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A PREDICTIVE MODEL OF EDGE EFFECTS

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Abstract. Edge effects are among the most extensively studied ecological phenomena, yet we lack a general, predictive framework to understand the patterns and variability observed. We present a conceptual model, based on resource distribution, that predicts whether organismal abundances near edges are expected to increase, decrease, or remain unchanged for any species at any edge type. Predictions are based on whether resources are found predominantly in one habitat (decreased abundance in preferred habitat, increase in non-preferred), divided between habitats (predicts an increase near both edges), spread equally among habitats (predicts a neutral edge response), or concentrated along the edge (increase). There are several implications of this model that can explain much of the variability reported in the edge literature. For instance, our model predicts that a species may show positive, negative, *and* neutral responses, depending on the edge type encountered, which explains some intraspecific variability observed in the literature. In addition, any predictable change in resource use (for example, by region or season) may explain temporal or spatial variability in responses even for the same species at the same edge type. We offer a preliminary test of our model by making predictions for 52 bird species from three published studies of abundance responses near forest edges. Predictions are based solely on general information about each species' habitat associations and resource use. Our model correctly predicted the direction of 25 out of 29 observed edge responses, although it tended to under-predict increases and over-predict decreases. This model is important because it helps make sense of a largely descriptive literature and allows future studies to be carried out under a predictive framework.

Key words: *ecological boundary; ecotone; edge responses; habitat edge; predictive model; resource distribution.*

INTRODUCTION

Changes in species' distributions near habitat edges are among the most extensively studied phenomena in ecology because edge responses are a key component to understanding the influence of landscape structure on habitat quality. Edges can be defined as the boundary between patches with differing qualities; thus, the identification of edges will depend on how researchers define patches (Strayer et al. 2003). Increases in avian richness and abundance at forest edges have been noted for several decades (Lay 1938, Johnston 1947) and led to early claims that edge habitat was beneficial for wildlife. However, the discovery that many songbirds experience higher predation and parasitism rates near forest edges (Gates and Gysel 1978, Chasko and Gates 1982) led to a fundamental shift from a positive to

negative view of edge effects and brought critical attention to the issue of habitat fragmentation (Brittingham and Temple 1983). Since these seminal reports, there have been hundreds of studies describing edge responses for many taxa, with much of the focus remaining on forest edges (for reviews, see Paton 1994, Murcia 1995, Risser 1995, McCollin 1998, Lidiker 1999, Lahti 2001, Chalfoun et al. 2002, Sisk and Battin 2002).

Despite this extensive interest, the field has remained largely descriptive, with no underlying framework to make sense of the variability reported, giving the impression that general patterns of edge responses are elusive (Murcia 1995, Sisk and Battin 2002). Most edge response studies are observational, have low replication, do not control for factors known to interact with edge dynamics (Murcia 1995), and are carried out with no a priori predictions, so it is difficult to interpret the meaning of the patterns and variability reported in a rigorous fashion. However, the importance of this topic

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to ecology and its applications to conservation call for a synthesis of proposed mechanisms into a conceptual model that can make sense of previously reported patterns and allow future studies to be conducted within a theoretical framework. This will lead to a greater understanding of the factors that influence edge responses and allow for predictions, even for poorly studied species in a variety of landscapes. Therefore, our objectives were to (1) summarize the major patterns and proposed mechanisms reported in the literature; (2) present a conceptual model based on those mechanisms that predicts edge abundance responses for any species at any edge type; (3) explore the variability in the literature on edges and its potential underlying causes within the framework of our model; and (4) offer a preliminary test of our model by determining how well it predicts the nature of edge responses for over 50 bird species, as reported in three published studies.

EDGE RESPONSE PATTERNS AND MECHANISMS

Results from dozens of field studies confirm that many species respond to habitat edges in a variety of ways. Species may show increases, decreases, or no change in abundance, depending on the specific edge type encountered. These changes may be due to abiotic or biotic changes in the environment (Murcia 1995) caused by ecological flows across edges (Cadenasso et al. 2003), changes in interspecific interactions (Fagan et al. 1999), or a combination of these and other factors. In the avian literature, increased abundances near edges (also called positive edge responses) are generally more common than decreases or negative edge responses (Villard 1998, Sisk and Battin 2002). There currently is insufficient evidence to determine whether this pattern extends to other taxa. Neutral edge responses (no change in abundance near the edge) are probably underreported due to publishing bias and have received little attention, despite their potential importance in understanding general underlying mechanisms.

Three mechanisms have been cited most commonly to explain increased abundances near edges: (1) spillover, (2) edges as enhanced habitat, and (3) complementary resource distribution. Increased abundances near edges have often been attributed simply to spillover or "mass effects" (Shmida and Wilson 1985), which occur when individuals disperse into non-habitat by crossing the boundary from their preferred habitat. This results in elevated abundances near edges (within non-habitat), and is due solely to proximity and the fact that organisms are not likely to penetrate very deeply into a patch of non-habitat. In addition, the quality of the edge in non-habitat patches may also be enhanced by its adjacency to higher quality habitat, which also may lead to increased abundances near edges within non-habitat. For instance, forest habitat near open edges tends to be more similar to the bordering open habitat (hotter, drier, and with more light) compared to the forest interior (Chen et al. 1999). Conversely, open

habitat near forest edges experiences increased shading, resulting in lower temperatures and higher humidity (Cadenasso et al. 1997). In both cases, the environment near the edge is likely to be more hospitable to organisms adapted to conditions of the adjacent patch interiors.

Another way edges may be enhanced is by containing resources absent or rare in both adjoining patches. This concentration of resources near edges may support increased abundances of species that rely on those resources. One common example is shrub-dependent birds being attracted to forest edges that have developed a shrub layer rare or absent in either bordering habitat (Mills et al. 1991, Berg and Part 1994). In this case, if habitats were mapped finely enough, the edge might be identified as a unique habitat type and the observed response would not be considered a true "edge effect." However, most vegetation maps cannot capture such fine distinctions in habitat, and in many cases the increase in resource availability near edges may not constitute a unique vegetation class. This may be especially true when an organism that is responding to the presence of an edge provides the resource base for another organism, which may then also show an edge effect. Spotted Owls (*Strix occidentalis*) present a good example of this phenomenon. When their prey base is dominated by wood rats (*Neotoma* spp.), a species that shows an increased abundance near edges, the owls also show an increase near edges. On the other hand, when their prey base is dominated by flying squirrels (*Glaucomys sabrinus*), a species that shows no edge effect, the owl also shows no response to edges (Zabel et al. 1995). Another example is the butterfly *Lopinga achine*, an edge-associated species whose host plant is found in highest concentrations near forest edges, while shading from shrubs at these edges provides the most suitable microclimatic conditions for larval growth (Bergman 1999). These types of cascading edge effects may be very common.

The third mechanism, complementary resource distribution, occurs when two bordering patches contain different resources, and being at the edge allows the most convenient access to both (Dunning et al. 1992, McCollin 1998, Fagan et al. 1999). In this case, resources available only in one patch "complement" the resources available in the adjacent one. In complementary resource distribution, no particular resource is concentrated at the edge, but the juxtaposition of resources results in higher quality habitat at edges by offering greater access. One classic example is the Brown-headed Cowbird (*Moluthrus ater*), which forages in open pastures but parasitizes forest-dwelling songbirds (Brittingham and Temple 1983). Many other taxa that are associated with forest edges are assumed to be foraging in the open, yet obtaining other resources from the forest, including deer (Alverson et al. 1988) and numerous bird species (Gates and Gysel 1978, McCollin 1998). In contrast, we refer to resource dis-

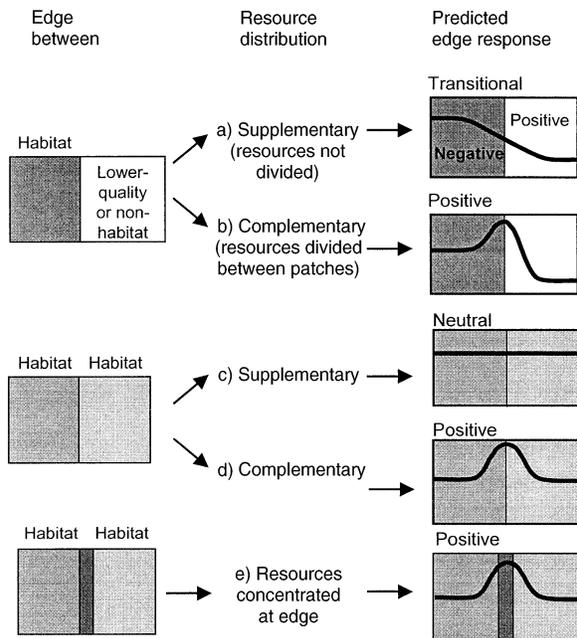


FIG. 1. A predictive model of edge effects. This general model predicts changes in population abundance near habitat edges based on resource distribution. When (a) resources are concentrated in one patch and those in the lower quality patch are supplementary, then a transitional edge response is predicted. However, when (b) resources in the lower quality patch are complementary (different), then being on the edge allows increased access and a positive response is predicted in both patches. When resource availability is relatively equal between patches, a neutral response is predicted when (c) resources are supplementary, and a positive one when (d) resources are complementary. When (e) resources are concentrated along the edge, a positive response is once again predicted.

tribution as “supplementary” when two adjacent patches both contain resources, but there are no resources in one patch not also available in the other. In that case, being near the edge offers no benefit with respect to access to resources.

Edge avoidance (decreased abundance near edges) is most commonly reported for habitat-specific species, usually forest “interior” species. Examples include the Ovenbird, *Seiurus aurocapillus* (Burke and Nol 1998), the Red-eyed Vireo, *Vireo olivaceus* (King et al. 1997), the red-backed vole, *Clethrionomys gapperi* (Mills 1995), and the plant *Trillium ovatum* (Jules 1998). These species are generally assumed to be avoiding changes in the environment near edges that make them hostile to species adapted to interior conditions. This has been well documented for the Ovenbird (*S. aurocapillus*) where the hotter, drier conditions near forest edges are associated with lower densities of their prey items (Burke and Nol 1998). Species associated with open habitat have also shown decreased abundances near forest edges, including butterflies (Haddad and Baum 1999) and grassland birds (O’Leary and Nyberg

2000, Fletcher and Koford 2003). Although these species may avoid less-preferred habitat, they may still spill over into bordering patches. Therefore, when a patch of suitable habitat borders a patch of lower quality habitat, a gradual transition from the highest densities in the interior of the preferred habitat patch to the lowest densities in the interior of the adjoining patch is expected (Sisk and Margules 1993, Lidiker 1999). This transition in abundance is assumed to reflect a gradient in habitat quality that may ultimately be based on resource availability and abiotic factors such as microclimatic shifts across the edge zone (Murcia 1995). All of the mechanisms presented relate either to the availability or proximity of resources, and led us to develop a conceptual model that uses resource distribution as a basis for predicting general edge responses.

A RESOURCE-BASED MODEL OF EDGE EFFECTS

For this model, we assume a simple landscape composed of two adjacent patches. Habitat quality in each patch is determined by the relative amount of available resources, so “lower quality” habitat refers to a patch that has fewer resources than the adjacent patch. When no resources are available in a patch, it is defined as non-habitat. Resources may include provisions such as food or nest sites, service-providers such as pollinators and seed dispersers, or abiotic resources such as light. Density levels in patch interiors are assumed to reflect relative differences in habitat quality, so low-quality and non-habitat patches will have lower or zero densities in those patch interiors. This model is therefore a patch-based model with edges defined as the boundaries between patches. While patch definition may vary among researchers, the fact that patch *quality* is defined here by the relative amount of resources means that our model should be broadly applicable even when landscapes are classified under different schemes. Our model predicts the expected change in abundance near edges, based on patterns of resource distribution between those two patches, as illustrated in Fig. 1.

When habitat borders lower quality or non-habitat and resources in the lower quality habitat are supplementary (so offer nothing not already found in the higher quality patch), then individuals are predicted to show a transitional response across the edge. This transitional response is characterized by a gradual decrease in density from a maximum in the interior of the higher quality habitat patch to a minimum in the interior of the lower quality or non-habitat patch (Fig. 1a). It is important to note that most empirical studies report responses within only one patch type (on one side of the edge), so a transitional response will appear to be either positive or negative, depending upon the reference point of the observer (see responses on either side of the edge in Fig. 1a). In contrast, when resources in the lower quality patch are complementary (offer something not found in the higher quality patch), then an

increase in abundance is predicted on both sides of the edge (Fig. 1b). This is because, in both patches, being near the edge allows access to additional resources only available in the adjacent patch.

For situations in which both patches provide relatively equal resource availability, responses are again expected to vary depending on how those resources are distributed. When resources are supplementary (not divided) between patches, no edge response is predicted (Fig. 1c). However, when resources are complementary (divided between patches), then being near the edge offers increased access to both sets of resources, so the species in question is again predicted to increase in abundance near edges (Fig. 1d). Predictions of positive abundance responses, based on complementary resource distribution (Fig. 1b, d), are most applicable to mobile organisms because they can most easily gain access to resources in two patches. However, some sessile organisms could also demonstrate such responses if advantages at the edge could be realized via, for example, root or branch growth. Finally, when resources are concentrated along the edge, then a positive edge response is again predicted (Fig. 1e). In this case, the concentration of resources along the edge distinguishes this prediction from those resulting from adjacent resources that may be distributed evenly within each patch (Fig. 1b, d).

VARIABILITY EXPLAINED BY THE MODEL

By synthesizing many of the mechanisms that have been proposed in the edge literature into a single conceptual framework (Fig. 1), we suggest that many of the patterns and much of the variability reported in the edge literature may be explained. For instance, this model predicts that all species may show positive, negative, and neutral edge responses, depending on the specific edge type encountered. This may explain reports of variable edge responses for the same species at different edge types (Murcia 1995, Lidiker 1999). Thus, the claim that certain species or groups are intrinsically edge avoiding (such as "forest interior" species) or edge exploiting (such as predators), may be an artifact of a focus on a single edge type (edges between forest and open patches). This may also explain the lack of congruence between edge responses and area sensitivity that has been noted in some studies (Villard 1998) because patches may be surrounded by a variety of different habitat types; although in general edge responses do correlate with changes in density found in different patch sizes (Bender et al. 1998, George and Brand 2002). As future field studies target different taxa and more edge types, we expect that most species will show a variety of edge responses, although there may be groups of species that are particularly insensitive to edges.

Another implication of this model is that changes in the use or distribution of resources may lead to changes in edge responses, even for the same species at the

same edge type. When these changes are predictable, more refined edge response predictions are possible. For example, avian edge responses have been shown to vary between seasons (Noss 1991, Hansson 1994), and this may be due to predictable changes in resource use throughout the year. Many birds are known to show different habitat associations during winter and breeding seasons (which is intuitive based on the fact that nesting resources are not needed during the nonbreeding season) and in those cases, our model will predict different edge responses during summer and winter, even at the same edge type. Likewise, regional variation in edge responses has been suggested for birds in the eastern vs. western U.S. (Sisk and Battin 2002). While this is difficult to test due to a paucity of studies in the west (Sisk and Battin 2002), such differences would be predicted by our model for any species showing regional differences in resource use.

One consequence of conducting research under this model framework is that characterization and comparison of edge responses requires investigators to account for habitat quality on both sides of the edge in their study design. Our model assumes that the relative availability of resources between patches is one of the main drivers of edge responses (Fig. 1). While a general classification of habitat, such as "forest" or "open," may often be a good proxy for resource availability, that need not be the case. Many published studies include different habitat types under a single, broad classification such as "open," pooling, for example, grassland, crops, roads, or development, all of which may present very different resource availability for different species. When using general vegetation classifications to represent habitats (a common practice that is probably the most sensible approach in most cases), it is necessary to know to what extent resource availability is associated with each habitat class. Unfortunately, this information is not often provided in the literature, hindering attempts to understand variability in edge responses reported in many studies. We suggest that future edge studies include information on relative habitat quality and resource distribution on *both sides of the edge*. Only when that information is available are a priori predictions possible.

VARIABILITY NOT EXPLAINED BY THE MODEL

Despite the potential for our model to explain much of the inter- and intraspecific variability that has been reported in the literature, it is clear that even when factors such as habitat quality, resource distribution, and seasonal or regional variation in resource use are controlled for, some variability will remain. However, we suggest that unexplained variability is largely restricted to finding both a consistent unidirectional edge response (either positive *or* negative) and neutral responses. For instance, Sisk and Battin (2002) reviewed edge responses for 12 bird species whose results were reported in multiple studies, all at forest edges and all

located in the eastern U.S. No species showed both positive *and* negative responses, but most were reported to show neutral responses in some studies, as well as significant, unidirectional responses in others. For instance, the Ovenbird (*S. aurocapillus*) showed negative responses in two studies, with two additional studies reporting neutral responses. Similarly, the Red-eyed Vireo (*V. olivaceus*) had negative responses reported in three studies and a neutral response reported once.

One reason for this type of intraspecific variability is that there are several ecological factors that are known to influence the pattern of resource distribution relative to edges, as well as a species' response to that pattern. As these different ecological factors interact, realized edge responses will range along a continuum from strong to weak, and in some cases the effects may disappear altogether. Although there are likely several ecological factors that interact to change the strength of a species' edge response, those that have received the most attention are edge orientation and edge contrast (Murcia 1995). Edge orientation has been most rigorously explored within the plant literature. Several studies have shown how the directional orientation of the edge within the landscape may influence both the strength and depth of penetration of edge effects, but not the direction of the response (Wales 1972, Ranney et al. 1981, Palik and Murphy 1990, Fraver 1994). Edge contrast describes the degree to which bordering patches differ structurally from each other. Unfortunately, most studies have not controlled for habitat quality on both sides of the edge while varying edge contrast, making it difficult to separate the influence of edge contrast from habitat quality. However, Fletcher and Koford (2003) showed that the magnitude of negative edge responses for a grassland bird was stronger at forest (high-contrast) compared to agricultural (low-contrast) edges, even though both constituted equally poor habitat. Landscape composition has also been shown to influence edge responses, with more highly fragmented landscapes showing stronger edge effects in some situations (Donovan et al. 1997) and weaker in others (Kremsater and Bunnell 1992). Another factor suggested to impact the magnitude of edge responses is internal patch heterogeneity (Noss 1991), and there are likely other factors that underlie the variable strength of some edge responses. Identifying these factors and determining how they predictably interact with resource distribution will allow for additional variation to be accounted for.

Another factor that may explain some unpredicted neutral edge responses is that certain species may be intrinsically less sensitive to the presence of habitat edges. However, there is currently little evidence to suggest that any species is particularly edge sensitive or insensitive, although Brand (2004) found that birds with smaller body sizes are less likely to show edge responses. Based on our model, all species are expected

to show positive, neutral, and negative edge responses depending on the edge type encountered. Therefore, to truly gauge "intrinsic" edge sensitivity, it is necessary to determine whether there are certain species or groups of species that either consistently show edge responses where they are predicted (edge-sensitive species) or *never* show edge responses, regardless of predictions (edge-insensitive species). This is currently difficult, because most studies have taken place at a single edge type (forest edges), and have not been carried out in a way that allows the separation of neutral responses into those that are predicted and those that are not. Only species that fail to show edge responses where predicted should be considered edge insensitive. However, there are reasons to suspect that certain species or groups may be differentially sensitive to edges, and several authors have suggested that specific life-history or ecological traits should be associated with this sensitivity, including body size, mobility, and defenses against predation (Wiens et al. 1985, Lidiker 1999). Other factors may include the scale at which organisms perceive the landscape or the cues they use to assess habitat quality. By using our model to separate neutral responses into those that are predicted and those that are not, it will be possible to determine if edge-insensitive species truly exist. If they do, it would be useful to determine if there are life-history or ecological traits that are predictably associated with intrinsic insensitivity to edges.

Ultimately, one of the difficulties of grappling with the underlying causes of variation in the nature and strength of edge responses is the limitation of many field studies. Most empirical studies of edge effects have low site replication and limited statistical power (Murcia 1995) and are unlikely to detect any but the strongest patterns. Therefore, it is difficult to determine if reported neutral edge responses are actually describing situations where a species is distributed evenly across an edge gradient (a truly neutral response) or if it is due to a lack of power to detect responses which may, in fact, be operative. Nevertheless, it is clear that there are many potential causes of the neutral responses that underlie much of the variability reported in the edge literature. Therefore, observing a *neutral* response when a positive or negative one is predicted may not indicate factors operating that conflict with the underlying framework of our model. Instead, the separation of predicted from unpredicted neutral responses should assist in future model development through the identification of the factors that underlie this variability (assuming a study had sufficient power to detect edge responses).

In contrast, we consider the observation of a significant response that was *not* predicted (for example, observing a positive response when a negative one was predicted or observing a positive or negative response when a neutral one was predicted) to be indicative of an incomplete knowledge of the distribution of critical

resources for the focal organism, which may have led to a spurious prediction, or the operation of a dynamic not captured by our model. For instance, some mammals have been shown to avoid edges to escape predation (Bowers and Dooley 1993, Jacob and Brown 2000), although we found no evidence of this for birds. There are also examples of interspecific competition driving edge responses that may not be predicted by our model (Suarez et al. 1998, Piper and Catterall 2003). In these cases, unpredicted responses may be used to identify situations where more complex species interactions are occurring.

A PRELIMINARY TEST OF THE MODEL

Rigorous testing of this model will involve determining the distribution of critical resources throughout the landscape for each species of interest, predicting edge responses based on that information, and collecting independent verification data to test predictions. Such detailed data on habitat quality are not usually reported in the edge literature, and obtaining them will require directed field efforts, which we suggest should become standard information reported in future edge studies. However, habitat associations and general resource use are well described for some taxa, particularly birds, and it is possible to apply the model absent local information on resource use and distribution, although predictions are likely to be affected by the relative coarseness of this information. In order to perform a preliminary test of our model, we made predictions for bird species whose edge-abundance responses had been reported in the recent literature. We then compared model predictions with observed responses to determine how well our model performed. We focused on North American birds because habitat associations are well described for most species. We limited our search to studies of multiple species at abrupt edges between forest and open habitats (because habitat associations are well described relative to both of those habitat types). In order to allow the most robust comparisons of predicted and actual responses, we selected studies where quantitative data on edge responses were presented, with statistics, for multiple species. We restricted our search to studies of multiple species to avoid publication biases that may lead studies to remain unpublished if no significant effect was found, an outcome that is most likely for single-species studies. In addition, we required at least three replicate sets of sampling points to increase the likelihood that edge responses, if present, were detected.

Three edge response studies met our criteria. Germaine et al. (1997) studied edge effects at small openings (0.4 ha) created by timber cuts in a hardwood forest in Vermont. These cuts had >95% of trees removed and contained few shrubs (Germaine et al. 1997). Five independent study areas were established, with surveys being conducted within patch cuts, and inside the forest at three distance classes (50, 100, and

200 m) from forest edges. June surveys were conducted in 1991 and 1992, and data on the edge responses of 25 species were presented. Sisk et al. (1997) reported edge responses for 26 birds at oak woodland–grassland edges in central, coastal California (detailed statistics were reported in Sisk 1992). Four transects were surveyed during the 1988 and 1989 breeding season, with plots placed at the edge, 100, and 200 m into the oak woodland and grassland habitats. Brand and George (2001) studied edge effects of 14 species within redwood forest patches bordered by open habitat, including flood plains, prairies, and human-altered habitat including developments, roads, and power line corridors. They established 12 rectangular plots extending 400 m into the forest (no surveys were conducted in open habitat) and performed surveys during the 1996 and 1997 breeding seasons. For all three studies, we examined edge responses within the forest patches.

Because all three of our focal studies took place within forest patches bordered by openings of various sizes and types, we needed to classify each species relative to their associations with forest and open habitat. For this test of the model, we assumed that habitat association, as reported independently in the bird literature, relative to patch type (forest vs. open) was a suitable proxy for resource distribution. However, this assumption did not seem appropriate for shrub-dependent species because shrubs are often associated with both forest and open habitat. Therefore, shrub-dependent species were excluded from this test. We used detailed accounts from the Birds of North America series (individual references given in the Appendix) to classify each species. When these accounts were unavailable, we used less-detailed information found in Ehrlich et al. (1988). All information on edge associations was ignored when making predictions. Each of the 59 species represented in the three studies was placed into one of the four following categories. (1) Forest: species was associated solely with forest. (2) Open: species was associated solely with open habitat, which included any habitat with no overstory (including scrub). (3) Both: species was associated with both forest and open habitats. This included any species that was identified as being associated with openings in forests or solely with open woodlands (thus, habitat associations were defined at a finer scale than the patch). Species that were classified as both were further classified as to whether resource distribution was complementary or supplementary. When resource distribution was described as divided between habitats (always in reference to nesting and foraging), resource distribution was listed as complementary. Absent this information, species accounts simply did not give any information on resource use, so we classified resource distribution as unknown. (4) Shrub-dependent: These species were excluded from the analysis.

Of the 59 species classified, seven were shrub-dependent and so were excluded from the model test. Five

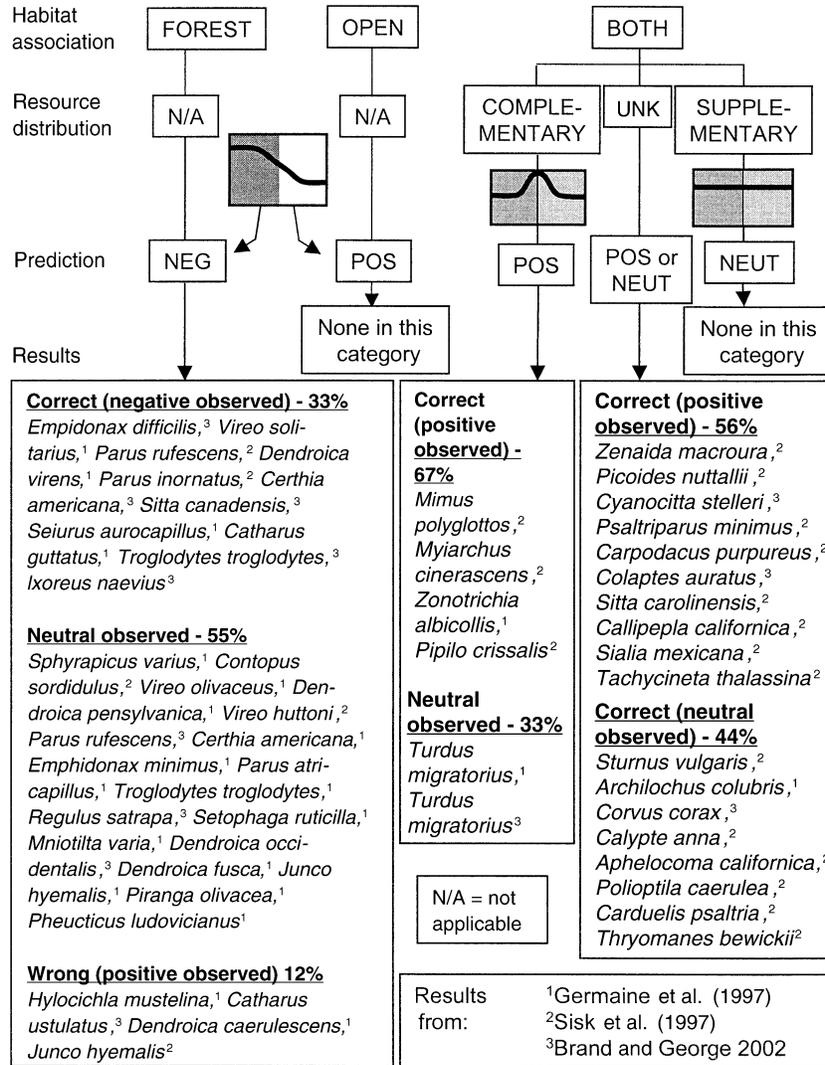


FIG. 2. This flowchart demonstrates how edge response predictions were generated for 52 bird species, and how those predictions compare with observed edge responses, as reported in three published studies. Model predictions were based on the habitat associations of each species and the distribution of resources on both sides of the habitat edges (see Appendix for species-by-species details). From this information, a positive (POS), neutral (NEUT), or negative (NEG) edge response was predicted based on our model (see Fig. 1 for details). In some cases, resource distribution was not known (UNK), so we predicted *either* a positive or neutral response, while excluding the possibility of a negative response. Results are shown for each species reported in three studies (Germaine et al. 1997, Sisk et al. 1997, Brand and George 2002). The superscript numbers indicate the study reporting the observed responses. Species are grouped where model predictions were correct and incorrect. Incorrect predictions were further divided into cases where the model failed to predict a positive or negative edge response (wrong) and where an unpredicted neutral response was observed (neutral).

of the remaining 52 species were represented in two studies, so there were 57 separate opportunities to test the predictions of our model. Fig. 2 shows the classification of each of the 52 species relative to habitat associations, resource distribution, the resulting prediction, and the response observed in each study. Details on each of these species predictions, including common names, references for all habitat information, a brief habitat description, and the categories assigned to each species, are found in the Appendix. Of those 52 species, 29 were classified as forest-associated, and

therefore predicted to show a negative response at forest edges. No species was identified as being solely associated with open habitat. The remaining 23 species were classified as being associated with both forest and open habitat, and, of those, five were shown to have complementary resource distribution and therefore predicted to show a positive edge response. For the remaining 18 species, we lacked the information to determine if resource use was complementary or supplementary, so we predicted either a positive or neutral response, but excluded the possibility of a negative one.

Our model did well in predicting edge responses for the 57 cases from these three empirical studies (Fig. 2). With only the most basic information on habitat associations and resource use, we were able to correctly predict 25 out of 29 cases (86%) when positive or negative edge responses were reported, a significantly better result than would be expected if predictions were made at random ($\chi^2 = 15.21$, $df = 1$, $P < 0.0001$). Our model did best when predicting positive responses. In four of the six cases when a positive response was predicted, it was observed with neutral responses occurring in the remaining two cases (Fig. 2). When we lacked information to differentiate between neutral and positive responses, but were able to exclude the possibility of predicting a negative response (18 cases), only neutral or positive responses were observed (Fig. 2). Finally, our model was least successful in predicting negative edge responses. Of the 33 cases where negative responses were predicted, they occurred only 11 times, with 18 neutral and four positive responses observed (Fig. 2). As explained above, the observed neutral responses may be due to lack of statistical power, insufficient detail regarding habitat quality, or intrinsic edge insensitivity. However, the four positive responses directly contradict the predictions of the model. One species (the Dark-eyed Junco, *Junco hyemalis*) is known to be associated with open-canopy forests and was listed as an edge-exploiter in its species accounts, information that we ignored when generating predictions. Another species (Swainson's Thrush, *Catharus ustulatus*) may be responding to an increase in shrubs along edges in the study area (T. L. George, *personal communication*). However, we have no explanation for the responses of the remaining two species (Wood Thrush, *Hylocichlla mestelina*, and Black-throated Blue Warbler, *Dendroica caerulescens*), both of which have strong forest associations. It is possible that there was a complementary resource in the bordering open habitat that may have caused the increase in density near the edge (Fig. 1b). As better site-specific information on resource use and distribution becomes routinely reported within the literature, cases such as these, where observed edge responses are in direct contradiction of predictions, can be more rigorously explored.

Although this preliminary test was successful in making predictions for most observed edge responses, we tested only a subset of the several mechanisms incorporated into our model (Fig. 1). There were no species in our three studies associated with open habitat, so the increase predicted in less-preferred habitat for the transitional edge response (Fig. 1a) was not tested. However, another study that measured the response of an open-habitat bird within forest edges (the Southern Emu-wren, *Malurus lamberti*) found the increase within forest edges (Baker et al. 2002) that is predicted by our model. Also, because all three studies in our preliminary test took place at only one edge type, all during the breeding season, it was not possible to test the

ability of our model to account for intraspecific variability. However, a recent test of this model for 15 butterfly species at 12 edge types of varying structures found that the model was successful in explaining different observed edge responses for most species even at different edge types (Ries 2003). Further tests of the model, especially through directed field efforts, will continue to test the different mechanisms proposed in Fig. 1 and evaluate the ability of this model to account for both inter- and intraspecific variability, as well as highlight other ecological factors that are important in edge responses and may be used to explain additional variability.

CONCLUSIONS

Our predictive model of changes in abundance near edges presents a framework for understanding the broad patterns and much of the variability reported in a large, mostly descriptive literature. This literature reports variable edge responses for many species, suggesting complex mechanisms and few general patterns. However, when viewed in the light of this relatively simple model, it is clear that variability in edge responses should be expected, and that most of these responses are predictable based on the patterns of resource distribution and use by each species. We also present a framework for investigating variation in edge responses that is not explained by our model, through the exploration of ecological factors that may underlie the variable strength of edge responses, the search for life-history or ecological traits associated with intrinsic edge sensitivity, and the possibility of higher-order species interactions. By examining previous studies under the umbrella of this predictive framework, and incorporating modest habitat characterizations into future edge studies, a more mechanistic understanding of edge effects will emerge. As habitats become increasingly fragmented, conservation decisions will necessarily rely on predictive models of how multiple species are expected to respond to complex and continuously changing landscapes. This model of edge responses fills a gap in a larger conceptual framework that attempts to explain how habitat heterogeneity and the spatial patterning of landscapes impact the abundance and distribution of a broad range of organisms.

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APPENDIX

Information used to generate predictions for 52 bird species whose edge responses were reported in the recent literature is available in ESA's Electronic Data Archive: *Ecological Archives* E085-093-A1.