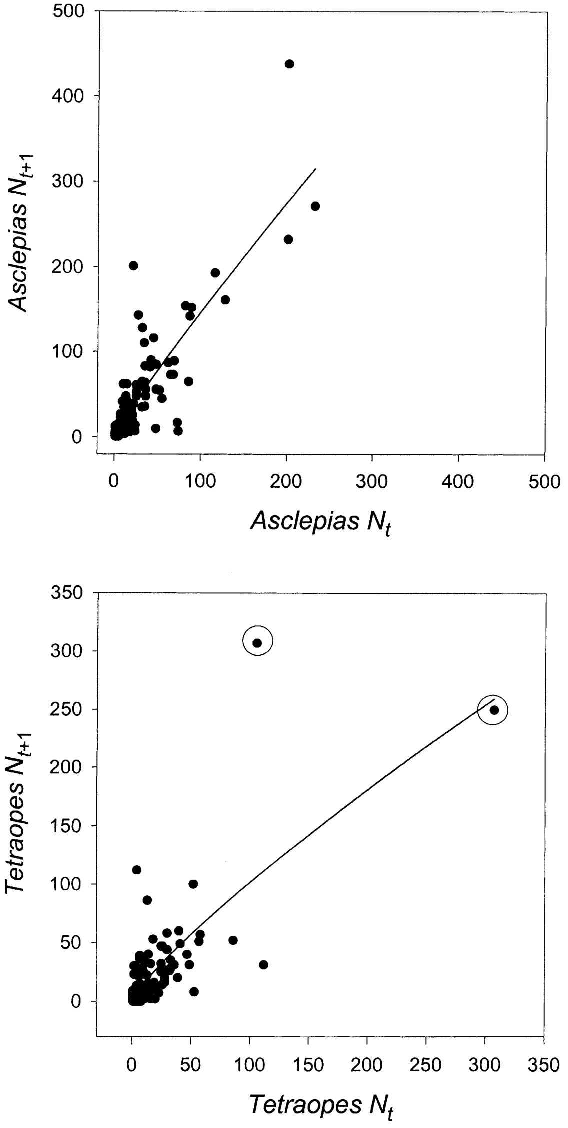

Fig. 1. Growth of milkweed patches (top) and local beetle populations (bottom). Patch size (number of ramets) or the number emerging beetles in year t is plotted vs. the number for the same patch (N) in year $t+1$. Non-linear regression of the form $N_{t+1} = rN_t^B$ were fit to the data (statistics in text). The circled points in the bottom panel have strong leverage on the estimates of beetle growth. If the point to the right is removed, growth is 1.39 and density dependence is 0.95. If both points are removed, growth is 5.37 and density dependence is 0.51. However, there is no biological justification to remove these populations from the analysis.

of these two estimates. To examine temporal trends in the density–area relationship for the *Tetraopes–Asclepias* system, 500 simulations of 35 generations were run beginning with the number of patches, patch sizes, and beetle population sizes seen in 1997.

2.3. Model validation

The model using the parameters described above was validated using the configuration of patch sizes and beetle abundances observed in 1995. Comparisons were made to the observed correlation between beetle density and patch size, number of patches, mean patch size, and abundance of beetles seen in 1997. Simulated data from the model showed a good concordance with observed data (Fig. 2). The observed data fell within one standard deviation of the mean of all simulated distributions. Thus, the model captures the dynamics of this system while maintaining the variability inherent in the system.

2.4. General model

The *Tetraopes–Asclepias* model was generalized to examine how the rate of dispersal, death and establishment of patches, and density dependence in the growth of patches and insect populations affect the density–area relationship (Table 1). The general model follows the same structure as the *Tetraopes–Asclepias* model. Because there were differences in

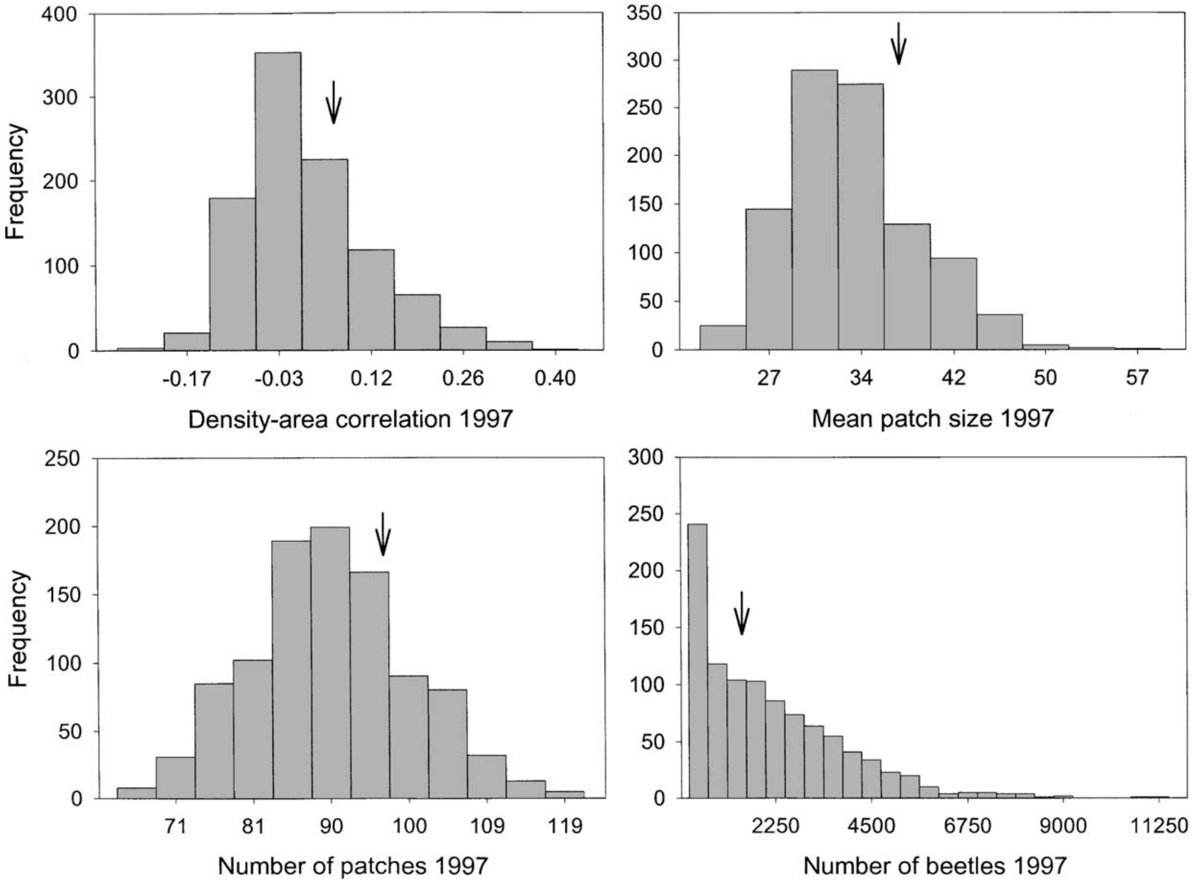

Fig. 2. Model validation distributions. Data shown are the model-predicted distributions for 1997 based on 1000 simulations using observed data from 1995. The observed values in 1997 (indicated by arrows on the histograms) were 0.08 for the correlation between density and area, a mean patch size of 37, 97 patches, and 1448 beetles.

Table 1
Parameters for the *Tetraopes–Asclepias* system and factor levels used in the general model

Parameter	*Tetraopes–Ascepias*	Simulation values			
Density dependence in patch growth	0.90 ± 0.04	0.85	0.90	0.95	1.00
Density dependence in insect growth	0.85 ± 0.06	0.85	0.90	0.95	1.00
Patch death rate	0.05 ± 0.03	0.00	0.02	0.04	0.06
Patch birth rate	0.17 ± 0.06	0.00	0.20	0.40	0.60
Proportion dispersing	0.61	0.20	0.40	0.60	0.80

In the general model, the growth rate of both patches and insect populations was 1.3 ± 0.2. The birth and death rates of patches and proportion of insects dispersing were constant parameters, while density dependence in the growth rates of both patches and insects were drawn from normal distributions with a mean of the parameter value and a S.D. of 0.05.

the density–area relationship depending on whether the landscape was near an equilibrium number of patches or not (see results), the general model was assumed to be near equilibrium, which will not apply to all situations. For this model, the birth and death rates of patches and the proportion of insects dispersing were not drawn from distributions, but were fixed variables (Table 1). Size dependence in the growth rates of both patches and insects were drawn from normal distributions with a mean of the parameter value and a standard deviation of 0.05. Additionally there was no ‘yearly’ variation in the growth rate of insect populations. Both local insect and patch growth rates were set at $r = 1.3 \pm 0.20$. Parameter values used in the general model were chosen to bracket the range seen for the *Tetraopes–Asclepias* system while simulating reasonable values for insect–host plant systems.

To begin each simulation, a landscape containing 50 patches was created. Initial patch sizes and insect densities were drawn from log-normal distributions with means of 50 and 1.0, respectively. Log-normal distributions were used because they represent the distributions seen for the *Tetraopes–Asclepias* system, i.e. there were mostly small patches and densities, but also a few large patches or high densities. Each simulation lasted 25 generations. Ten replicates of each factorial combination of parameter values were run totaling 10,240 simulations. The mean and temporal variance in the correlation between density and patch size were calculated over the 25 generations for each simulation.

2.5. General model analysis

I fit a full factorial ANOVA model to examine how each factor affects the correlation between population density and patch size and temporal variation in the correlation. ANOVA was adopted because the functional forms of the relationships were not known. What is of interest in these analyses is not the significance of any factor, but the amount of variation accounted for by each factor. Partitioning the effects due to a single factor in all its forms estimates the sensitivity of the dependent variable to each independent variable (Pearman and Wilbur, 1990; Matter, 1999, 2001a,b). To determine the sensitivity of a specific factor, I totaled the sum of squares attributable to each significant source in which a factor was involved (i.e. both main effects and interaction terms). It should be noted that this summed variance is not independent, as variation due to interactions contributes equally to each factor in that term.

Variance attributable to each factor also depends on the range of values investigated. Thus, sensitivity as expressed here must be gauged within the range of parameter values used. The correlation coefficient was transformed to Fisher’s Z prior to analysis to meet the assumptions of ANOVA (Sokal and Rohlf, 1981).

3. Results

3.1. Tetraopes–Asclepias model

The correlation between population density and patch size varied over both the 35 generations and the 500 simulations (Fig. 3). The correlation between density and patch size became negative after four to five generations, and significantly so after approximately 15 generations. There appears to be a difference depending on whether the system is at an equilibrium number of patches or not. When the landscape was below the carrying capacity of patches, and thus a greater number of new patches were entering the system, the correlation was slightly less negative, and not significantly different than 0.0. After the landscape reached its carrying capacity for the number of patches, the correlation became slightly more negative and significantly less than 0.0.

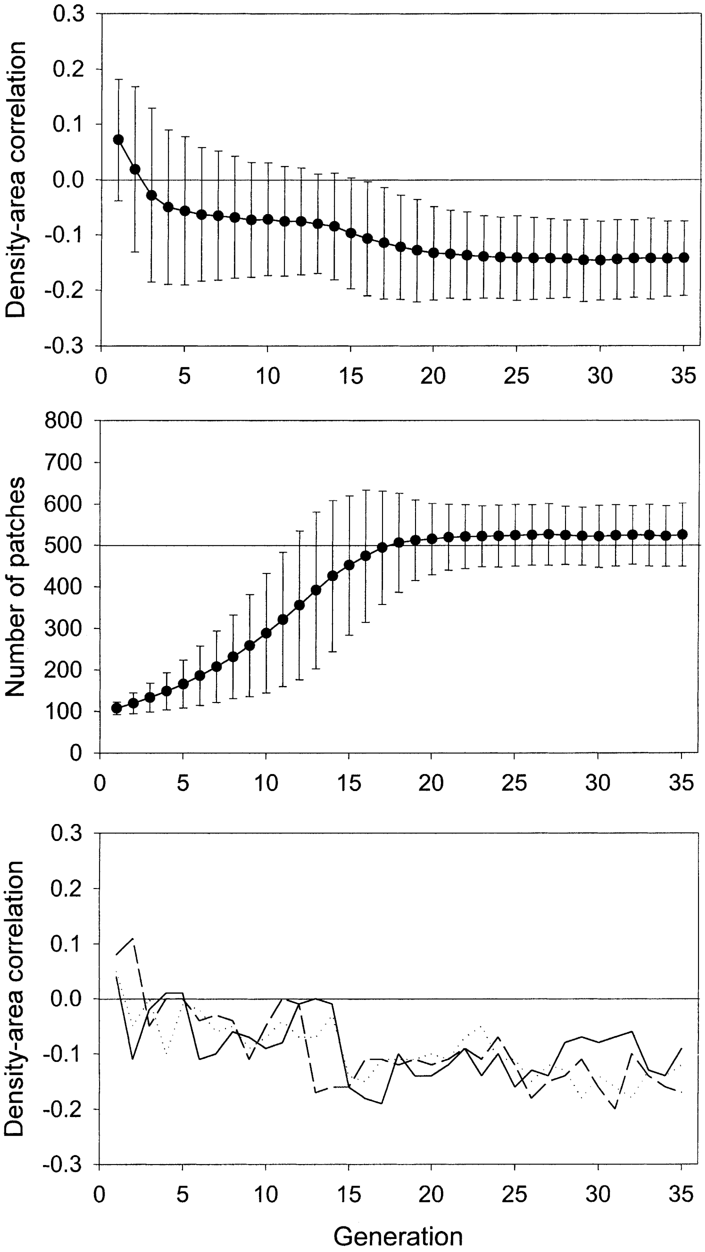

Fig. 3. Predicted temporal patterns in the correlation between *T. tetraophthalmus* density and *A. syriaca* patch size (top) and the number of *A. syriaca* patches (middle). Mean (±2 S.D.) of 500 simulations are shown for 35 generations. Simulations began using the observed values for 1997. The bottom graph shows the temporal pattern for three simulations.

Twenty random simulations were examined for temporal autocorrelation in the density–area relationship. A positive autocorrelation (lag-one) was found in the density–area relationship (mean $r = 0.55$), indicating that although there is variation in the relationship across simulations, the relationship has ‘inertia’ and depends on the prior relationship (Fig. 3).

3.2. *Genera model*

Over all simulations, the mean correlation between density and patch size was -0.098 ± 0.162 and the mean temporal variation in the correlation over the 35 generations was 0.021 ± 0.015. Analyses show that the correlation between density and patch size was most sensitive to density dependence in insect growth, followed by density dependence in the growth rate of patches, the birth rate of patches, the death rate of patches, and dispersal rate of insects (Table 2). Most of the variation was explained by the main effects, although there were significant two-, three-, and four-way interactions. The correlation between density and patch size increased with decreasing strength of insect density dependence. In other words,

Table 2
Density–area relationship—ANOVA table for the effects of parameters on the correlation between insect density and patch size

Source of variation	Sum of squares (SS)
Density dependence in insect growth (IG)	201.35
Density dependence in patch growth (PG)	59.47
Patch birth rate (PBR)	30.19
Patch death rate (PDR)	17.66
Proportion of insects dispersing (DSR)	5.18

Source	d.f.	SS	*F*	*P*
PDR	3	6.04	1169.90	<0.01
IG	3	173.32	33549.73	<0.01
PG	3	27.52	5328.82	<0.01
DSR	3	0.78	151.54	<0.01
PBR	3	18.26	3534.06	<0.01
PDR × DSR	9	0.67	43.12	<0.01
PDR × IG	9	0.04	2.92	<0.01
PDR × PG	9	1.29	82.97	<0.01
IG × PG	9	23.62	1521.21	<0.01
IG × DSR	9	0.20	13.06	<0.01
PG × DSR	9	0.72	46.36	<0.01
PDR × PBR	9	7.42	478.92	<0.01
IG × PBR	9	0.19	12.28	<0.01
PG × PBR	9	1.81	116.50	<0.01
DSR × PBR	9	0.58	37.08	<0.01
PDR × IG × PG	27	0.47	10.11	<0.01
PDR × IG × DSR	27	0.09	1.96	<0.01
PDR × PG × DSR	27	0.10	2.21	<0.01
IG × PG × DSR	27	2.21	47.54	<0.01
PDR × IG × PBR	27	0.30	6.39	<0.01
PDR × PG × PBR	27	0.58	12.56	<0.01
IG × PG × PBR	27	0.36	7.67	0.01
PDR × DSR × PBR	27	0.11	2.46	<0.01
IG × DSR × PBR	27	0.02	0.48	0.99
PG × DSR × PBR	27	0.24	5.16	<0.01
PDR × IG × PG × DSR	81	0.20	1.45	0.01
PDR × IG × PG × PBR	81	0.34	2.44	<0.01
PDR × IG × DSR × PBR	81	0.02	0.16	>0.99
PDR × PG × DSR × PBR	81	0.06	0.43	>0.99
IG × PG × DSR × PBR	81	0.06	0.43	>0.99
PDR × IG × PG × DSR × PBR	243	0.06	0.14	>0.99
ERROR	9216	15.87		

The top table shows the total sums of squares attributable to each significant factor. This value was used to judge sensitivity of the dependent variable to each factor (see text). Below are the statistics for individual factors and interactions.

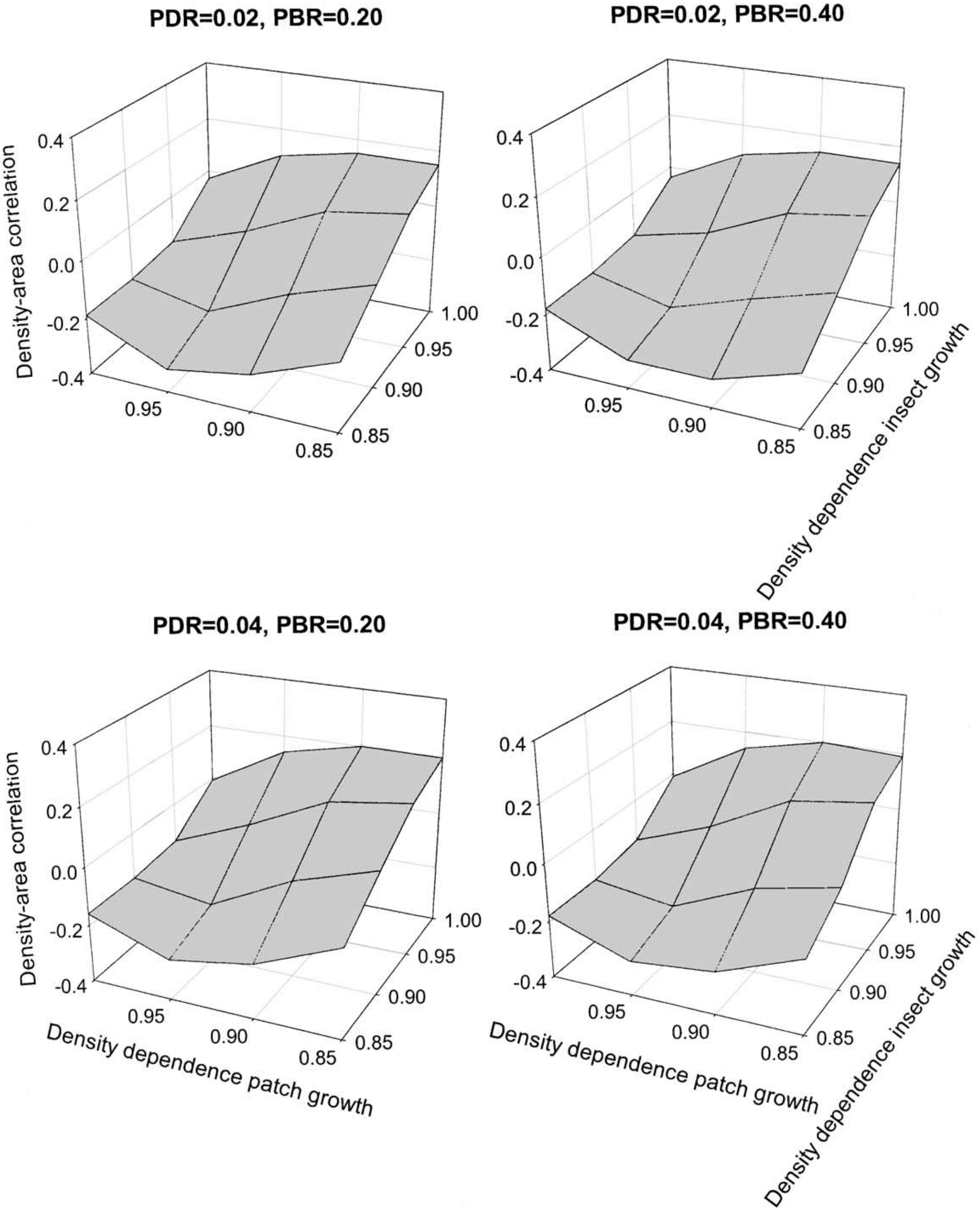

Fig. 4. General model results for the density–area correlation. Two levels of patch death rate (PDR) and patch birth rate (PBR) are shown. Data shown is averaged across all levels of the dispersal rate ($N = 40$) which had little effect on the correlation.

densities were higher in larger patches when density dependence in insect growth was low (Fig. 4). The density–area correlation tended to become more positive as density dependence in patch growth increased. Interestingly, interactions between density dependence in patch and insect growth result in the most negative correlations between density and patch size occurring when density dependence in insect growth is strongest and density dependence in patch growth is intermediate (0.90–0.95). The correlation became increasingly positive as both the birth and death rates of patches increased.

Temporal variation in the correlation between insect density and patch size was most strongly affected

Table 3
Temporal variation in the density–area relationship—ANOVA table for the effects of model parameters on the temporal variation in the correlation between insect density and patch size

Source of variation	Sum of squares (SS)
Density dependence in patch growth (PG)	1.050
Density dependence in insect growth (IG)	0.374
Patch birth rate (PBR)	0.340
Patch death rate (PDR)	0.225
Proportion of insects dispersing (DSR)	0.150

Source	d.f.	SS	*F*	*P*
PDR	3	0.029	121.00	<0.01
IG	3	0.075	317.10	<0.01
PG	3	0.680	2857.62	<0.01
DSR	3	<0.001	0.54	0.65
PBR	3	0.085	356.46	<0.01
PDR × DSR	9	0.027	37.44	<0.01
PDR × IG	9	0.018	24.70	<0.01
PDR × PG	9	0.009	12.76	<0.01
IG × PG	9	0.112	156.67	<0.01
IG × DSR	9	0.014	19.55	<0.01
PG × DSR	9	0.054	76.08	<0.01
PDR × PBR	9	0.032	45.43	<0.01
IG × PBR	9	0.043	59.93	<0.01
PG × PBR	9	0.081	113.20	<0.01
DSR × PBR	9	0.022	30.62	<0.01
PDR × IG × PG	27	0.050	23.21	<0.01
PDR × IG × DSR	27	0.002	0.99	0.47
PDR × PG × DSR	27	0.006	2.79	<0.01
IG × PG × DSR	27	0.011	5.36	<0.01
PDR × IG × PBR	27	0.022	10.37	<0.01
PDR × PG × PBR	27	0.015	7.10	<0.01
IG × PG × PBR	27	0.012	5.77	<0.01
PDR × DSR × PBR	27	0.004	1.80	0.01
IG × DSR × PBR	27	0.004	1.67	0.02
PG × DSR × PBR	27	0.007	3.08	<0.01
PDR × IG × PG × DSR	81	0.004	0.67	0.99
PDR × IG × PG × PBR	81	0.013	2.07	<0.01
PDR × IG × DSR × PBR	81	0.003	0.54	>0.99
PDR × PG × DSR × PBR	81	0.004	0.62	>0.99
IG × PG × DSR × PBR	81	0.006	0.86	0.80
PDR × IG × PG × DSR × PBR	243	0.003	0.13	>0.99
ERROR	9216	0.731		

The top table shows the total sums of squares attributable to each significant factor that was used to judge sensitivity of the dependent variable to each factor (see text). Below are the statistics for individual factors and interactions.

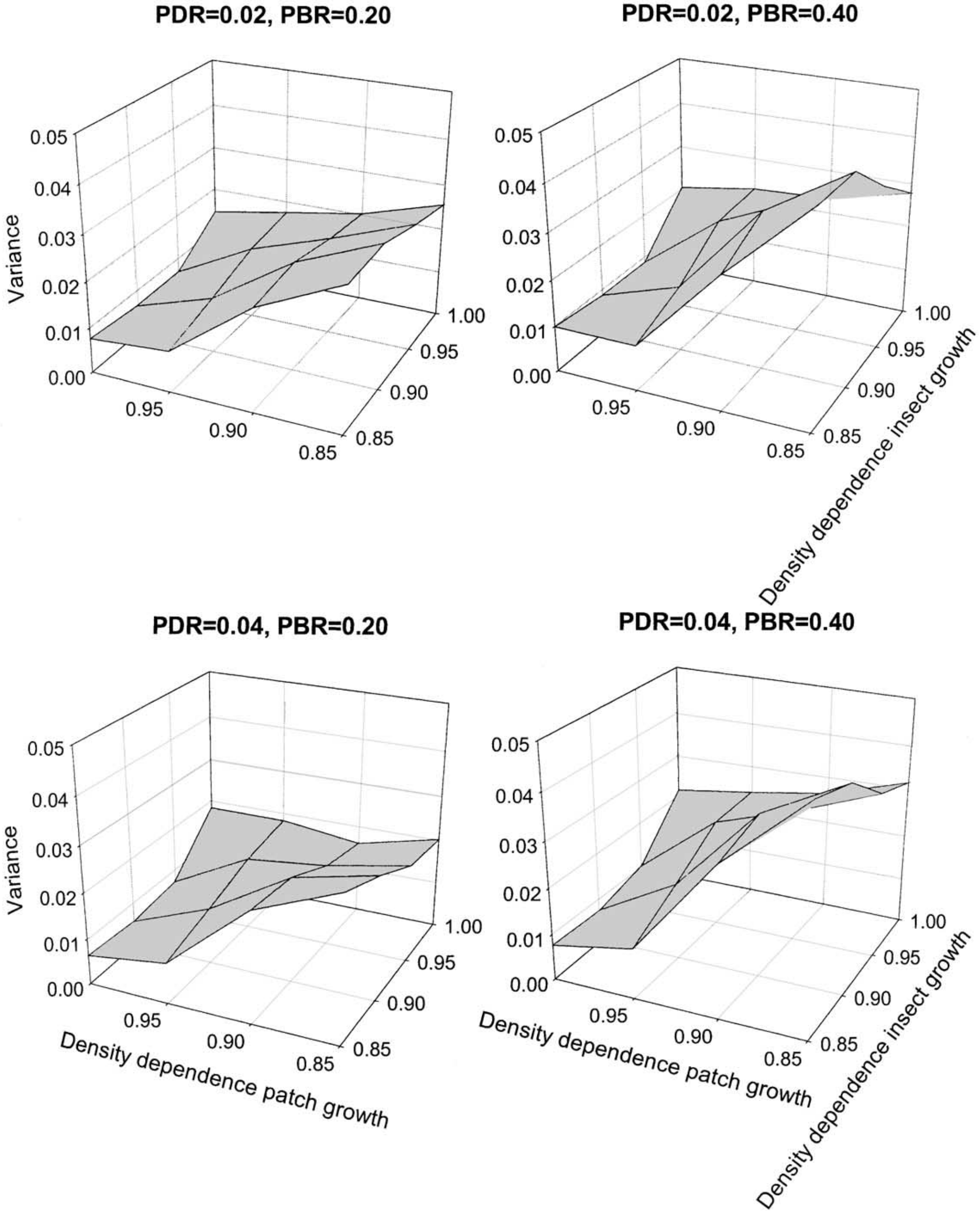

Fig. 5. General model results for temporal variation in the density–area correlation. Two levels of patch death rate (PDR) and patch birth rate (PBR) are shown. Data shown is averaged across all levels of the dispersal rate ($N = 40$), which had little effect on temporal variation in the correlation.

by density dependence in patch growth followed by density dependence in the growth rate of insect populations, the birth rate of patches, the death rate of patches, and the proportion of insects dispersing (Table 3). The bulk of variation was attributable to the main effects. Temporal variation in the correlation between density and patch size increased with increasing density dependence in patch growth (Fig. 5), and tended to increase with decreasing density dependence in insect growth. Increasing patch birth and death rates tended to increase temporal variability in the correlation, however, the effect was not uniform across all factor combinations.

4. Discussion

For the *Tetraopes–Asclepias* system, over the long-term, densities should tend to be lower on larger patches than on smaller patches. This prediction differs from Connor et al.'s (2000) observation that, in general, the densities of insects tend to increase with patch size. However, among the insects they investigated, the density of many did decrease with increasing patch size, indicating that this pattern is not uncommon. Studies not included in their review have also shown patterns of decreasing insect density with patch size (Förare and Solbreck, 1997; Krauss et al., 2003; Matter et al., 2003). The long-term prediction of the model differs somewhat from previous empirical observations for this system where densities increased (1992; Matter, 1997), decreased (1995), or were constant with patch size (1996, 1997). Although the model predicts that density should decrease with increasing patch size, the trajectories of individual simulations indicate that moving between patterns of increasing and decreasing density with patch size can be expected in the short-term. Additionally, point estimates and variance indicate that the magnitude of the relationship may not deviate strongly from showing effect of patch size on density, especially before an equilibrium number of patches is reached. As indicted by the lag-one autocorrelation in the simulation, large changes between generations should be uncommon. Predictions from the general model also reveal that conditions near those seen for the *Tetraopes–Asclepias* system should result in comparatively high temporal variability in the density–area relationship.

The general model shows that density dependence in patch and insect population growth rates have considerable influence on the density–area relationship. That these factors are important should not be surprising as both are components of population size. Because local population density is the number of insects on a patch divided by patch size, the effects of these two factors on the relationship between population density and patch size should have opposing effects. It is expected that density dependence in insect growth should result in decreasing density with increasing patch size. Large populations on large patches would grow at a slower rate than small populations on small patches. Exactly this result is seen in the simulation. For patch growth, the denominator of density, density dependence in patch growth is expected to produce increasingly higher densities as patch size increases. This trend is apparent in the simulation results; however, the effects are not as strong as for density dependence in insect growth and are not consistent across all factor levels. The difference in strength is explained by the fact that the range of patch sizes is narrower than for insect populations, thus given equal coefficients for density dependence the effect will be greater for insect populations because they span a larger range of abundances. The non-linear response of the correlation to density dependence in patch growth arises through interactions. When density dependence in insect growth is weak, we see the expected pattern with respect to density dependence in patch growth. When density dependence in insect population growth is strong, the correlation is more positive than expected when density dependence in plant growth is weak.

Temporal variability in the density–area relationship has largely been neglected. Most empirical assessments of the density–area relationship have been conducted only over one season and the relationship between density and area has almost been regarded as a species characteristic. Indeed there has been a good deal of concordance in density–area relationships between studies of the same species but in different locals (Bowers and Matter, 1997). The general model and empirical results from the *Tetraopes–Asclepias* system show that the relationship can be variable and that variability in the relationship is largely affected by density dependence in patch growth. High density dependence in patch growth or rate of change in habitat size will result in greater temporal variability in the density–area relationship. If density–area relationships are to be used in conservation strategies, an appreciation of temporal variability is crucial.

That change in the number and size of patches within a landscape can affect the density–area relationship should not be surprising. It was somewhat surprising that factors related to the number of patches in the system had relatively little impact. We might expect that the production of new patches should result in increasing density with patch size, especially if there is any lag until new patches are colonized. Such a lag is not present in this system or in the general model. For the *Tetraopes–Asclepias* system, new patches generally appear before the emergence of beetles. The models use both densities before and after dispersal, averaging the effects of between and within generation processes. Density–area relationships calculated before dispersal (not presented) do show a strong effect of factors related to the number of new patches. In these situations, density increases markedly with patch size. Thus, systems where there is a lag until colonization, or where population density is estimated before dispersal, may show results that differ from this model. Population density is likely to increase with patch size in systems where there are uncolonized or new patches (Bowers and Matter, 1997).

The model produces useful predictions concerning where certain density–area patterns may be found and when we may expect temporal variability in the relationship. In general, we should expect that insects experiencing strong density dependence in population growth will exhibit decreasing density with increasing patch size. The converse, that highly positive density–area relationships are associated with insects that show weak density-dependent population growth, may not be true due to interactions between factors contributing to the density–area relationship. This prediction should hold, whether the landscape is variable or not. The observations of Connor et al. (2000) show that the density of insects increases with patch size, in combination with the results of this model indicate that, in general, there is only weak density dependence in insect growth under field conditions (Podoler and Rogers, 1975; Stubbs, 1977). However, extrinsic density-dependent factors such as parasitism, predation, or disease may also be affected by landscape structure, thus density dependence due to these factors may not vary in a similar manner (Roland and Taylor, 1997).

Few studies have been conducted to test the predictions of this model. Förare and Solbreck (1997) examined the relationship between the density of the moth *Abrostola asclepiadis* and the size of patches of its host plant, *Vincetoxicum hirundnaria* over a 5-year period. Their system varied little in the size and number of patches during study (Förare and Solbreck, 1997). Averaged across the 5 years, they found a decreasing density of larvae with increasing patch size. Unfortunately, they provide no data concerning the temporal variation in the relationship. For this system, it appears that there is little density dependence in insect population growth. Assuming no change in the landscape, the model would predict the negative density–area relationship which is congruous with their observations, however, patch size-dependent dispersal and oviposition by females play an important role in the density–area relationship for this moth (Förare and Solbreck, 1997).

Despite the general nature of these simulations, predictions will not apply to all situations. Effects of insects on their host plants, shown for this system (Matter, 2001b) were incorporated in the growth rates of patches, rather than explicitly modeled. Systems akin to host–parasitoid models where the growth of 'patches' are linked may show different patterns. The scale of patch use also must be considered. Systems where patches are foraging units, or inhabitants are not autonomous populations, may not respond similarly (Hastings and Harrison, 1994). Where the net flux of individuals varies with the size of patches (e.g. Root, 1973; Kareiva, 1985; Turchin, 1986), the results may differ, although effects of dispersal are generally less important than between-generation processes (Matter, 1999). Finally, as shown by the *Tetraopes–Asclepias* simulations, results may differ depending on whether the system is near an equilibrium number of patches or not.

5. Conclusions

Density–area relationships are central to debate concerning conservation refuge design, metapopulation dynamics, and spatial population theory. These theories and related issues generally assume that density does not vary with habitat size and that it is temporally invariant (Connor et al., 2000). Results of this study suggest that in situations where there is density dependence in the growth of populations or where the landscape is variable, as is often the case in conservation studies where habitat loss or degradation is an issue, the relationship between density and area may differ compared to assumptions of a stable or homogeneous system. Examining the relationship between density and area is only a first step in applying it to theory or conservation. A mechanistic understanding of the factors responsible for the relationship is needed before recommendations based on individuals–area relationships are applied.

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References

Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals with different proportions of suitable habitat: a review. Oikos 71, 355–366.

Bach, C.E., 1988. Effects of host plant patch size on herbivore density: patterns. Ecology 69, 1090–1102.

Bender, D.J., Contreras, T.A., Fahrig, L., 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79, 517–533.

Bowers, M.A., Harris, L.C., 1994. A large-scale metapopulation model of interspecific competition and environmental change. Ecol. Model. 72, 251–273.

Bowers, M.A., Matter, S.F., 1997. Landscape ecology of mammals: relationships between density and patch size. J. Mammal 78, 999–1013.

Bowers, M.A., Gregorio, K., Brame, C.J., Matter, S.F., Dooley, J.L., 1996. Use of space and habitats by meadow voles at the home range, patch, and landscape scales. Oecologia 105, 107–115.

Bowman, J., Cappuccino, N., Fahrig, L., 2002. Patch size and population density: the effect of immigration behavior. Conserv. Ecol. 6, 9 (online) URL: http://www.consecol.org/vol6/iss1/art9.

Connor, E.F., Courtney, A.C., Yoder, J.M., 2000. Individuals–area relationships: the relationship between animal population density and area. Ecology 81, 734–748.

Denno, R.F., Raupp, M.J., Tallamy, D.W., 1981. Organization of sap-feeding insects: equilibrium versus non-equilibrium coexistence. In: Denno, R.F., Dingle, H. (Eds.), Insect Life History Patterns: Habitat and Geographic Variation. Springer-Verlag, New York, pp. 151–181.

Förare, J., Solbreck, C., 1997. Population structure of a monophagous moth in a patchy landscape. Ecol. Ent. 22, 256–263.

Gaston, K.J., Matter, S.F., 2002. Individuals–area relationships: comment. Ecology 83, 288–293.

Gaston, K.J., Blackburn, T.M., Gregory, R.D., 1999. Does variation in census area confound density comparisons? J. Appl. Ecol. 36, 191–204.

Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecol. Appl. 9, 623–633.

Haila, Y., 1988. Calculating and miscalculating density: the role of habitat geometry. Ornis Scand. 19, 88–92.

Hanski, I., 1994. A practical model of metapopulation dynamics. J. Anim. Ecol. 63, 151–162.

Harrison, S., Thomas, C.D., Lewinson, T.M., 1995. Testing a metapopulation model of coexistence in the insect community on ragwort (*Seneco jacobea*). Am. Nat. 145, 546–562.

Hastings, A., Harrison, S., 1994. Metapopulation dynamics and genetics. Annu. Rev. Ecol. Syst. 25, 167–188.

Hochwender, C.G., Marquis, R.J., Stowe, K.A., 2000. The potential for and constraints on the evolution of compensatory ability in *Asclepias syriaca*. Oecologia 122, 361–370.

Kareiva, P.M., 1983. Local movement in herbivorous insects applying a passive diffusion model to mark-recapture field experiments. Oecologia 57, 322–327.

Kareiva, P.M., 1985. Finding and loosing host plants by *Phyllotreta*: patch size and surrounding habitat. Ecology 66, 1809–1816.

Krauss, J., Steffan-Dewenter, I., Tscharntke, T., 2003. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? J. Biogeog. 30, 889–900.

Matter, S.F., 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. Oecologia 105, 447–453.

Matter, S.F., 1997. Population density and area: the role of within and between patch processes. Oecologia 110, 533–538.

Matter, S.F., 1999. Population density and area: the role of within- and between-generation processes over time. Ecol. Model. 118, 261–275.

Matter, S.F., 2000. The importance of the relationship between population density and habitat area. Oikos 89, 613–619.

Matter, S.F., 2001a. Synchrony, extinction, and dynamics of spatially segregated, heterogeneous populations. Ecol. Model. 141, 217–226.

Matter, S.F., 2001b. The effects of above and below ground herbivory by *Tetraopes tetraophthalmus* (Coleoptera: Cerambycidae) on the growth and reproduction of *Asclepias syriaca* (Asclepidacae). Environ. Ent. 30, 333–338.

Matter, S.F., Roland, J., Keyghobadi, N., Sabourin, K., 2003. The effects of isolation, habitat area and resources on the abundance, density and movement of the butterfly, *Parnassius smintheus*. Am. Midl. Nat. 150, 26–36.

Pearman, P.B., Wilbur, H.M., 1990. Changes in population dynamics resulting from oviposition in a subdivided habitat. Am. Nat. 135, 708–723.

Pease, C.M., Lande, R., Bull, J.J., 1989. A model of population growth, dispersal and evolution in a changing environment. Ecology 70, 1657–1664.

Podoler, H., Rogers, D., 1975. A new method for the identification of key factors from life-table data. J. Anim. Ecol. 44, 84–114.

Pulliam, H.R., 1988. Sources sinks and population regulation. Am. Nat. 132, 652–661.

Raupp, M.J., Denno, R.F., 1979. The influence of patch size on a guild of sap-feeding insects that inhabit salt marsh grass *Spartina patens*. Environ. Ent. 8, 412–417.

Risch, S.J., 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. Ecology 62, 1325–1340.

Roland, J., Taylor, P.D., 1997. Insect parasitoid species respond to forest structure at different spatial scales. Nature 386, 710–713.

Root, R.B., 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards, *Brassica oleracea*. Ecol. Monogr. 43, 95–124.

Schoener, T.W., 1986. Patterns in terrestrial vertebrate versus arthropod communities: do systematic differences in regularity exist? In: Diamond, J., Case, T.J. (Eds.), Community Ecology. Harper & Row, New York, pp. 556–586.

Smallwood, K.S., Schonewald, C., 1996. Scaling population density and spatial pattern for terrestrial mammalian carnivores. Oecologia 105, 329–335.

Sokal, R.R., Rohlf, F.J., 1981. Biometry, 2nd ed. Freeman, New York, 859 pp.

Stubbs, M., 1977. Density-dependence in the life-cycles of animals and its importance in K- and r-strategies. J. Anim. Ecol. 46, 677–688.