

Nonlinear responses to food availability shape effects of habitat fragmentation on consumers

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Abstract. Fragmentation of landscapes is a pervasive source of environmental change. Although understanding the effects of fragmentation has occupied ecologists for decades, there remain important gaps in our understanding of the way that fragmentation influences mobile organisms. In particular, there is little tested theory explaining the way that fragmentation shapes interactions between consumers and resources. We propose a simple model that explains why fragmentation may harm consumers even when the total amount of resources on the landscape they use remains unchanged. In particular, we show that nonlinearity in the relationship between resource availability and benefits acquired by consumers from resources can cause a decrease in benefits to consumers when landscapes are subdivided into isolated parts and when the distribution of consumers in fragments is not matched to the distribution of resources. We tested predictions of the model using a laboratory system of cabbage looper (*Trichoplusia ni*) larvae on artificial landscapes. Consistent with the model's predictions, survivorship of larvae decreased when landscapes with heterogeneous resources were fragmented into isolated parts. However, average mass of surviving larvae did not change in response to fragmentation. With basic knowledge of consumer resource use patterns and landscape structure, our model, supported by our experiment, contributes new understanding of the resource-mediated effects of fragmentation on consumers.

Key words: cabbage looper; connectivity; consumer–resource interactions; food distribution; Jensen's inequality; landscape fragmentation; landscape heterogeneity; nonlinearity; patchiness; resource distribution; *Trichoplusia ni*.

INTRODUCTION

Fragmentation, the dissection of landscapes into spatially isolated parts, is a major driver of environmental change worldwide (Fischer and Lindenmayer 2007). Landscape fragmentation customarily refers to a reduction in connectivity between parts of a landscape (Zhu et al. 2006) or the conversion of the landscape into a mosaic of cover types, some of which differ from the original habitat (Southworth et al. 2004, Gonzalez-Abraham et al. 2007). The ecological implications of these changes remain largely unresolved (Bowman et al. 2002, McGarigal and Cushman 2002, Stephens et al. 2003, Ryall and Fahrig 2006).

This absence of consensus in studies of fragmentation can be explained, at least in part, from ambiguity in terminology. The term “fragmentation” has been used in the literature to encompass a broad variety of changes in landscapes, changes that include reduction in habitat

area, increased isolation of habitat patches, extension of the length of edges between habitats, and amplified contrast between habitat and the surrounding matrix (Wiens 1995, Jaeger 2000, Fahrig 2003, Southworth et al. 2004, Zhu et al. 2006, Gonzalez-Abraham et al. 2007). These manifold changes in landscapes are often confounded, for example, when patches of forest remain standing within land cleared for agriculture (Castellon and Sieving 2006). In this case, “fragmented” forest patches are simultaneously smaller and more widely separated; there is more edge between forested and agricultural land, and a new type of habitat (plowed ground) has appeared. Thus, the term “fragmentation” serves as a catchall for four confounded changes in the landscape. Referring to a collection of changes as if they were a single one is virtually certain to create ambiguity in interpreting fragmentation research.

To remedy this problem, several researchers have recommended using the term fragmentation to imply loss of connectivity within a landscape apart from habitat loss or changes in landscape composition, thereby making a clear distinction between these types of landscape change (Fahrig 1997, Harrison and Bruna 1999, Ryall and Fahrig 2006). Here, we follow this recommendation and limit the use of the term fragmentation to mean the loss of connectivity that occurs from

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the breaking apart of a constant amount of habitat (Fig. 1A, B) or to imply that the effects of loss of connectivity are distinct from the effects of reductions in habitat area or change in landscape composition (Fig. 1C). This definition of fragmentation has a functional component (*sensu* Kotliar and Wiens 1990); landscape changes may limit the mobility of some species and not others. For example, construction of a highway across an otherwise intact landscape might compress the movements of small mammals while exerting minor effect on birds (Forman and Alexander 1998).

Empirical studies of fragmentation and habitat loss offer a wide array of conclusions (see reviews in Fahrig 2002, Ewers and Didham 2006) and the absence of clear, predictive theory on effects of fragmentation contributes to the lack empirical consensus (Ryall and Fahrig 2006). A large body of theory predicts the population-level consequences of loss of connectivity among habitat patches (Roff 1974, Wiens 1976, Cantrell and Cosner 1991, 2001, Tischendorf et al. 2005, Wiegand et al. 2005). However, at the level of the individual, theory of effects of fragmentation is less well developed. In particular, there is no theory that predicts how fragmentation, narrowly defined (Fig. 1), influences the condition of individuals. These individual-level influences have consequences for populations and can help to explain population level responses.

Building on established theory of resource matching (Morris 2003), there is growing evidence (Galvin et al. 2007, Hobbs et al. 2008, Hobbs and Gordon 2010) that mobility of consumers across landscapes is critical to their foraging success, allowing them to exploit heterogeneity through selectivity. It follows that limiting mobility by fragmenting landscapes into isolated parts may harm consumers, even when the amount and quality of resources on a landscape remains unchanged. Yet, theory on how fragmentation influences consumers is poorly developed. In this paper, we present a simple, general model that portrays how fragmentation interacts with the spatial distribution of resources on the landscape to alter benefits to consumers. We then challenge the model experimentally by comparing its predictions with observation of the effects of fragmentation on growth and survival of the cabbage looper (*Trichoplusia ni*) in the laboratory.

A MODEL OF RESOURCE-MEDIATED EFFECTS OF FRAGMENTATION ON CONSUMERS

Consider a population of mobile consumers occupying a landscape that is divided into fragments such that consumers can move freely within fragments but cannot move among them (Fig. 1A, B, right panels). The landscape contains a quantity of resources that limits the growth of the consumer population. For the example here, we will consider these resources to be food, but they could be any limiting resource. We assume that the benefit that accrues to an individual consumer from exploiting resources is a decelerating function of per

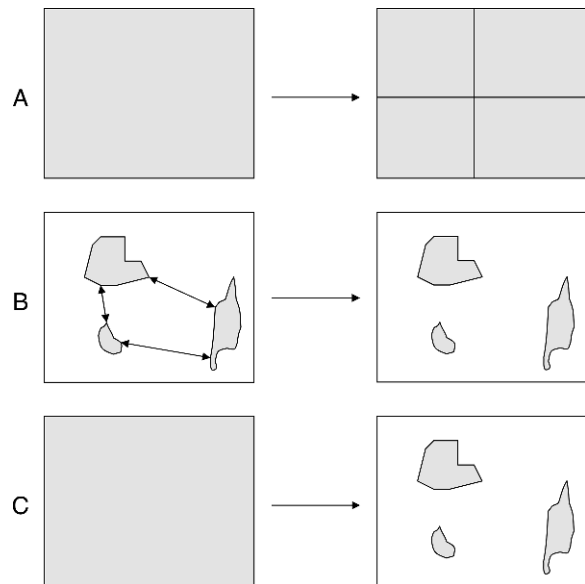


FIG. 1. We define fragmentation as the loss of connectivity among areas of the landscape that occurs from the breaking apart of a constant amount of habitat. This can occur (A) when an intact landscape is subdivided by barriers to movement, or (B) when connectivity among patches is eliminated without an accompanying reduction in their area. Our model also has implications for the case in which (C) isolated habitat patches are created by land conversion because the predictions of the model imply that the effect of fragmentation can add to the effect of habitat loss.

capita resource availability (Fig. 2). If the rate of increase in benefits to consumers decelerates with increasing resource availability, as is commonly the case (Spalinger and Hobbs 1992, Stelzer 2001, Bayliss and Choquenot 2002, Polishchuk and Vijverberg 2005), then the benefit function will be monotonically increasing and asymptotic (Fig. 2). The asymptote represents the maximum benefits accrued by consumers when resources are unlimited.

Because we assume that the landscape is subdivided into fragments without altering the total quantities of resources or consumers on the landscape, the overall average resource availability (measured as food per consumer or food per area) remains unchanged with fragmentation. However, the resulting average benefit to consumers in the fragmented environment will be lower than the average benefit in the intact one whenever the per capita resource availability differs among fragments (Fig. 2). The decrease in benefits to consumers on the fragmented landscape occurs as a result of Jensen's inequality (Jensen 1906), which states that the mean of the output of a convex-up, nonlinear function will always be less than the function of the mean of the inputs (Fig. 2). This occurs as the result of the differences in the slope of the function above and below the point representing the average resource availability on the landscape. When resource availability–benefit functions are convex-up, the set of fragments with lower

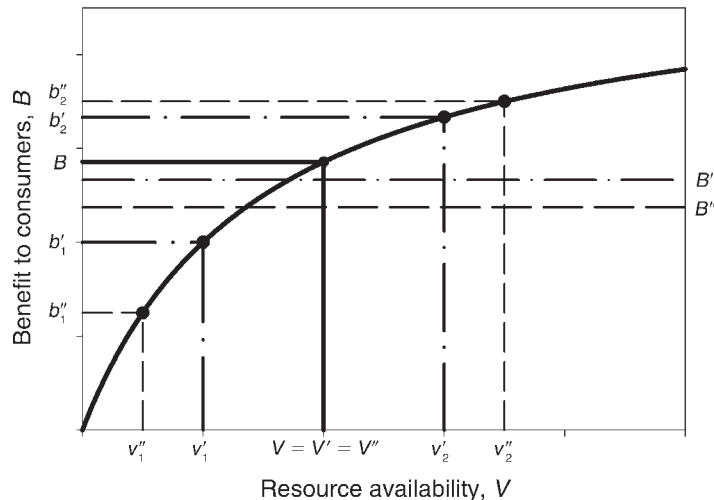


FIG. 2. Illustration of a decrease in average benefit after fragmentation, without overall change in food availability. An intact landscape has food availability V and resultant consumer benefit B . After division into two fragments, the food availabilities of the two fragments are v'_1 and v'_2 , and the average food availability on the landscape is $(v'_1 + v'_2)/2 = V'$. The benefit after fragmentation is $(b'_1 + b'_2)/2 = B'$. Average food availability is unchanged ($V = V'$). Gains in the average benefit due to b'_2 are smaller than losses to the average benefit due to b'_1 ; therefore, the average benefit is decreased as a result of nonlinearity in the function and $B' < B$. Division of the landscape into two fragments with food availabilities (v'_1 and v'_2) that have greater variance than v'_1 and v'_2 results in average benefit (B'') that is lower than B' .

than average resource availability has a greater effect on the mean benefit than the set of fragments above the average resource availability. This causes a reduction in the mean benefit among fragments in the fragmented landscape relative to the unfragmented landscape when resource availability differs among fragments.

A mechanism for effects of fragmentation on consumers

The theory developed in the preceding section predicts that fragmentation will harm the population of consumers on the landscape whenever the per capita availability of resources is heterogeneous over space, that is, when the resources differ among fragments. This suggests that some of the harmful effects of fragmentation on consumers are a result of preventing them from matching their spatial distribution to the distribution of resources. If the spatial distribution of consumers is proportional to the spatial distribution of resources, all consumers experience the same average supply of resources; we will refer to this situation as a matched distribution. Graphically, this means that the per capita resource availabilities for all consumers occupy a single point on the benefit function (Fig. 2). Therefore, we predict that when animals and resources are distributed in a matched manner among newly created fragments, fragmentation will not affect consumer performance because there is no heterogeneity in availability of resources per individual. However, if resources and consumers are distributed in a way in which demand is unmatched with availability, Jensen's inequality compels a reduction in the average benefit acquired by consumers relative to the unfragmented case. We emphasize that this reduction must occur despite the

fact that the total amount of resource on the landscape remains unchanged.

Model predictions

The theory we developed above motivates the following predictions. The spatial distribution of resources relative to consumers will have no effect on the performance of mobile consumers in intact landscapes because consumers are able to match their foraging to the distribution of resources. However, consumers with convex-up resource use functions in fragmented, spatially heterogeneous landscapes will show reduced benefits, on average, relative to consumers in intact landscapes if consumer distributions are not matched to resources within fragments. Fragmentation operates by preventing consumers from matching their distribution to resources. Thus, the effect of fragmentation depends on resource distributions that are unmatched to consumer density in habitat fragments.

METHODS

Experimental design

To test these predictions, we conducted two experiments (Fig. 3). In Experiment 1, we created a homogeneous distribution of consumers across the landscape and allowed them to exploit foods in two spatial distributions (homogeneous vs. heterogeneous) at three levels of fragmentation (none, low, high). Thus, in Experiment 1 we compared matched and unmatched consumer distributions that occurred as a result of differences in the spatial distribution of food within fragments used by the same distribution of consumers. In Experiment 2, we used a heterogeneous distribution

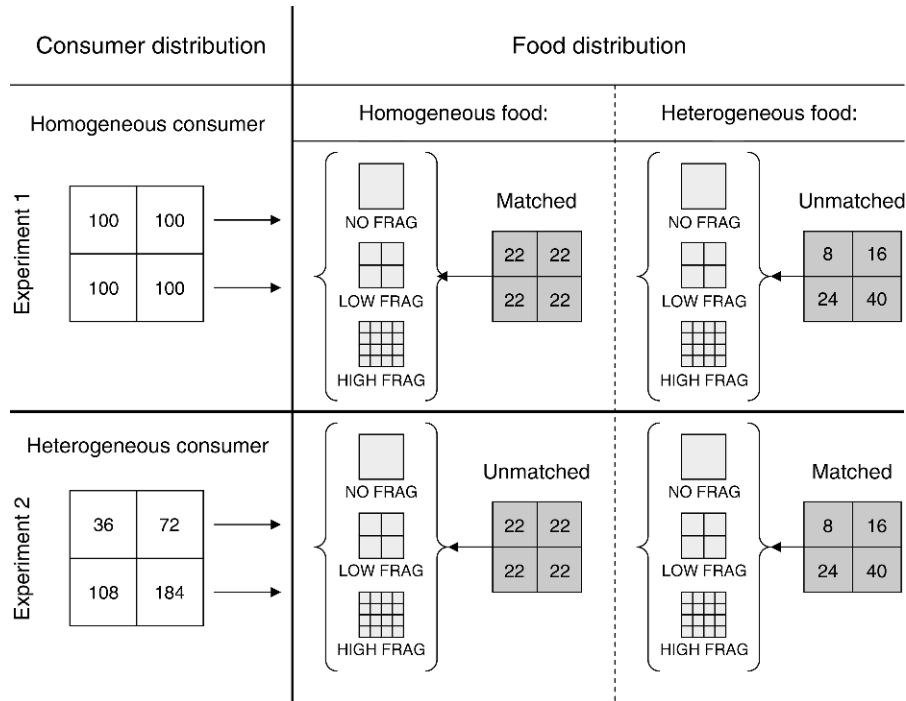


FIG. 3. Experimental design. We examined matched and unmatched consumer distributions in experimental landscapes that were fragmented and intact, using a laboratory system of cabbage looper (*Trichoplusia ni*) larvae on artificial landscapes. Food per consumer ratios are similar among all fragments in matched treatments. In unmatched treatments, food per consumer ratios are more dissimilar than in matched treatments. Each experimental block contains six landscapes, consisting of one class of consumer distribution (homogeneous in Experiment 1 or heterogeneous in Experiment 2), two classes of food distribution (homogeneous and heterogeneous), and three levels of fragmentation. Levels of fragmentation are labeled as follows: NO FRAG, no fragmentation; LOW FRAG, low fragmentation; HIGH FRAG, high fragmentation. Numbers in boxes are the numbers of larvae or units of food in each quarter of the landscape.

of consumers across the landscape and allowed them to exploit foods that were either homogeneously or heterogeneously distributed at three levels of fragmentation (none, low, and high). Thus, in Experiment 2, we could compare matched and unmatched consumer distributions that occurred as a result of differences in the spatial distribution of food within fragments using a heterogeneous distribution of larvae. We predicted that a fragmentation effect would occur only when food distributions were unmatched with consumer distributions. The two experiments combined allowed us to test for effects of fragmentation and to test the causal mechanism by which it affects consumers: nonlinear averaging of benefits when the distribution of food fails to match the distribution of consumers.

Experimental procedure

The cabbage looper, *Trichoplusia ni* (Lepidoptera: Noctuidae), has been widely used as a model organism because it is easy to raise in large numbers in the laboratory and because of its importance as an agricultural pest (McEwen and Hervey 1960). Larvae feed on the leaves of a wide range of cultivated plants, particularly crucifers and cotton (Soo Hoo et al. 1984).

Cabbage looper larvae can be reared at high densities on artificial diet and reach pupation at two weeks to more than six weeks from hatch (McEwen and Hervey 1960). The rate of development is largely dependent on temperature (Shorey et al. 1962, Toba et al. 1973).

We obtained *T. ni* eggs before each replication of the two experiments (Benzon Research, Carlisle, Pennsylvania, USA) and portioned them onto artificial diet substrate (Southland Products, Lake Village, Arkansas, USA) in covered 236.6-mL squat Styrofoam cups (30 eggs/cup). Eggs for each experimental replicate were laid on the day before receipt and hatched 48–96 hours after receipt. Individuals hatched in the cups and fed on the substrate until seven days from hatch, when they were distributed on artificial landscapes. At the time of distribution, 80% of larvae measured ~1.2 cm.

We constructed artificial landscapes to implement the experimental design. These landscapes were square, uncovered acrylic boxes (40.64 × 40.64 cm, 10.16 cm in height). The construction of the landscapes imposed the three levels of fragmentation using internal barriers. Barriers were absent in the no-fragmentation treatment level. We divided the landscape into four fragments of equal size for the low-fragmentation level, and into 16

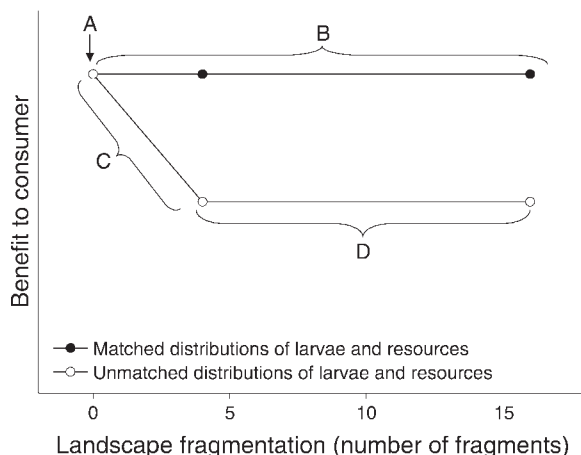


FIG. 4. Form of the hypothesized results of the experiment. We expect no effect of resource matching (A) when landscapes are intact because mobile consumers can adjust their densities to match resources. (B) In the case in which consumer distributions are matched to resources, we expect no effect of increasing fragmentation. (C) We expect that the low- and high-fragmented treatments will show lower benefits than the intact treatment in the unmatched landscape or any of the treatments in the matched landscape. (D) However, we expect no difference between the low- and high-fragmentation levels in the unmatched landscape because the ratio of resources to individuals is the same in these treatments.

fragments of equal size for the high-fragmentation level. Heated barriers topping all internal subdivisions and the inside of the external wall were used to contain larvae within fragments (McEwen and Hervey 1960). Heated barriers consisted of nickel chromium wire covered in thermally conductive, electrically insulating epoxy. When electrical current was applied to the wire through a rheostat at 65 V, the epoxy was warm enough to prevent the larvae from crossing but caused no apparent injury to the larvae testing the barrier. Pilot studies indicated that temperature inside the landscapes was fairly consistent across treatments (within 2°C). Humidity in the room was kept above 60%.

We filled polyethylene tubing with artificial diet; when the diet cooled, the tubing was cut into uniform lengths of 1.27 cm and was distributed in the landscapes over damp paper towels. In all landscapes, there were a total of 400 introduced *T. ni* larvae and 88 units of food (one unit contained 0.465 g food, $\sigma^2 = 0.003$).

To achieve a heterogeneous distribution of food, we distributed 8, 16, 24, and 40 units of food (sum = 88) among four quarters of the landscape (Fig. 3). Homogeneous distributions were achieved by allocating 22 units of food for each quarter. To achieve a heterogeneous distribution of consumers, we distributed 36, 72, 108, and 184 consumers in each quarter of a landscape; homogeneous consumer distributions had 100 individuals in each quarter. Food and consumers were distributed evenly within each quarter of a landscape at all fragmentation levels. Therefore, the

high-fragmentation treatments (in which the landscapes were divided into sixteenths) had four-sixteenths of each level of food availability. For example, one-quarter of the landscapes with heterogeneous food and heterogeneous consumers held eight units of food and 36 consumers; the corresponding quarter of the high-fragmentation landscape consisted of four fragments, each with two units of food and nine consumers.

Food was present in the landscapes when the larvae were introduced, and was reapplied 48 h and 76 h after larval introduction; 42 h after the last food addition, we collected, weighed, and counted surviving larvae. The average wet mass of survivors and the proportion of survivors served as the two response variables. Both experiments were repeated five times for a total of 10 runs.

Analysis

To estimate the shape of the relationship between consumer benefits and resource availability, we used data from the fragmented treatments of Experiments 1 and 2, each of which provided four different levels of per capita resource availability (0.08, 0.16, 0.24, and 0.4 units of food per consumer in Experiment 1; 0.12, 0.20, 0.3, and 0.61 units of food per consumer in Experiment 2). We fit a quadratic model to the resource–benefit curves to test for convexity; if the quadratic term was significant, the form of the function was convex.

We predicted that there would be no influence of resource matching when landscapes were intact because, in this case, consumers were free to adjust their distributions to the distribution of resources (Fig. 4A). We predicted that there would be no effect of increasing levels of fragmentation on the matched landscape (Fig. 4B). However, we predicted that both levels of fragmentation on the unmatched landscape would show reduced benefits relative to those observed on the intact landscapes or on the fragmented levels of the matched landscape (Fig. 4C). We also compared the low with the high level of fragmentation on the unmatched landscape. Because these two levels contained the same ratio of consumers to resources, we predicted no effect of increasing fragmentation on consumer benefits between these levels (Fig. 4D).

Comparisons were made in SAS using a mixed-model ANOVA (proc MIXED) for linearity tests, a generalized linear mixed-model ANOVA (proc GLIMMIX) for survivorship data, and proc MIXED for the average mass of survivors. For average mass data, we used the mixed-model ANOVA rather than a general linear model (proc GLM) because there were missing data. Differences among temporal replications of the experiments necessitated comparisons within runs (using replicate number as an indicator variable) rather than pooling data across runs. All analyses were done using SAS version 9.1 (SAS Institute 2004). We assumed treatment differences to be statistically significant at $P \leq 0.05$.

RESULTS

Resource benefit functions

We observed convex-up relationships between food availability and survival in both experiments (Experiment 1, $F_{1,92} = 7.80$, $P = 0.0063$; Experiment 2, $F_{1,201} = 73.75$, $P < 0.0001$; Fig. 5A). We also observed a convex-up relationship between food availability and average mass of survivors in Experiment 1, when consumers were homogeneously distributed across heterogeneous food ($F_{1,92} = 20.20$, $P < 0.0001$; Fig. 5B), but not in Experiment 2, when consumers were heterogeneously distributed across homogeneous food ($F_{1,199} = 1.31$, $P = 0.2542$; Fig. 5B). Therefore, the only response variable *not* expected to show fragmentation effects predicted by our model was the average mass of larvae in Experiment 2, because in this case there was not a convex-up relationship for resource benefits relative to availability.

Survival

Observations of survivorship were consistent with the predictions of the model (Figs. 4, 6A, B). We observed no effect of resource or consumer distribution in the absence of fragmentation in either experiment, although some of these effects approached significance (Experiment 1, $t_{20} = -1.87$, $P = 0.0763$; Experiment 2, $t_{20} = 1.94$, $P = 0.0660$). In both experiments, fragmentation reduced survival in the unmatched treatments (Experiment 1, unfragmented vs. low fragmentation, $t_{20} = 3.19$, $P = 0.0046$; Experiment 2, unfragmented vs. low fragmentation, $t_{20} = 2.95$, $P = 0.0079$), but not in the matched treatments (Experiment 1, unfragmented vs. low fragmentation, $t_{20} = -0.41$, $P = 0.6849$; Experiment 2, unfragmented vs. low fragmentation, $t_{20} = 0.27$, $P = 0.7895$). Similarly, we observed effects of matching when the landscape was fragmented (Experiment 1, high-fragmentation treatment, $t_{20} = 2.98$, $P = 0.0075$; Experiment 2, low fragmentation, $t_{20} = 4.61$, $P < 0.0020$; Experiment 2, high fragmentation, $t_{20} = 4.27$, $P = 0.0004$). However, the effect of matching was not significant in the low-fragmentation treatment of Experiment 1 ($t_{20} = 1.74$, $P = 0.0979$). Thus, fragmentation influenced survival only when resources and consumer density were unmatched.

Body mass

Observations of average survivor mass were partially consistent with model predictions (Figs. 4, 6C, D). In Experiment 1, we observed no effect of consumer–resource distribution in the absence of fragmentation ($t_{20} = 1.44$, $P = 0.1643$). As expected, when resources and consumers were unmatched, average body mass of survivors in the low-fragmentation treatment was less than the average mass of those in the unfragmented treatment; however, this difference was not statistically significant (unfragmented vs. low fragmentation, $t_{20} = 1.41$, $P = 0.1740$). Fragmentation effects were not observed in the high-fragmentation treatment relative

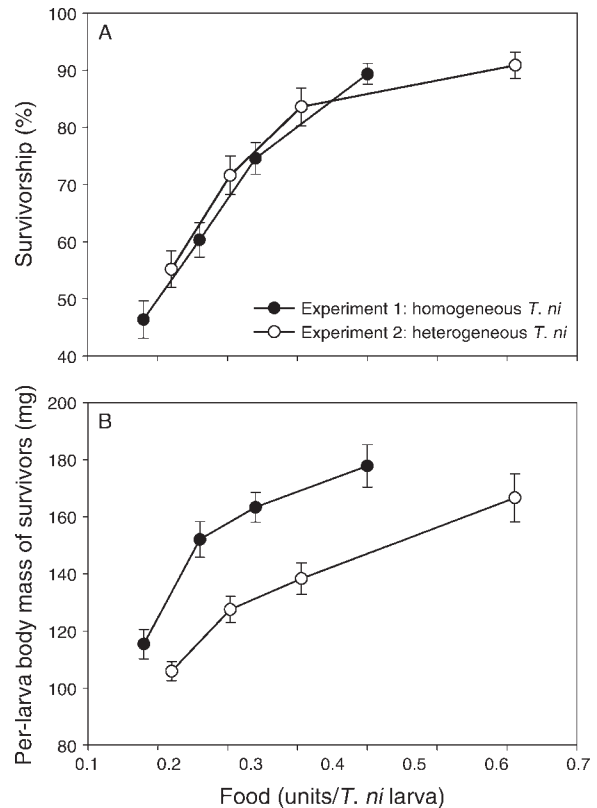


FIG. 5. Observed forms of the relationships between (A) survivorship and (B) average survivor mass and food availability for *T. ni* larvae in Experiments 1 and 2. Food is expressed as units per *T. ni* larva, with one unit defined as 1.27 cm of polyethylene tubing filled with artificial diet. Error bars show \pm SE. The quadratic term was significant in both sets of survivorship data (Experiment 1, $F_{1,92} = 7.80$, $P = 0.0063$; Experiment 2, $F_{1,201} = 73.75$, $P < 0.0001$; Fig. 5A) and in homogeneous *T. ni* average mass data ($F_{1,92} = 20.20$, $P < 0.0001$; Fig. 5B), indicating convexity. The quadratic term was not significant in Experiment 2 average mass data ($F_{1,199} = 1.31$, $P = 0.2542$; Fig. 5B). These relationships were evaluated using data from fragmented landscapes with unmatched distributions of larvae and food in both experiments.

to the low treatment (low vs. high fragmentation, $t_{20} = 0.95$, $P = 0.3545$). In the matched treatments, no effects of fragmentation were evident (unfragmented vs. low fragmentation, $t_{20} = 0.51$, $P = 0.6161$; low vs. high fragmentation, $t_{20} = -1.17$, $P = 0.2576$). In summary, Predictions A, B, and D (Fig. 4) were fully supported, and Prediction C (Fig. 4) was not strongly supported in Experiment 1.

Because the average mass of survivors was not found to be significantly nonlinear in Experiment 2, we did not expect to detect all predicted differences. In fact, the only statistically significant effect was an unexpected difference between the unfragmented and low-fragmentation treatments in the matched landscapes ($t_{20} = 2.17$, $P = 0.0425$; Fig. 6D). Other comparisons between

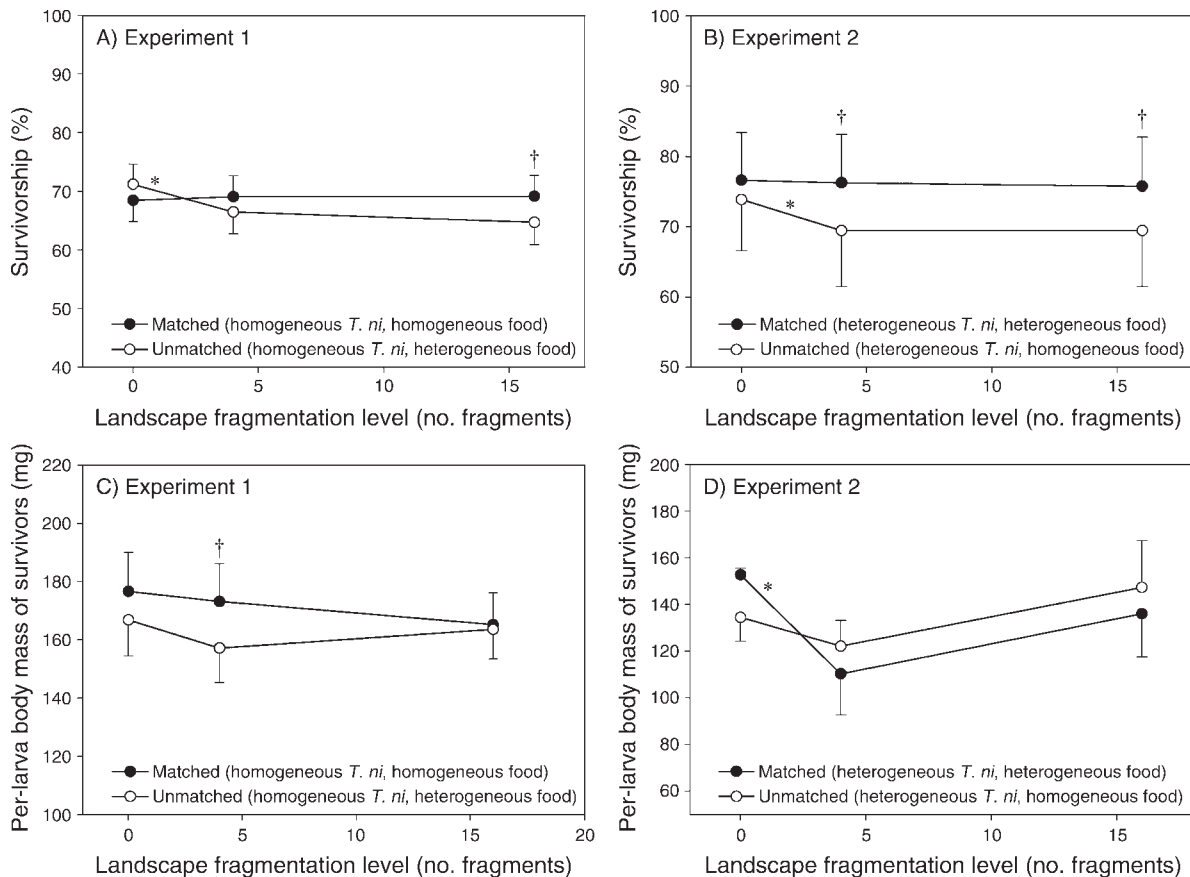


FIG. 6. Consumer benefit across three levels of fragmentation in matched and unmatched treatments. Three fragmentation levels (none, low, and high) have 0, 4, or 16 fragments. Statistically significant differences ($P < 0.05$) between fragmentation levels within matched or unmatched treatments are marked with an asterisk (*), and statistically significant differences ($P < 0.05$) between matched and unmatched treatments within a fragmentation level are marked with a dagger (†). Observations of effects of fragmentation and resource matching on survivorship (panels A and B) agreed closely with the predictions of theory. Observations of average body mass (panels C and D) were moderately consistent with model predictions. Panels (A) and (C) are results from Experiment 1 (homogeneous larval distribution); panels (B) and (D) are results from Experiment 2 (heterogeneous larval distribution). Error bars indicate \pm SE, which overlap in the graphs even when data are significantly different ($P < 0.05$); this is due to the inclusion of cross-replicate variance in the SEM. Replicate effects were large in our data; the statistical analysis compared treatments without incorporating among-replicate variability, but the error bars reflect the large variance among replicates and therefore do not accurately reflect statistical significance.

treatments were nonsignificant, and ranged from $P = 0.2019$ to $P = 0.5771$.

DISCUSSION

We developed a new, general model to explain how fragmentation affects interactions between individual consumers and resources. Our model exploits a simple observation: when resource–benefit functions are nonlinear and convex-up, dividing heterogeneous resources among fragments will diminish the average benefit to consumers relative to the case in which landscapes are intact. The mechanism mediating harmful effects of fragmentation on consumers is also simple: in fragmented environments, individuals are unable to match their distribution to the distribution of resources on the landscape. Thus, our model predicts that the effects of fragmentation on consumers depend in a truly funda-

mental way on the spatial distribution of consumers and resources and the shape of the relationship that governs the benefits that accrue from exploiting those resources.

Empirical observations were largely consistent with the predictions of the model. Fragmentation diminished consumer survival, but only when the distribution of consumers was not matched to the distribution of resources within fragments. Our experiment did not provide support for predictions on the effect of fragmentation on consumer body mass. There are two potential reasons for this result. First, response of body mass to food availability was not strongly nonlinear. We observed only weak nonlinearity in Experiment 1 and did not observe significant nonlinearity in Experiment 2. Thus, the model did not predict strong effects of fragmentation on body mass, and variance in the average mass data was high. Any weak effects may

have been masked by the high variance in mass responses among individuals. Second, there may have been a confounding effect of the survival response on the body mass response. Reduced survival of individuals in the low- and high-fragmentation treatments probably increased the per capita availability of resources for surviving individuals in those treatments, diminishing the potential effect of fragmentation on mass.

Consistent with the predictions of the model, fragmentation did not affect consumers when resource–benefit functions were not strongly nonlinear. The observation of different forms of the benefit–food function for different types of consumer responses is not unusual. Arrivillaga and Barrera (2004) found a convex-up effect of food availability on survival and resistance to starvation in a mosquito, but a linear effect on per capita mass of survivors. Similarly, Atlantic Puffins showed a linear response of body mass to food availability and a curvilinear response of several other measures of growth (Oyan and Anker-Nilssen 1996).

As with all manipulative experiments, ours imposed artificial conditions, and consequently, we need to be clear about its relevance to natural systems. We designed the experiment to challenge a theoretical prediction, and it is the theory, buttressed by experiment, that has broad application rather than the experiment itself. The situations in which our theoretical results are relevant are illustrated in Fig. 1. The theoretical prediction will apply when landscapes are fragmented by barriers to consumer movement that do not appreciably affect the area of habitat (Fig. 1A), for example, when intact landscapes are dissected by construction of roads or fences, a human action that is truly ubiquitous throughout the world (Forman and Alexander 1998, Serrano et al. 2002, Galvin et al. 2007, Hobbs et al. 2008). The prediction will apply when connections among habitat patches are severed without any change in patch area (Fig. 1B). Our model has implications for the case in which shrinking habitat patches simultaneously become disconnected (Fig. 1C), such as when habitat is converted to new habitat types. In this case, our model suggests that the effect of loss of connectivity may add to the effect of habitat loss.

Our work offers a necessary first step in understanding how fragmentation may affect consumers over the short term. Our experiment did not allow for a multi-generation, population response, which in temporally stable environments would presumably allow consumer populations to come into equilibrium with resources (Fretwell and Lucas 1970, Schwinning and Rosenzweig 1990). Thus, under such conditions, we would expect that per capita resource availability would become increasingly similar among fragments over time and we would expect the effect of fragmentation to fade as equilibrium was reached. However, there is a growing view that such equilibrial behavior may be the exception in nature rather than the rule (reviewed by Wiens 1977, Ellis and Swift 1988, Illius and O'Connor 1999, Galvin et al. 2007,

Owen Smith 2010). In systems where resources vary dramatically over time and are not correlated over space, density-independent forces will prevent the equilibration of consumers and resources, thereby preserving fragmentation effect over time. However, the possibility of long term-equilibrium does not contradict the fundamental prediction of our model and the empirical support we obtained for it: when resource–benefit functions are convex-up and consumer distributions are not matched with resources, fragmentation will lead to a reduction in the average benefit obtained by consumers from resources. Our model makes clear, testable predictions and our experiment suggests that testing these predictions in other systems is promising.

Negative effects of fragmentation on consumers within a heterogeneous landscape do not imply that spatial heterogeneity in resources is bad for consumers. Indeed, spatial heterogeneity has often been shown to be beneficial for consumer populations on intact landscapes (Senft et al. 1987, Mysterud et al. 2001, Choquenot and Ruscoe 2003, Said and Servanty 2005, Wang et al. 2006). Rather, it is the loss of access to spatially heterogeneous resources that negatively impacts populations. Although several workers have hypothesized such impacts (Mysterud et al. 2001, Boone and Hobbs 2004, Fryxell et al. 2005) and recent observational studies provide empirical evidence supporting them (Wang et al. 2006, Hebblewhite et al. 2008), there has been relatively little theoretically motivated experimental work showing evidence for loss of benefits to consumers in response to fragmentation in heterogeneous environments. Searle et al. (2010) showed experimentally that fragmentation can interfere with the ability of mobile herbivores to track pulses of high-quality resources that occur when phenology of plant patches varies asynchronously over space and time. Our results reinforce these findings by showing that fragmentation harms consumers by preventing them from matching their spatial distribution to the spatial distribution of resources.

It should not be surprising that isolation of individuals in suboptimum patches harms their performance. The unique contribution of this paper is to show that isolation caused by fragmentation prevents patches that are of high value from fully compensating for those that are of low value. As a result, fragmented landscapes offer diminished benefits to consumers, even when the total amount and quality of resources on those landscapes remains unchanged. This result occurs because of nonlinearities in resource use functions. Temporally and spatially nonlinear relationships abound in natural systems. However, nonlinearity in key relationships and the possible role of Jensen's inequality in ecological processes have not been widely considered. Davis et al. (2002) recognized the significance of Jensen's inequality for numerical responses and consumer population sizes. Consistent with Jensen's inequality, a convex-up numerical response decreased

long-term population growth rates when variance in the independent variable was high. Other examples include the effects of spatial variance of biodiversity on average plant productivity (Benedetti-Cecchi 2005) and the effects of environmental variation on optimal life history strategy (Pasztor et al. 2000). Ruel and Ayres (1999) cited several examples of the implications of Jensen's inequality for processes in physiological ecology, such as the effects of variability in environmental conditions on metabolic processes. Here, we show that nonlinearity in the relationship between resource availability and benefit to consumers has fundamental implications for the effects of landscape fragmentation on consumers.

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SUPPLEMENT

Survivorship, survivor mass, and individual mass of *Trichoplusia ni* larvae with multiple levels of landscape fragmentation, larval density, and food density (*Ecological Archives* E092-009-S1).