

Butterfly edge effects are predicted by a simple model in a complex landscape

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Abstract Edge responses have been studied for decades and form a critical component of our understanding of how organisms respond to landscape structure and habitat fragmentation. Until recently, however, the lack of a general, conceptual framework has made it difficult to make sense of the patterns and variability reported in the edge literature. We present a test of an edge effects model which predicts that organisms should avoid edges with less-preferred habitat, show increased abundance near edges with preferred habitat or habitat containing complementary resources, and show no response to edges with similar-quality habitat that offers only supplementary resources. We tested the predictions of this model against observations of the edge responses of 15 butterfly species at 12 different edge types within a complex, desert riparian

landscape. Observations matched model predictions more than would be expected by chance for the 211 species/edge combinations tested over 3 years of study. In cases where positive or negative edge responses were predicted, observed responses matched those predictions 70% of the time. While the model tends to underpredict neutral results, it was rare that an observed edge response contradicted that predicted by the model. This study also supported the two primary ecological mechanisms underlying the model, although not equally. We detected a positive relationship between habitat preferences and the slope of the observed edge response, suggesting that this basic life history trait underlies edge effects and influences their magnitude. Empirical evidence also suggested the presence of complementary resources underlies positive edge responses, but only when completely confined to the adjacent habitat. This multi-species test of a general edge effects model at multiple edge types shows that resource-based mechanisms can explain many edge responses and that a modest knowledge of life history attributes and resource availability is sufficient for predicting and understanding many edge responses in complex landscapes.

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Introduction

Understanding ecological responses to the presence of habitat edges is critical to understanding landscape-scale phenomena, such as the effects of habitat heterogeneity within a landscape mosaic and the impacts of habitat fragmentation (Murcia 1995). Edge effects have been studied for many decades (Lay 1938), with a tremendous number of

published studies emerging in the last 30 years, all confirming that many taxa respond behaviorally and numerically to the presence of habitat edges (for reviews, see Murcia 1995; Risser 1995; Lidicker 1999; Lahti 2001; Chalfoun et al. 2002; Sisk and Battin 2002; Ries et al. 2004). Edge responses have been shown to be far more common than responses to changes in habitat area per se; in fact, most patterns identified initially as area responses are probably scaled-up edge responses (Fletcher et al. 2007). Furthermore, incorporating knowledge of edge responses has improved predictions of species' distributions in fragmented landscapes (Temple 1986; Sisk et al. 1997; Ries 2003; Brand et al. 2006). Despite the importance of this topic, there has been no overarching theoretical framework (Murcia 1995; Cadnasso et al. 2003) or, until recently (Ries and Sisk 2004), a general model available to predict the responses of organisms to a variety of edge types.

This lack of a theoretical framework has made it difficult to make sense of the varied results reported in the edge literature. A specific example of this can be found in the limited literature on butterfly edge responses. Studies have shown that certain butterfly species either avoid (Schultz 1998; Haddad and Baum 1999) or are attracted (Ravenscroft 1994; Bergman 1999; Wahlberg 2001; Ide 2002) to certain edges. Although some of these studies include data showing how changes in microclimate or host plant distribution were associated with these patterns, there is no overarching framework to explain when specific butterfly species should be expected to avoid, be attracted to, or ignore specific edge types. Therefore, it is difficult to extrapolate these results to other species or landscapes or to develop a general understanding of which factors are most important in driving butterfly edge responses.

Focusing on the variability of edge responses may leave the impression that, despite decades of study, edge responses are so species and context specific that they constitute an idiosyncratic phenomenon that cannot be generalized. In contrast, in 2004 we proposed a general model of edge effects based on habitat associations and resource distribution (Fig. 1, Ries and Sisk 2004). Drawing on dozens of published studies on diverse species in a variety of landscapes, the model was able to correctly predict the direction of observed edge responses 83% of the time for birds (Ries and Sisk 2004), 91% of the time for plants, and 83% of the time for mammals (Ries et al. 2004).

The goal of the study reported here was to determine how well this model explains the great variability in edge responses observed for a suite of butterfly species in a complex riparian landscape characterized by several distinct edge types. To provide the first robust test of this model for an invertebrate taxon, we collected one of the largest datasets on butterfly edge effects and the first extensive effort in one of North America's centers of Lepidopteran diversity,

the San Pedro River riparian corridor in southeastern Arizona.

A resource-based model of edge effects

Edge effects can be caused by a variety of cascading ecological phenomena, from changes in microclimate to interactions with competitors or predators (see the mechanistic model presented in Ries et al. 2004). However, most of these factors integrate to cause predictable edge effects based on two main factors: (1) relative differences in habitat quality and (2) the distribution of key resources (Ries et al. 2004; Ries and Sisk 2004). By focusing on these two variables, we suggest that it is possible to predict how population density will change near edges for any species at any edge type. The model predicts that organisms should avoid edges adjoining non-habitat or lower quality habitats that offer only supplementary resources, they should show increased density near edges with higher quality habitat or habitat that contains complementary (different) resources, and they should show no response to edges adjoining similar quality habitat that offers only supplementary (similar) resources (Fig. 1). The more stark the contrast in habitat quality or resource division, the stronger the edge response should be (Ries and Sisk 2004). This model is a synthesis of ideas published in the edge literature; a detailed description of the underlying mechanistic framework is presented in Ries et al. (2004) and Ries and Sisk (2004). For this test of our model, information on habitat preferences and resource distribution (in this case, host and nectar plants) was used to generate predictions for 15 butterfly species at 12 different edge types within desert riparian habitats in southeastern Arizona. By applying this model to numerous butterfly species at multiple edge types, we created the

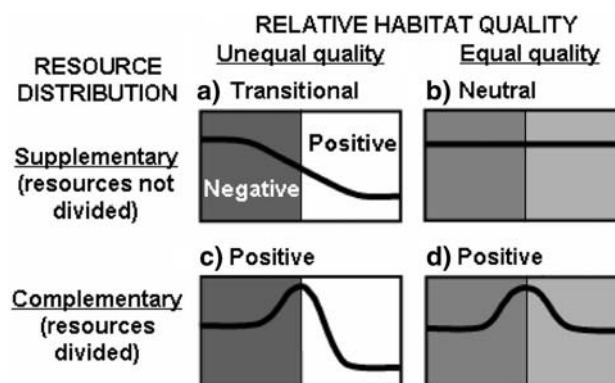


Fig. 1 Model predictions of edge responses are transitional (a), neutral (b) or positive (c, d) based on relative habitat quality and resource distribution. Lower habitat quality is indicated by a white box, while habitats of higher or equal quality are shaded. The same resources are either available in both habitats (supplementary), or different resources are divided between habitats (complementary). Adapted, with permission, from Ries and Sisk (2004)

opportunity not only to test the qualitative predictive power of the model (how often the edge responses predicted by the model are observed) but also to determine how strongly the two key model variables (habitat association and complementary resource distribution) correlate with the strength of observed edge responses.

Test system: butterflies in desert riparian habitat

Butterflies in desert riparian habitat present an ideal system for conducting an empirical test of the model. The structure of desert riparian habitat leads to a multitude of relatively abrupt and well-defined edges that vary from “classic” forest-grassland edges to more subtle edges, such as those between riparian grasslands and desert scrub. Butterflies are an excellent group for testing the general applicability of the model because much is known about their ecology, but they have received relatively little attention in the edge literature. For this study, we define edges as abrupt linear boundaries between two different habitat types, positive edge responses as increases in butterfly density near edges (relative to the interior of the habitat patch), and negative edge responses as decreases in butterfly density near edges.

This study took place along the Upper San Pedro River in southeastern Arizona, within the boundaries of the San Pedro Riparian National Conservation Area [SPRNCA, see Appendix 1a in Electronic Supplementary Material (ESM)], where grazing and agriculture have been excluded since 1987 (Kreuper et al. 2003). The Upper San Pedro River’s riparian corridor exists as a two-tiered system with a primary floodplain and upland riparian zone surrounded by desert scrub (Appendix 1a in ESM). The primary floodplain is dominated by Fremont cottonwood (*Populus fremontii*) and Gooding’s willow (*Salix goodingii*), which form a highly heterogeneous canopy structure with large openings throughout. The dominant woody vegetation in the upland riparian zone is mesquite (*Prosopis velutina*), although other shrubs are common. This zone also demonstrates a high degree of heterogeneity in canopy structure, ranging from open grasslands to dense riparian forests or “bosques”. Intermediate between these two extremes are areas akin to open woodlands, where tall mesquite are abundant, yet sufficiently spaced to allow for the development of a thick herbaceous layer. To reduce the effects of internal heterogeneity, we classified the upland riparian zone into three habitat types: grassland (GRASS), mesquite-dominated forests (MES) and grassland-mesquite mixes (MIX). The surrounding desert scrub is characterized by widely-spaced, low shrubs with a rocky ground cover that typically supports only a sparse herbaceous layer. The juxtaposition of the cottonwood-dominated floodplain (CW), the three categories of upland riparian habitat (GRASS, MIX, and MES), and the surrounding desert

scrub (DS) results in six combinations of adjacent habitat pairs of varying structural contrast (CW and GRASS, CW and MIX, CW and MES, GRASS and DS, MIX and DS, MES and DS). We considered edge responses separately on either side of the edges formed by these six habitat pairs, resulting in 12 edge types that were the focus of this study (Appendix 1b in ESM).

Material and methods

We established 17 study areas during a 3-year period (1999–2001) throughout the 70-km extent of the SPRNCA (Appendix 1a in ESM), with one additional site 50 km north of the boundary. Not all sites were sampled in all years due to the occurrence of wildfires. Most study areas were at least 1 km from the next closest area of the same edge type (Appendix 1a in ESM), although in one case, study areas were only 300 m apart (in 1 year only) and in two other cases, 500 m. For purposes of our analysis, each study area was considered to be one independent sample site within the boundaries of the SPRNCA. There were from two to six independent study areas established for each edge type in each year, with most edge types represented in four or five areas. Mesquite edge types were not surveyed in 2001.

Transects, placed perpendicular to the edge, consisted of contiguous 10 × 10-m plots that generally spanned both sides of the edge, extending up to 100 m into the interior of upland riparian habitat and 40–50 m into cottonwood and desert scrub habitat (Appendix 1b in ESM). There were one to three transects established for each edge type within each study area, with all transects for the same edge type located within 50–100 m of each other. Multiple transects for one edge type within a single area were not considered to be independent and were pooled for analysis. Each edge type in each year was represented by between three and 13 transects, with a mean of eight transects per edge type.

Butterfly surveys were conducted from mid-August through early October in 1999, 2000, and 2001. Three (in 2000, 2001) or four (in 1999) complete rounds of surveys were conducted during each year, with a survey round lasting 3–4 weeks. Surveys began at one end of the transect, with an observer surveying alternate plots to the end of the transect, then reversing direction and surveying the remaining plots on the way back. The starting point of each transect was alternated between rounds. Surveys were only begun when the sun was not obscured by clouds. Each 10 × 10-m plot was searched for 3 min, and all butterflies seen were identified and recorded. Nectaring and oviposition activities were recorded, including the plant species on which each activity occurred. At the end of each survey, the presence of each plant species that was a potential nectar

source was recorded. In order to identify the distribution of host plants, once each field season we conducted separate surveys on herbaceous plants. A 10×2 -m area along the edge of each plot was searched to determine the presence or absence of ten herbaceous taxa identified as important local host plants, including *Aristolochia watsoni*, *Viguiera dentata*, *Helianthus annuus*, *Matalea* sp., *Sarcostemma* sp., *Cassia leptocarpa*, *Cassia roemeriana*, *Lepidium thurberi*, *Sphaeralcea* sp., and *Sida* sp. Surveys of the woody host species *Atriplex* sp. and *Celtis* sp. were conducted once, in 2001.

Data analysis

Fifteen species were sufficiently abundant to permit detailed analysis. Data from survey rounds during peak flight periods, identified separately for each species, were pooled to arrive at a single density estimate for each plot in each year. Information on habitat preferences and resource distribution was used to generate predictions from our model (see Fig. 1). We used ANOVA to determine if there were significant differences in density for each butterfly species between each of the six pairs of adjacent habitat types. Edge plots were not used in this analysis in order to avoid confounding habitat preferences and edge responses. Where one habitat type supported equal or higher densities relative to the adjacent habitat type, it was necessary to determine whether host and nectar plant distributions were complementary or supplementary. We did this by calculating the relative probability of encountering nectar and host plants on the adjacent side of the edge. Given these parameters, a predicted edge response was generated for each species at each edge type. Empirical edge responses were determined to be positive, negative, or neutral based on finding a slope parameter significantly different from zero in a linear regression model. Because this study used plots within transects, which represent repeated measures along a non-independent sampling unit (Diggle et al. 1994), a mixed model was used with distance to edge as the fixed effect, study area as a random effect, and plots within transects specified as repeated measures (Littell et al. 1996). Examination of the residuals at varying distances indicated a decay in correlation strength as distance increased, so an autoregressive correlational structure was specified in the model (Diggle et al. 1994). The regressions were run with the number of transects in each area (one to three) used as a weighting factor.

For the subset of species/edge type combinations where we had sufficient data to make predictions, we compared those predictions to observed edge responses. For both generating and testing predictions, making a Type-II error (failing to detect an effect where one does in fact occur) has consequences as serious as a Type-I error. To try to balance

these two types of errors, we judged an alpha level of 0.10 to be appropriate for capturing biologically relevant trends in habitat associations and edge responses. In addition, we considered results in the range of $0.10 < P < 0.30$ to be “indeterminate”, and excluded them from further consideration because they provide little statistical basis for identifying or rejecting either habitat associations or edge responses. These cut-offs were used only to generate predictions and classify edge responses. The actual test of the predictive power of the model comes from comparing how often predictions match observations and from determining the strength of association between predictor variables and the observed edge responses. The *P* values resulting from these key tests can be considered individually to assess the strength of the support for the model. All analyses were done in SAS (v 8.2) or SAS-JMP (v 4.0.4) (SAS Institute, Cary, NC).

Model predictions

For this application of the general edge effects model, habitat preferences were assigned separately for each of the six habitat pairs based on a species having significantly higher densities in the interiors of one of the adjacent habitat types. While local densities can sometimes be a misleading indicator of local habitat quality (Van Horne 1983) due to factors such as source-sink dynamics, we use densities pooled across spatially replicated patches to broadly define general habitat associations (e.g., whether a species prefers MES over GRASS)—not to identify particular patches as being of particularly high or low quality. When there was a significant difference in butterfly densities in two adjacent habitat types, the habitat with the higher density was identified as “preferred”, and the habitat with the lower density as “less-preferred”. Habitat pairs were identified as being “equally preferred” when differences in density were not significant. For the determination of “equally preferred”, we used a *P* value of 0.30 to minimize Type-II errors. However, when *P* values fell between 0.10 and 0.30, no predictions were generated because habitat preferences could not be clearly determined from our data. In order to generate predictions from our model in these cases, more field data on habitat preferences would be needed. The analyses used to assign habitat preferences are detailed in Appendix 2 (ESM).

Local nectar and host plants preferences (listed in Appendix 3 in ESM) were identified through a combination of efforts, including: (1) associations published in a local field guide (Bailowitz and Brock 1991); (2) conversations with James Brock, an area host plant expert; (3) our own nectaring and oviposition observations; (4) observations of eggs and caterpillars on candidate host plants made throughout our 3-year study. For each plot, the presence or

absence of each resource was recorded, and the overall proportion of plots containing each of the key resources was calculated for each habitat type within an area. We considered resource distribution to be complementary if either nectar or host plant resources were at least twice as likely to be encountered in the adjacent habitat. Otherwise, resources were listed as supplementary. This cut-off presented a reasonable break-point between cases where resources were similarly available on both sides and cases where resource distribution was starkly different (see Appendix 3 in *ESM* for details). For five species, we had only limited data on host plant distribution between some habitat pairs; in those cases, our determination of resource distribution was partially based on observations we made throughout the 3-year study. In these cases where data on resource use or distribution was limited, we identified confidence in our resource data as “low”; otherwise it was identified as “high”. Confidence in resource distribution was subsequently examined to determine its influence on how well the model performed.

Qualitative comparison of predictions to observations

Edge response predictions were compared qualitatively to observations by building a 3×3 contingency table (Table 1) that tallied the number of times observations did or did not match predictions (e.g., how often did we see a positive edge response when one was predicted, etc.). When the predicted edge response was observed, the outcome was called “correct”. Cases in which the model was incorrect were divided into two categories: “neutral” (a neutral result was observed where a positive or negative edge response had been predicted) or “wrong” (an unpredicted positive or negative edge response was observed) (Table 1). While both types of incorrect predictions indicate avenues for future model improvement, the approaches may be different for each. For example, some species are thought to be generally insensitive to edges (Wiens et al. 1985, Lidicker 1999) and identifying the prevalence of “neutral” responses may allow us to identify those species and the life history traits associated with edge insensitivity. In contrast, an unpredicted “wrong” response may be due to incomplete data on that species’ resources relative to the focal edge type or to the presence of a dynamic not incorporated in the current model construction. By separating incorrect outcomes into these two categories, we can separately explore the implications of each.

To gauge overall model performance, we determined if the number of “correct” outcomes was more frequent than expected by chance. To do this, we performed two goodness-of-fit tests. The first compared the observed distribution of outcomes in the 3×3 table (Table 1) to an independent distribution among rows (predictions) and

Table 1 Evaluation of model performance

Prediction	Observation		
	–	0	+
–	Correct	Neutral	Wrong
0	Wrong	Correct	Wrong
+	Wrong	Neutral	Correct

A 3×3 contingency table illustrates cases where the model is correct (the predicted edge response was observed), wrong (an unpredicted positive or negative response was observed), or neutral (a neutral response was observed when a positive or negative response was predicted)

columns (observations). Residuals, adjusted to cell totals (as per Agresti 1996), were then examined to determine if there were more “correct” observations than would be expected by chance. We refer to this test as the “Residuals Test”. We used Fisher’s Exact Test to determine if those residuals were significantly different from zero. A second goodness-of-fit test examined the subset of cases where positive or negative edge responses were predicted to determine how often observed responses were in the predicted direction. We refer to this as the “Direction Test”. We used a chi-square test to determine if observed responses were in the predicted direction more than 50% of the time (the proportion expected if results were randomly distributed). In addition, both the Residuals Test and the Direction Test were stratified by habitat type and species to allow an exploration of whether the model performed particularly well or poorly in particular habitats or for certain species.

Quantitative comparison of predictions to observations

Although our model does not make specific quantitative predictions about the strength of edge responses (for example, predicting that densities will be twice as high at the edge vs. the interior), we specifically predict stronger edge responses when there are stronger differences in habitat associations and/or complementary resources in adjoining habitats (Ries and Sisk 2004). We therefore examined the strength of the relationship between the magnitude of the differences between habitat types for each of our two predictor variables (habitat association and resource distribution) and the slope of the measured edge responses. Differences in habitat association were calculated by subtracting, separately for each species at each edge type in each year, the density in the focal habitat from the density in the adjacent habitat. To be included in this analysis, differences in habitat associations within years need not have been statistically significant (however, the species must have shown a significantly different association between the two habitat types across years). Using this approach, we were able to look at the entire spectrum of

responses—from strongly negative, to weak or absent, to strongly positive. A mixed-model regression, with species as the random component, was performed.

To explore the impact of complementary resource distribution, we calculated the mean slope of all edge responses for species in the following three categories: (1) those with no habitat associations and where resources in the adjacent patch are only supplementary (so no edge response is predicted); (2) those with no habitat association, but for which a complementary resource was concentrated in the adjacent patch (so a positive edge response is predicted); (3) those with no habitat association and complementary resources were restricted to the adjacent patch (so a stronger positive edge response is predicted). We performed a mixed-model ANOVA with slope as the fixed variable and species as the random variable on the three groups (supplementary, complementary-concentrated, complementary-restricted).

Results

Empirical edge responses

All 15 species showed at least one edge response for at least one of the 12 edge types over the 3 years of study (results for each species at each edge type over all 3 years are given in Appendix 4 in [ESM](#)). However, there was substantial variation in responses, both across species and among edge types. Of the 15 species studied, 12 showed positive, neutral, and negative edge responses at one or more of the different edges. Most observed responses were neutral, with positive or negative responses observed 21% of the time (32% if statistically marginal cases are excluded). Where a species showed more than one significant edge response across years at the same edge type, edge responses were in the same direction 93% of the time (highlighted in Appendix 4 in [ESM](#)).

Model predictions

An example of how we used data to generate—and then test—predictions is illustrated for one species (*Phoebis sennae*) at the edge between CW and GRASS habitats (Fig. 2a–d). The first step in generating predictions was to consider habitat preference. *Phoebis sennae* prefers GRASS habitat (Fig. 2a). Similar comparisons were made for all 15 species at all six habitat pairings. A significant habitat preference was found in 53 cases ($P < 0.10$), no habitat preference was found in 44 cases ($P > 0.30$), and no predictions were possible in the 25 remaining cases, where P values fell between 0.10 and 0.30 (see Appendix 2 in [ESM](#)). When habitat was either equally or more preferred, information on resource distribution (complementary or

supplementary) was necessary to make predictions. In the case of *P. sennae*, the host plant is confined to the CW habitat, while nectar sources are more equally distributed (Fig. 2b, c). This result means that their host plant represents a complementary resource when they are in a GRASS habitat, so we predict a positive edge response on both sides of the edge (Fig. 1). No information on resource distribution is necessary when habitat is less preferred (in those cases, edge responses are always predicted to be positive, see Fig. 1). Appendix 3 in [ESM](#) shows when resources were identified as complementary or supplementary, for cases where that information was necessary to make a prediction.

Comparing qualitative model predictions with field observations

We compared observed edge responses with model predictions for all cases where predictions were possible. As noted above, a positive edge response was predicted for *P. sennae* on both sides of the CW–GRASS habitat edge. Based on our data, we observed a positive response in the GRASS habitat (so a “correct” outcome), but a neutral response in the CW habitat (so a “neutral” outcome) (Fig. 2d). A tally of outcomes and the associated residuals are detailed in Table 2, both combined and stratified by habitat and species. For all habitats and species combined, the model was able to predict the observed edge response more often than expected by chance ($P = 0.01$), as indicated by the positive value for the adjusted residuals in the “correct” category for all habitat types combined (Fig. 3a). When the model was incorrect, it was 2.6-fold more likely that no response was observed when a positive or negative response was predicted, rather than observation of an unpredicted positive or negative (“wrong”) response (Fig. 3a). For cases where a significant edge response was observed, the Direction Test showed the responses were in the predicted direction 70% of the time for all habitats combined ($P < 0.001$, Fig. 3b).

We also applied the Residuals and Direction Tests stratified by habitat. In these cases, sample sizes were too low to test for statistical significance, but the stratified comparisons indicated whether model performance was particularly good or poor in certain habitat types. Model performance was best in the upland riparian zone (GRASS, MIX, MES) and lowest in the CW and DS habitats (Fig. 3a). Model performance was also highest in the same habitats for the Direction Test (Fig. 3b) and again lowest for CW, with observed responses in the predicted direction only 17% of the time (Fig. 3b). We explore this result in greater detail below; however, in order to examine the relationship between the magnitude of habitat and resource differences, on one hand, and the magnitude of edge responses on the

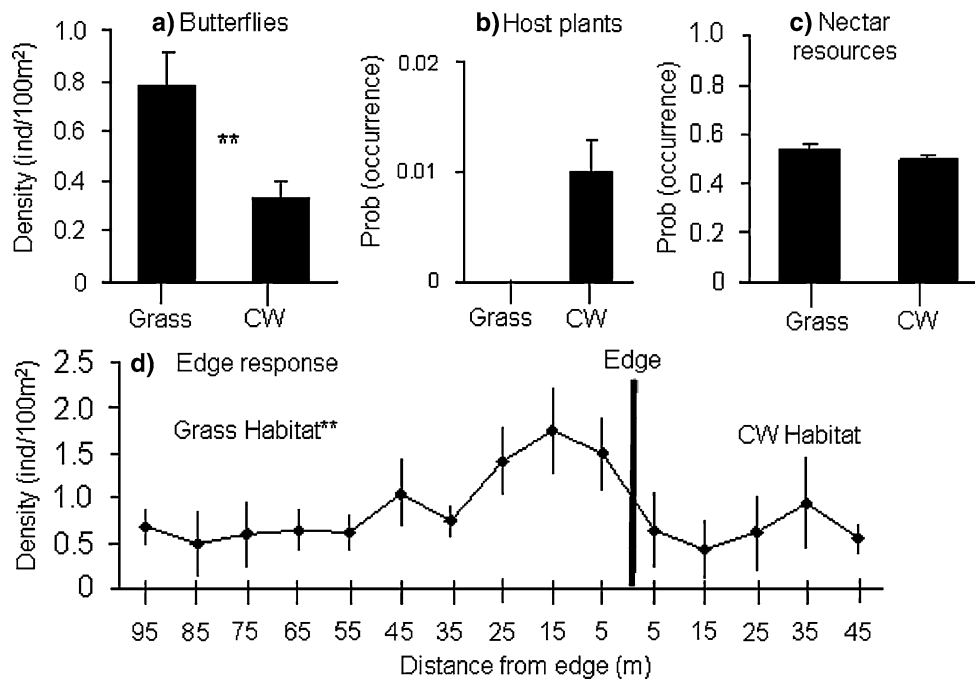


Fig. 2 An example of the evaluation of model performance for the edge responses of *Phoebis sennae* butterflies on either side of the Grasslands (GRASS)–Cottonwood (CW) habitat edge in Arizona, USA during 1999–2001. The observed distribution of butterflies (a), host plants (b), and nectar resources (c) suggest that *Phoebis sennae* prefers the GRASS habitat (a), but have complementary resources in the CW

zone (b). The model therefore predicts a positive response at both edges (see Fig. 1c). The densities of *P. sennae* across the GRASS–CW edge (d) show that the model correctly predicted the positive edge response observed in GRASS habitat ($P < 0.05$), but not the neutral response in the CW habitat. Means and standard errors are shown with significant differences (** $P < 0.05$) indicated

other, further evaluations omit results from the CW habitat. Given this caveat, nine of the 14 species had more “correct” outcomes than expected by chance (Table 2). Inspection of the data revealed no influence of confidence of resource distribution (“low” or “high”) on any outcomes (analysis not presented).

Comparing quantitative model predictions with field observations

There was a significant ($P < 0.0001$) positive relationship between the magnitude of the habitat preference and the measured slope in the edge model (Fig. 4). This result is consistent with the qualitative predictions of the model (that positive edge responses are expected in a less preferred habitat and negative edge responses are expected in a more preferred habitat—see Fig. 1). As the strength of habitat preferences increased, the magnitude of the slope of the edge responses also increased (Fig. 4). The results for complementary resource distribution were less clear. Only cases where complementary resources were entirely restricted to the adjacent habitat showed any trend towards positive edge responses ($P = 0.07$). In contrast, when complementary resources were available on both sides (although concentrated in the adjacent habitat), there was no trend towards positive responses at all ($P = 0.42$). Species show-

ing no habitat preference and supplementary resources were predicted to have no edge response, and indeed the mean edge response slope for this group was also zero ($P = 0.31$).

Discussion

Edge responses for several butterfly species at a wide range of edge types were, when observed, largely predictable and consistent. This result strongly supports our general model of edge effects, the only currently available model that allows specific edge response predictions to be made. The use of this model helps make sense of much of the variability observed in systems with multiple species and multiple edge types. The model performed significantly better than expected by chance (Fig. 3a) and was able to predict the correct direction of edge responses about 70% of the time for this diverse assemblage of riparian butterflies (Fig. 3b). Earlier reviews (Ries and Sisk 2004; Ries et al. 2004) showed that the model was also successful for birds, plants and mammals, predicting the correct direction of observed edge responses 83, 91, and 83% of the time, respectively. These combined results suggest that many edge responses can be understood by considering habitat associations and resource distribution, rebutting previous conclusions that

Table 2 Comparison of model predictions to field observations. Evaluations of overall model performance are illustrated in Fig. 3

Prediction:	–			0			+			Residuals ^c		
	Observation: ^a											
	–	0	+	–	0	+	–	0	+	C	N	W
Model performance: ^b	C	N	W	W	C	W	W	N	C	C	N	W
All habitats	19	36	5	8	44	9	13	55	22	7.0	–1.5	–5.5
Cottonwood	0	2	0	6	15	2	5	14	1	–1.8	1.1	0.5
Grass	6	12	4	0	1	1	2	8	8	3.0	–0.0	–3.1
Mix	10	18	0	0	9	3	2	6	3	4.9	–0.9	–3.9
Mesquite	3	4	0	1	13	1	0	1	0	3.3	–1.1	–2.3
Desert scrub	0	0	1	1	6	2	4	26	10	–0.5	–1.1	1.5
Species summaries (cottonwood excluded)												
All species	19	34	5	2	29	7	8	41	21	8.6	–1.7	–6.9
<i>Battus philenor</i>	0	5	0	0	0	0	3	5	1	–0.7	0	0.7
<i>Brephidium exilis</i>	2	4	0	0	0	0	0	0	1	3.3	0	–3.3
<i>Chlosyne lacinia</i>	0	7	1	0	0	1	0	2	1	–1.4	1.0	0.4
<i>Colias cesonia</i>	1	2	0	1	6	0	0	1	0	1.2	–0.3	–0.9
<i>Colias eurytheme</i>	2	3	0	0	5	0	0	3	1	5.1	–1.4	–3.7
<i>Danaus gilippus</i>	1	4	0	0	1	0	0	3	0	1.3	–0.2	–1.1
<i>Euptoieta claudia</i>	4	0	0	1	2	0	0	0	0	3.9	–1.9	–1.9
<i>Eurema nicippe</i>	0	0	0	0	1	2	1	5	4	–1.3	0.5	0.8
<i>Eurema proterpia</i>	0	0	0	0	5	0	1	1	2	4.2	–2.4	–1.8
<i>Libytheana carinenta</i>	0	1	1	0	3	3	2	9	0	–4.3	0.9	3.4
<i>Nathalis iole</i>	0	0	2	0	5	0	0	1	0	1.5	–2.2	0.7
<i>Pholisora catullus</i>	0	0	0	0	0	1	1	2	2	–1.9	0.8	1.1
<i>Phoebis sennae</i>	1	2	0	0	1	0	0	3	9	6.1	–0.6	–5.4
<i>Pontia protodice</i> ^d	1	0	0	0	0	0	0	0	0			
<i>Pyrgus albescens</i>	7	6	1	0	0	0	0	6	0	1.5	0	–1.5

^a A tally of observed edge responses separated by habitat type and species where negative (–), neutral (0), and positive (+) edge response predictions were made

^b Model performance is separated into cases where a prediction was correct (C), an unpredicted neutral response was observed (N), and cases where an unpredicted “wrong” positive or negative response was observed (W)

^c Adjusted residuals showing the relative occurrence of each outcome are also shown (positive residuals indicate an outcome happened more frequently than expected by chance and vice-versa)

^d Residuals could not be calculated due to a lack of data

edge effects are idiosyncratic and difficult to understand or predict. In these studies, the majority of negative edge responses can be attributed to species avoiding edges with less-preferred habitat. Positive edge responses can be largely explained by increased densities near a preferred, adjacent habitat, or by proximity to resources restricted to adjacent patches.

We found a significant relationship between the strength of the habitat association and the strength of the edge response. Our model predicts that species should decrease in abundance as they approach edges with less preferred habitat, but may “spill over” into the adjacent habitat, causing a positive edge response (Fig. 1a). In such cases, the magnitude of the difference in habitat preference should be reflected in the strength of the edge response (Sisk and Ries 2004), and indeed this was true for butterflies in this study (Fig. 4). These results support the use of habitat associations as a predictor in the model and suggest that the strength of habitat preferences could be used to infer the magnitude of edge responses.

The relationship between complementary resource distribution and the strength of the edge response was not so clear. In fact, complementary resource distribution was not

a useful predictor except in situations where the complementary resources were entirely restricted to the adjacent habitat. Although complementary resource distributions (also known as cross-boundary subsidies) have been suggested as mechanisms underlying edge responses (Fagan et al. 1999), no empirical work has attempted to quantify how divided the resources must be to have an impact on edge responses. This study suggests that, at least for butterflies, the separation of resources must be very stark in order to trigger positive edge responses. When conducting future tests of the model, researchers should consider being more conservative than we were in defining what constitutes a complementary resource.

In cases where model predictions were incorrect, it was more than twice as likely that no response was observed where a positive or negative response had been predicted, as opposed to cases where unpredicted positive or negative edge responses were observed. This general trend was observed in past tests of the model for bird, mammal, and plant taxa (Ries et al. 2004), suggesting that the model is prone to over-predicting directional edge responses but that it is quite successful in predicting the nature of directional responses (positive or negative) when they occur. This

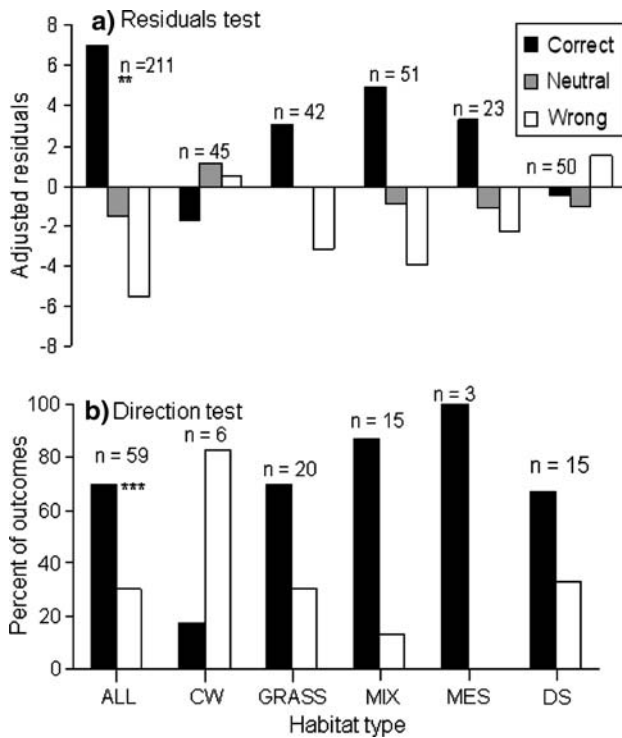


Fig. 3 Evaluation of model performance using the Residuals Test (a) and Direction Test (b) for 15 butterfly species at 12 edge types within five different habitats. Responses are pooled for all species among habitats (ALL) and stratified by habitat type [CW, GRASS, mesquite-dominated forests (MES), grassland-mesquite mixes (MIX), surrounding desert shrub (DS)]. The residual test indicates whether the correct, neutral, or wrong responses (see Table 1) were observed more (positive values) or less (negative values) often than expected by chance. The P value is based on Fisher’s Exact Test. The Direction Test (b) indicates the percentage of times the direction of observed edge responses was correctly or wrongly predicted. The P value is based on a χ^2 test that compares observed percentages to an expected value for random response (50%). ** $P < 0.05$, *** $P < 0.01$. Statistical tests were only carried out for the ALL category due to low sample sizes when stratified by habitat type

result suggests that model improvement may hinge on an improved understanding of the ecological factors that lead to edge insensitivity.

Insensitivity to edges could be caused by physical factors, such as edge orientation and edge contrast (Ries et al. 2004), or species-specific factors, such as body size or mobility (Wiens et al. 1985). Despite the popularity of classifying certain species as edge sensitive or insensitive, it is currently impossible to say which species are truly insensitive to the presence of habitat edges (Ries et al. 2004). Only species that consistently fail to show edge responses where they are predicted to occur should be considered edge-insensitive. Using our model, these outcomes are represented by the two “neutral” cells in Table 1, in contrast to the center cell, where a neutral result is both predicted and observed. However, any model that uses a biological basis to predict when edge responses should occur could be used

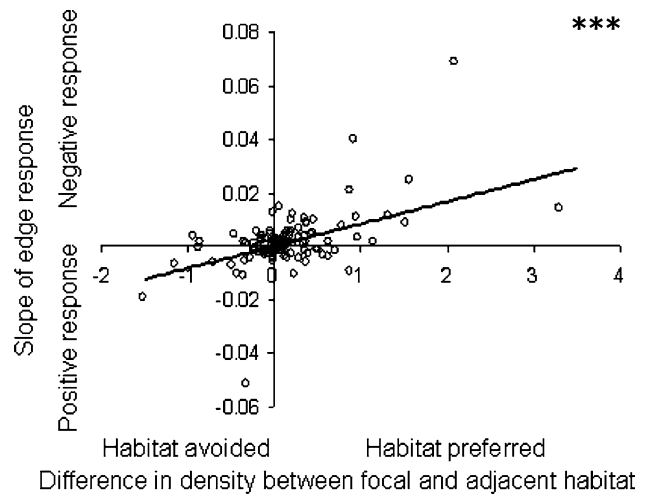


Fig. 4 The relationship between differences in individual density from focal to adjacent habitats (from strongly preferred to strongly avoided), and the slope of the edge response for species with supplementary distribution. All responses were included, regardless of whether the habitat associations for that year where significant or not, so that a full spectrum could be observed. Note that a positive slope for an edge response indicates a negative edge response, and vice-versa. *** $P < 0.0001$, value based on a mixed-model regression

as a framework for identifying edge-insensitive species. Despite the current difficulty in classifying species as edge sensitive or insensitive, to do so would represent a significant advance in the study of edge effects. If common traits underlying edge insensitivity could be found, then model predictions could be significantly enhanced. For instance, Brand (2004) found that the likelihood of birds exhibiting edge responses was associated with body size, incubation period, and nest location and type.

Although observed edge responses were rarely in the opposite direction of those predicted (i.e., there were few “wrong” predictions), it is important to examine these results and determine their potential causes. The model did not do equally well in all habitats (Fig. 3a) or for all species (Table 2). As noted above, the model performed poorly in the CW habitat, with observed responses in the predicted direction only 17% of the time (Fig. 3b). One factor that clearly distinguished the CW from the upland habitat was its internal heterogeneity, which has been suggested as a factor influencing edge responses in birds (Noss 1991). Heterogeneity was addressed in the upland riparian habitat by separating it into three classes, based on canopy structure. However, we elected to consider the CW zone as a single habitat type despite its highly heterogeneous nature. In retrospect, it may have been more appropriate to separate the CW habitat into several classes based on canopy cover, similar to what was done in the upland area. This finding suggests that the initial way that habitat patches are defined within a landscape can influence the definition of edges and our ability to predict effects. Indeed, model performance is

profoundly influenced by a researcher's ability to define landscape elements in a way that is meaningful for the focal species. Model performance was also weak in the DS habitat (Fig. 3a) although observed edge responses were generally in the predicted direction (Fig. 3b). Unlike the CW habitat, the DS habitat has a simple structure of widely dispersed low shrubs, so internal heterogeneity is not a likely explanation. One possible factor is the low overall density of butterflies in this habitat type, which may make gradients more difficult to detect.

Model performance differed among species, with the model performing well (based on observing more "correct" responses than expected by chance) for nine of the 14 species (Table 2). For the remaining five species it is possible there was a gap in our knowledge about the primary local host or nectar plants. Alternatively, there may have been other resources that were driving those species' distribution patterns that were not considered here, such as the availability of roosting sites, minerals, or water (Dennis 2003). More detailed ecological studies of those species' critical resources and their distribution may help resolve why model performance was poor for these species. Using this modeling framework offers an opportunity to focus future studies on species whose edge responses are not easily explained and where more complex ecological interactions may be occurring (see Ries et al. 2004 for a discussion of future research directions).

A knowledge of local resources is particularly crucial for identifying complementary resource distribution. Our results suggest that identifying complementary resources only improved model predictions when resources were entirely restricted to the adjacent habitat, and even in those cases there was substantial variation in results. Although this mechanism is well supported in the edge literature (Fagan et al. 1999; Ries et al. 2004), the best studied examples involve cases where resources are almost completely partitioned between adjacent habitats (for example, brown-headed cowbirds are well-known edge exploiters who parasitize the nests of forest birds but forage in adjacent livestock pastures). Further research is needed to determine how the degree of segregation of complementary resources influences edge responses. This research will affect how conservative one should be when defining a resource as complementary.

Despite the difficulty we had effectively using complementary resource distribution to predict positive edge responses, it is worth noting that the species which we identified as having no difference in habitat preference between adjacent habitat pairs showed only significant positive edge responses or no edge response, never a negative edge response. Under these circumstances, the model only predicts positive or neutral edge responses with the critical difference in the prediction being due to whether comple-

mentary resources are present or not (Fig. 1c, d). The model never predicts a negative response under any circumstances, and indeed we never observed negative responses in the field. The congruence between model and empirical results suggests that the biological basis of the model construction is valid, while the variability in results suggests that we did not always do a good job of identifying complementary resources in this study system. The unpredicted positive responses seen at edges between habitats where species showed that no clear preference could have been due to the presence of unidentified complementary resources. Conversely, the many neutral edge responses we observed in cases where we predicted positive responses may indicate that the complementary resources we identified were actually supplementary or unimportant. Clearly, the correct identification of resources and determinations about their spatial distribution represent a challenging component of the model. While habitat associations are often known and generally consistent among regions, local resource use—for butterflies and other animal taxa—can vary and may require a more detailed knowledge of the biology of focal species.

Conclusions

Our study suggests that edge responses are more predictable and consistent than is commonly believed. At first glance, the 267 edge responses we report in Appendix 4 (in ESM) for 15 butterfly species at 12 edge types over 3 years may seem like an intractable list of conflicting results that are not readily interpretable; however, when viewed within the conceptual framework of our predictive edge effects model, many of the results make ecological sense. Negative edge responses can be largely attributed to the avoidance of a non-preferred habitat, while positive responses are due to increased access to resources near the edge of a preferred habitat or to particular complementary resources that are confined to the adjacent patch. Although we detected many more neutral edge results than predicted, when multiple edge responses were observed for the same species at the same edge type, they were remarkably consistent. Our results highlight the need for a better understanding of neutral edge responses, and they suggest future avenues of research that could identify factors, including landscape variables and species-level traits, that may underlie edge insensitivity. Our modeling framework makes it tractable to explore factors, both extrinsic and intrinsic to the study species, which are associated with the likelihood of observing a predicted edge response, allowing a more focused exploration of mechanisms driving edge dynamics.

Our model tests revealed that habitat associations, the most widely available type of ecological information, are

consistent and effective predictors of edge responses. These tests also indicated that complementary resource distribution is an important factor influencing response, but that obtaining this information may be more challenging than expected and that resource separation may have to be quite stark before its influence on butterfly distributions is detectable. Although the application of our model to riparian butterflies involved consideration of host and nectar plant resources, the model could be applied to a wide variety of situations where habitat associations and general resource distributions are known. Previous tests of the model based on literature reviews showed that it was successful in predicting responses for birds (Ries and Sisk 2004), mammals, and plants (Ries et al. 2004), suggesting that this model has general applicability. Despite decades of study and hundreds of published reports, a coherent, general framework for understanding edge responses has remained elusive because most studies were largely descriptive, with no underlying conceptual model to put variable observations into a theoretical context (Murcia 1995; Cadenasso et al. 2003; Ries et al. 2004; Ries and Sisk 2004; Ewers and Didham 2005). This study represents an important step forward in placing edge responses into a predictive framework, and develops a blueprint for future studies by suggesting which factors should be taken into account when examining variation in edge responses.

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