Conservation Biology

Review

Potential Negative Ecological Effects of Corridors

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Abstract: *Despite many studies showing that landscape corridors increase dispersal and species richness for disparate taxa, concerns persist that corridors can have unintended negative effects. In particular, some of the same mechanisms that underlie positive effects of corridors on species of conservation interest may also increase the spread and impact of antagonistic species (e.g., predators and pathogens), foster negative effects of edges, increase invasion by exotic species, increase the spread of unwanted disturbances such as fire, or increase population synchrony and thus reduce persistence. We conducted a literature review and meta-analysis to evaluate the prevalence of each of these negative effects. We found no evidence that corridors increase unwanted disturbance or non-native species invasion; however, these have not been well-studied concerns (1 and 6 studies, respectively). Other effects of corridors were more often studied and yielded inconsistent results; mean effect sizes were indistinguishable from zero. The effect of edges on abundances of target species was as likely to be positive as negative. Corridors were as likely to have no effect on antagonists or population synchrony as they were to increase those negative effects. We found 3 deficiencies in the literature. First, despite studies on how corridors affect predators, there are few studies of related consequences for prey population size and persistence. Second, properly designed studies of negative corridor effects are needed in natural corridors at scales larger than those achievable in experimental systems. Third, studies are needed to test more targeted hypotheses about when corridor-mediated effects on invasive species or disturbance may be negative for species of management concern. Overall, we found no overarching support for concerns that construction and maintenance of habitat corridors may result in unintended negative consequences. Negative edge effects may be mitigated by widening corridors or softening edges between corridors and the matrix. Other negative effects are relatively small and manageable compared with the large positive effects of facilitating dispersal and increasing diversity of native species.*

Keywords: connectivity, dispersal, disturbance, diversity, edge effects, fragmentation, invasive species

Efectos Negativos Potenciales de los Corredores

Resumen: *A pesar de que muchos estudios demuestran que los corredores incrementan la dispersión y la riqueza de especies de taxones diversos, todavía persisten preocupaciones sobre si los corredores pueden tener efectos negativos no intencionados. En particular, algunos de los mismos mecanismos que subyacen a los efectos positivos de los corredores sobre las especies de interés de conservación también pueden incrementar la expansión y el impacto de especies antagonistas (p. ej.: depredadores y patógenos), fomentar los efectos*

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negativos de los bordes, incrementar la invasión de especies exóticas, incrementar el esparcimiento de perturbaciones no deseadas como incendios o incrementar la sincronía de poblaciones y así reducir la persistencia. Llevamos a cabo una revisión de la literatura y un meta-análisis para evaluar la prevalencia de cada uno de estos efectos negativos. No encontramos evidencia alguna de que los corredores aumenten las perturbaciones no deseadas o la invasión de especies no nativas; sin embargo, estos problemas no han sido bien estudiados (1 y 6 estudios, respectivamente). Otros efectos de los corredores fueron estudiados con mayor frecuencia y produjeron resultados inconsistentes; el tamaño promedio de los efectos no fue distinguible de cero. El efecto de los bordes sobre la abundancia de especies determinadas fue tan probable de ser positivo como negativo y los corredores tenían la posibilidad de no tener efecto sobre antagonistas o sincronía de poblaciones, así como de incrementar esos efectos negativos. Encontramos 3 deficiencias en la literatura. Primero, a pesar de los estudios sobre cómo los corredores afectan a los depredadores, hay pocos estudios sobre consecuencias relacionadas con el tamaño y persistencia de la población de la presa. Segundo, estudios diseñados sobre los efectos negativos de los corredores son necesarios en los corredores naturales a escalas mayores que aquellas que se consiguen en sistemas experimentales. Tercero, se necesitan estudios para probar hipótesis más enfocadas cuando los efectos mediados por corredores sobre especies invasoras o perturbaciones puedan ser negativos para especies de importancia para el manejo. En general, no encontramos apoyo dominante para preocuparse de que la construcción y el mantenimiento de corredores de hábitat puedan resultar en consecuencias negativas no intencionadas. Los efectos negativos de borde pueden mitigarse al ampliar los corredores o suavizar los bordes entre los corredores y la matriz. Otros efectos negativos son relativamente pequeños y manejables, comparados con los grandes efectos positivos de facilitar la dispersión e incrementar la diversidad de especies nativas.

Palabras Clave: Conectividad, dispersión, diversidad, efecto de borde, especies invasoras, fragmentación, perturbación

Introduction

Conservation corridors are among the most popular landscape-level strategies for biodiversity conservation (Hilty et al. 2006). Numerous studies have tested their functions and show that in general they promote dispersal of native plants and animals between otherwise isolated habitat fragments (Haddad et al. 2003; Gilbert-Norton et al. 2010) and maintain species richness (Gonzalez et al. 1998; Damschen et al. 2006). The popularity of corridors is increasing as land managers seek ways to ensure that species can shift their ranges through fragmented landscapes as climate changes (Krosby et al. 2010; Beier 2012).

Although most empirical studies show that the ecological effects of corridors are positive (Gilbert-Norton et al. 2010), concerns remain about whether and when such benefits may be outweighed by potential costs (Hilty et al. 2006) (Fig. 1). Simberloff and Cox (1987) and Simberloff et al. (1992) first drew attention to possible unintended negative ecological effects of corridors by noting the potential for corridors to increase dispersal of species antagonistic to conservation targets (e.g., predators or pathogens), create edge, increase dispersal of exotic species, facilitate spread of disturbances (e.g., fire), and synchronize population dynamics and increase the likelihood of metapopulation extinction. Thus, they recognized that the same mechanisms that promote the positive effects of corridors on dispersal and diversity of conservation targets could promote unintended negative effects.

However, in the more than 25 years since these concerns were raised, there has been no synthetic review of research assessing their validity. This deficiency reflects in part the few scientific studies on negative effects in general. Comprehensive publications about corridors have only been able to speculate on negative effects, and they offer little guidance on what to do about them (Hilty et al. 2006; Rudnick et al. 2012). Evidence demonstrating that a particular negative effect is frequent or strong might help guide conservation in a way that increases positive effects of corridors but mitigates potential negative effects. The possibility of severe negative effects might even cause conservation practitioners to reconsider whether to use corridors for conservation. Alternatively, hypothetical negative effects with little empirical support could be safely ignored in corridor design. There are now a sufficient number of studies for a synthesis to provide guidance about potential negative effects of corridors.

We reviewed corridor studies to assess the role corridors play in promoting 5 unintended negative effects. We conducted a meta-analysis of the data on 2 effects that have been relatively well-studied. From our review and meta-analysis, we identified a subset of negative effects that are likely to be of concern in conservation and gaps in knowledge that future research should target.

Methods

Systematic Review and Selection of Papers

We reviewed all papers that addressed any of 5 general categories of potential negative ecological effects identified by Simberloff and colleagues (Simberloff & Cox 1987; Simberloff et al. 1992): dispersal and impact of species

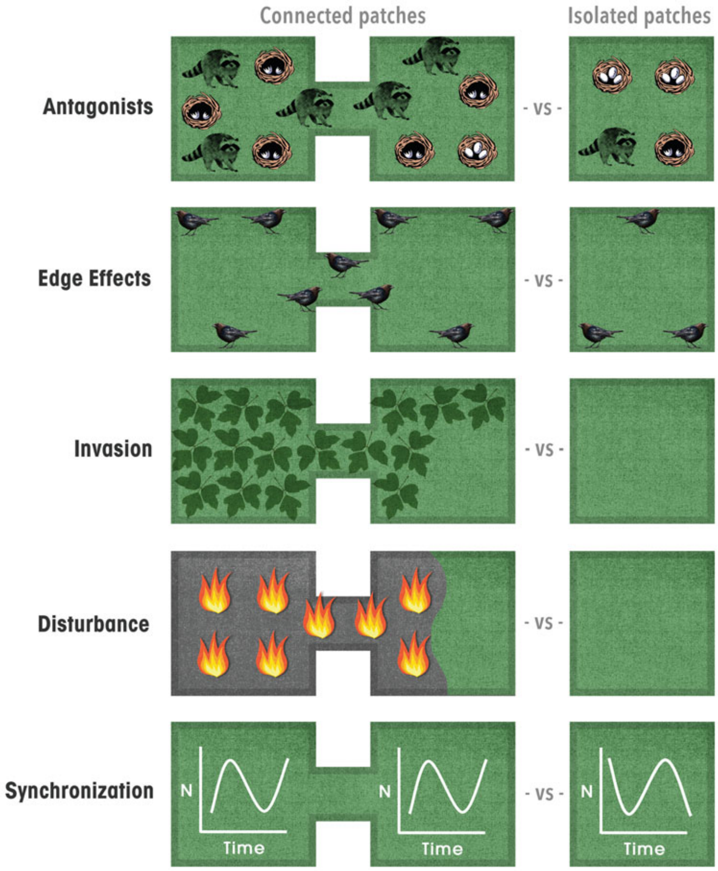

Figure 1. Examples of the potential negative effects of corridors: increase in the spread of antagonistic species (e.g., raccoons [Procyon lotor] *that depredate bird nests); creation of negative edge effects (e.g., increase presence of Brown-headed Cowbird* [Molothrus ater]*); facilitation of the spread of invasive species (e.g., kudzu* [Pueraria lobata]*); increase in the spread of disturbance (e.g., fire); and increase in population synchronization (population cycles in phase in connected patches, out of phase in unconnected patches; n, population size). Image by Neil McCoy.*

antagonistic to species that are conservation targets (e.g., predators, pathogens); enhancement of negative edge effects due to the creation of long and narrow corridors; spread and increased abundance of invasive species; spread of disturbance such as fire; and synchronization of population dynamics in connected patches, which increases the likelihood of simultaneous extinction. We did not investigate one potential negative effect noted by Simberloff and Cox (1987), the possibility that corridors increase outbreeding depression (Orrock 2005), because we found no empirical tests of this effect. We also did not consider nonecological effects, such as opportunity costs associated with corridors when other viable conservation strategies are available.

In June 2013, we searched for papers published in peer-reviewed journals, as identified in the ISI Web of Science. We used the search terms "*corridor** and (*ecol** or *conserv**)" (an asterisk indicates a wildcard character that can take the form of any suffix) to restrict papers to studies of corridors that were structurally similar to the patches they connect and typically narrow relative to the size of patches and to exclude other uses of the term *corridor*, most commonly in human transportation and infrastructure. Corridor research belongs to a subset of a broader group of studies on landscape connectivity. We focused specifically on studies of corridors because they were the focus of Simberloff and Cox (1987), they are the most direct way to restore connectivity in conservation, and corridor-connected fragments have a clear comparison group of unconnected fragments. With one exception (edge effects), we would expect the mechanisms by which corridors exert negative effects to be identical to those exerted by connectivity more broadly.

We also included in our search specific terms for each potential negative effect, as described later. From the resulting list of papers, we reviewed all abstracts and read all relevant papers that focused on one or more species in at least one landscape with corridors. We restricted our review to empirical studies, a criterion that allowed us to focus on empirical evidence in real populations and communities. We searched for studies of corridor effects on dispersal, populations, or communities within patches connected by corridors. We also included papers that focused on responses within corridors relative to other areas. We excluded 34 papers that focused specifically on human transportation or utility corridors (e.g., roads, powerline right-of-ways, canals) because these landscape elements are not created for conservation and disturbance associated with their creation and maintenance often confounds their role in connectivity (Trombulak & Frissell 2000). For papers that met our criteria (Supporting Information), we recorded the number of species studied and for those species the number of negative, positive, or neutral effects of corridors as determined

Table 1. Number of papers on potential negative effects of corridors included in this review, and the number that are based on experimental studies.*

Factor affecting corridor effects	*Total papers*	*No. of experiments*	*SRS corridor experiments*
Antagonists	17	15	9
Edge effects	17	15	12
Invasive species	6	3	3
Disturbance spread	1	1	1
Population synchronization	5	5	1

**Because they were such a large fraction of the total number of "studies tallied," the number of experimental studies from the SRS Corridor Experiment are noted separately.*

by the authors. For 2 negative effects that had sufficient numbers of studies, on antagonists and edge creation, we extracted means, sample size, and measures of variation for a meta-analysis (described later).

Examination of Potential Negative Effects

To examine how corridors might alter the movement or population impacts of species that are antagonists of focal conservation species (i.e., their predators, parasites, competitors, or pathogens), we added the following additional search terms to those listed above: "*predat** or *parasit** or *competit** or *diseas** or *antagon**." This search identified 276 papers. Of these, we considered only those that analyzed antagonists' dispersal, abundance, or impact in patches connected by corridors versus those in unconnected patches or in patches versus in corridors. Applying these criteria yielded 17 studies (Table 1); 14 focused on predators and 3 focused on pathogens.

To examine negative effects of corridors on edge creation, we included the following additional search term: "*edg**." This search identified 233 papers. Corridors are typically longer than they are wide, which may magnify edge effects. We selected those papers that examined responses in patches of equal area that varied in shape (patches with corridors and greater edge vs. more compact patches of equal area but with less edge), those that compared edge effects between connected and unconnected patches, and those that compared edge effects within corridors with edge effects within patches. In this way, we attempted to separate corridor effects on patch shape and edge effects from corridor effects on connectivity. We did not consider 11 studies of edge effects that occurred solely within corridors because they did not include a comparison group (e.g., Sinclair et al. 2005; Pryke & Samways 2012). We also did not include studies that focused on how edges may modify the behavior of dispersing animals (e.g., Haddad 1999; Pryke & Samways 2001; Berggren et al. 2002; Levey et al. 2005) because it was difficult to attribute a positive or negative effect of the potential change in behavior. These criteria reduced our total pool of papers focused on edge effects and corridors to 17 (Table 1).

To examine the negative effects of corridors on species invasion, we included the additional search terms "*inva** or *exotic**." This search resulted in 232 papers. Of these, we included studies of dispersal, occupancy, or abundance in patches connected versus unconnected by corridors. We did not include studies that reported abundance of invasive species within corridors if there was no comparison with connected or unconnected patches (e.g., Stohlgren et al. 1998; Ives et al. 2011). We did not include studies that speculated on corridor use based on observations of animal behaviors only within patches or corridors (e.g., Deckers et al. 2008; Bridgman et al. 2012), and we did not include studies investigating increased connectivity through sources other than corridors (e.g., Alofs & Fowler 2010). These criteria reduced our total pool of papers focused on invasive species and corridors to 6 (Table 1).

For spread of disturbance, we included the additional search terms "(*disturbance* or *fire*) and (*spread* or *propagation*)." This search resulted in 21 papers. Of those, we considered only papers in which corridors were found or postulated to spread disturbance between patches relative to controls. Only a single paper met our criteria (Table 1).

For population synchronization, we included the additional search terms "*synchron** or *cycle**." This search yielded 38 papers, most of which were theoretical. The 5 studies that empirically examined effects of corridors on population synchronization and compared responses in connected and unconnected patches were included in our review (Table 1).

Meta-Analysis

Two potential negative effects on antagonists and edge effects yielded sufficient numbers of studies for a meta-analysis. For each species or species group studied in each paper, we used the program DataThief III (www.datathief.org) to digitize graphics and then extract the mean and a measure of variation (typically standard deviation, standard error, or 95% CI) of responses for measures taken in patches with and without corridors. We then computed 2 measures of effect size: Hedges' d, computed as in Gilbert-Norton et al. (2010), and the natural log of the ratio of the response in connected relative to unconnected patches. Hedges' d weights responses by the variance in effect size and accounts for differences in replication among studies, but, because factors other than replication affect variance, it can be misleading when large sampling variance swamps an otherwise clear signal. In the end, our results were similar with both metrics. Thus, to be consistent with another meta-analysis of corridors (Gilbert-Norton et al. 2010), we report results for Hedges' d. All measures of variation were converted to standard deviation. In one case, d was computed from a t test. Three studies were not included in the meta-analysis. In 2 cases (Hoyle & Gilbert 2004; Johnson et al. 2011), no measure of responses was reported for a nonsignificant effect. In another case, there was no replication and thus no variation (Agostinho et al. 2012). Finally, we assigned the sign of the response to reflect whether the response was positive or negative as determined by the study's authors. For edge effects, positive effects were generated by higher abundances of target species, lower abundances of antagonists, lower predation rates, or higher species richness caused by higher edge effects in connected relative to unconnected patches. For antagonists, positive effects were generated by lower predation, higher persistence of prey populations, and lower (if predators were antagonists) or higher (in the case of biocontrol) predator abundances. Each species was treated as an independent sample in the analysis.

Results

Thirty-three papers met our general criteria, some of which investigated multiple negative effects of corridors (Supporting Information). Of those, 26 papers (79%) reported experiments. The Savannah River Site Corridor Experiment (which involves the authors of this review) was the study location of 17 (52%) papers, a percentage comparable to that found in the most recent review of positive effects of corridors (Gilbert-Norton et al. 2010).

Of the 17 papers we examined that focused on predation and parasites, the number of studies showing that corridors had negative effects by increasing abundance of predators, increasing rates of predation on target species, or reducing persistence of target prey species was about half the number that showed no effect on predators or predation (Fig. 2). Two different microcosm studies showed that corridors had positive effects by increasing persistence of prey species (Holyoak 2000*a*, 2000*b*). Across all studies, effect sizes were not distinguishable from zero (Hedges' d, mean $= -0.11$, 95% CI $= -0.58, 0.36$). Nearly all (15 of 17) papers stemmed from experiments; the 2 observational studies showed no effect of corridors on antagonist population size or spread (Johnson et al. 2011; Krewenka et al. 2011). Over half (4 of 7) the studies that showed evidence for negative corridor effects on predation came from the Savannah River Site Corridor Experiment and focused on antagonists of plant species of restoration interest. Corridors increased prevalence of biotically dispersed plant parasites (Sullivan et al. 2011) and rates of seed predation by small mammals (Orrock et al. 2003; Brinkerhoff et al. 2005; Orrock & Damschen 2005). Corridors had no effect on wind-dispersed parasites of plants (Johnson & Haddad 2011; Sullivan et al. 2011), on leaf herbivory, or on the abundance of generalist herbivores such as grasshoppers (Evans et al. 2012).

Corridor effects mediated through edge creation were nearly equally divided. Eight studies showed that corridors had negative effects on target species due to edge effects, 6 showed positive effects, and 8 showed no effect. The 17 papers that tested for negative effects of corridors via edge creation considered a total of 36 species, of which 10 showed negative responses, 11 showed positive responses, and 15 showed no response to corridors. The evenness in response to edge creation was confirmed by our meta-analysis results (Fig. 3; Hedges' d Mean $=$ 0.85, 95%, CI $= -2.05, 3.75$). Nearly all (15 of 17) studies of edges in relation to corridors were experimental, and most (12) were conducted in the Savannah River Site Corridor Experiment, which was specifically designed to separate edge effects from connectivity effects produced by corridors. The negative effects of edges included increased predation of migrant birds (nestlings) and fish, creating ecological traps for edge-loving species (Erikson et al. 2001; Weldon & Haddad 2005; Agostinho et al. 2012), and reduced abundance (Haddad & Tewksbury 2005; Orrock et al. 2011; Evans et al. 2012; Åström & Pärt 2013) or diversity (Chisholm et al. 2011) of some insects and other arthropods.

Of the 6 studies that investigated the role of corridors in increasing invasion by exotic species, none found evidence of negative corridor effects. Non-native species appeared to either remain where they initially established and did not spread or, perhaps because they are good dispersers, tended to be cosmopolitan in distribution regardless of the presence of a corridor (Minor et al. 2009). At the Savannah River Site Corridor Experiment, there was no evidence that corridors increased species richness of non-native plants (Damschen et al. 2006).

The single study of corridor effects on fire was conducted in the Savannah River Site Corridor Experiment. Experimental sites were subjected to controlled burns every 2–3 years. Corridors locally increased fire temperature due to a "bellows effect" whereby wind was directed down corridors and intensified burning (Brudvig et al. 2012). This increase in fire intensity by corridors was beneficial in this case because it accelerated restoration by promoting warm-season bunch grasses. Although corridors increased fire intensity, there was no evidence that corridors influenced fire spread—sampling locations in connected and unconnected patches ignited with similar probability.

Of the 5 studies that investigated effects of corridors on population synchronization, 3 showed that corridors synchronize population dynamics and 2 showed no effects of corridors on synchronization. Of the 3 studies that showed synchronization, 2 were conducted in experimental microcosms with protozoans. The third showed that connectivity can lead to short-term synchrony in seed loss through rodent foraging.

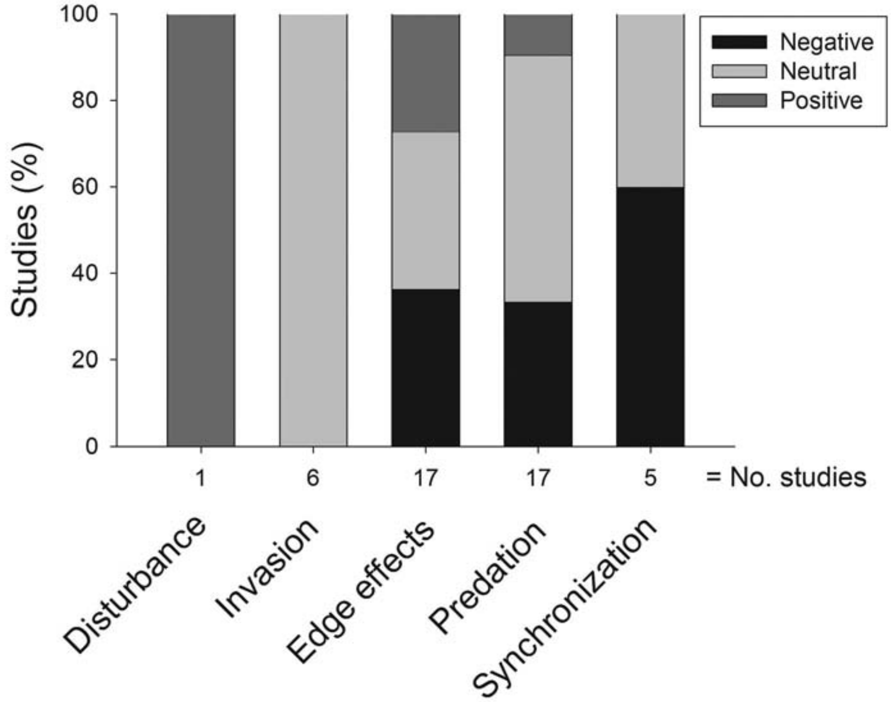

Figure 2. Proportion of studies that have identified negative, neutral, or positive effects of corridors on target species. Some studies included species that responded in more than one way, so it is possible for an individual study to appear in more than one category of response (increase in disturbance, facilitation of invasive species; increase in predation; increase in synchronization of population dynamics; effects are ordered from lowest to highest proportion of negative effects).

Discussion

We found no consistently negative effect of corridors. Our review yielded mixed evidence for 3 of the potential negative effects of corridors—concerns over whether they affect populations by facilitating antagonists, creating edges, or synchronizing population cycles. For the 2 potential negative effects that have been evaluated most frequently, our meta-analysis on antagonists and edge effects in corridors showed no clear direction of those effects across studies. We found no evidence that corridors have negative effects by increasing invasions or disturbance. Our results make it clear the particular types of negative effects that can be a concern and thus should be mitigated in conservation, the negative effects that are rarely of concern, and the negative effects that need further research.

First, the only negative effect of corridors that clearly reduces the population size or persistence of target species is the creation of edge, and even this effect is negative in only a fraction of cases. Except in the very widest corridors (>1 km) (Ewers & Didham 2008), edges inevitably exert some effect in corridors and in the patches they connect. Conservation biologists have a strong understanding of when edges reduce abundances of target species and when landscapes harbor antagonistic species that exploit edges (Leopold 1933; Ries et al. 2004). This knowledge suggests that negative effects of corridors through edges might be mitigated through creation of wider corridors or reduction of contrast between corridors and the surrounding matrix (i.e., softer edges). However, we noted a lack of research evaluating these hypotheses directly. In all tests of corridor effects, edge effects must be controlled or accounted for when assessing how corridors operate and the ecological impacts they provide through connectivity.

Second, 2 effects of corridors that have been a source of concern—the spread of invasive species and disturbance—are currently not consistent with published findings. Of the two, corridor effects on invasive species have received more attention. In our review, corridors were found to have no effect because invasive species within these studies were ubiquitous and presumably did not need corridors to increase their dispersal. We know of one exception to this general pattern: an example in which corridors increase invasion (Resasco 2013). In that instance, the weakly dispersing form of the invasive fire ant (*Solenopsis invicta*) that is particularly damaging to ecosystems also benefits from corridors, whereas the strongly dispersing form is unaffected by corridors. In cases such as this one, corridor promotion of weak dispersers may pose a conservation danger. A case not identified by our review in which corridor restoration seems likely to increase invasion is dam removal, which increases potential for spread of aquatic invasive species (Bednarek 2001; Rahel 2013). In terrestrial systems, where most invasive species are strong dispersers, conservation corridors are unlikely to promote their spread and impact. The relationship that we hypothesize exists between the dispersal capacity of harmful invasive species and the potential role of corridors in facilitating their dispersal merits further testing as corridors are created or restored in conservation (Wilkerson 2013).

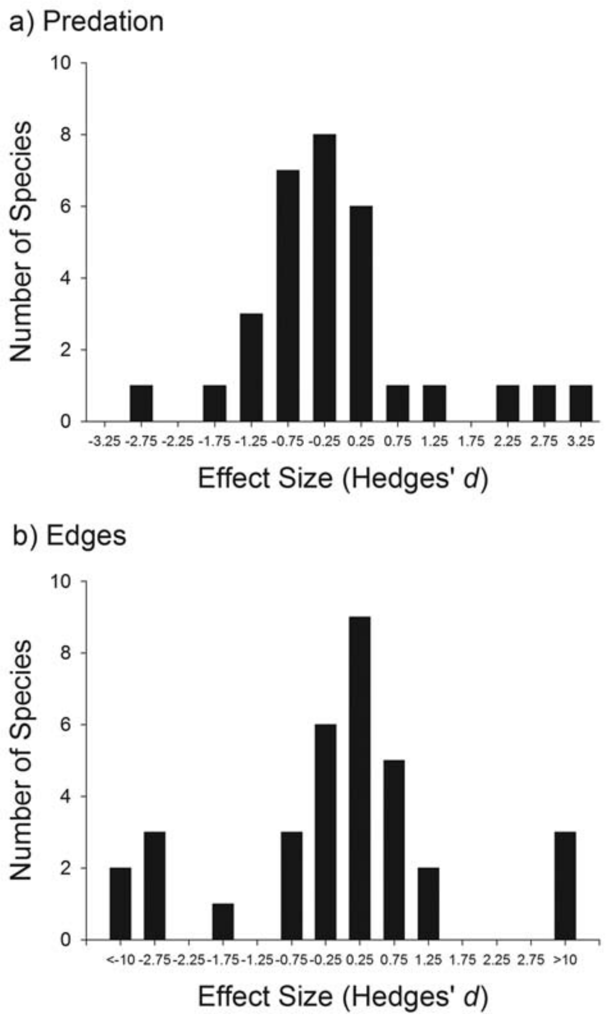

Figure 3. Number of species affected by corridors through (a) predation and (b) edges in 22 and 17 studies, respectively. For edges, positive Hedges' d *values indicate an increase in the abundance, persistence, or diversity of target species with edge creation. For predation, negative values represent increases in predator abundance or impact on target species. One to 5 species (i.e., individual taxonomic groups) were considered per study.*

As to effects of corridors on disturbance, we found only one study that showed corridors can increase the effects of disturbance intensity, but these impacts were positive for the focal ecosystem (Brudvig et al. 2012). Although Simberloff and Cox (1987) assume promotion of fire via corridors has a negative effect, fire typically has positive effects for fire-dependent ecosystems and their associated species of conservation concern (e.g., in systems where prescribed fire is used as a management tool). We recognize that situations exist for which the spread of disturbance is a significant concern to ecosystems, such as tropical forests that can become more fire prone following fragmentation, and to people, such as at the wildland–urban interface; thus, additional tests of corridor effects in these specific contexts would be particularly useful.

A third insight that emerges from our review is the rarity of studies on population dynamics in response to corridors (see also Gregory & Beier 2014). In the context of this review, more studies are needed to assess population consequences of antagonists and population synchronization of target species. Although we found some studies in which corridors increased the abundance or impact of predators or synchronized population dynamics, the implications of these responses are unclear. Less than half the studies in our review report that corridors increase the abundance or effects of antagonists, primarily seed predators (Orrock et al. 2003; Brinkerhoff et al. 2005; Orrock & Damschen 2005), plant parasites (Sullivan et al. 2011), and protozoans in microcosms (Burkey 1997; Cooper et al. 2012). Only in microcosm experiments did studies show that antagonists actually reduce population persistence of other species. In the Savannah River Site Corridor Experiment, there was no evidence that use of corridors by predators or parasites reduces the persistence of plant or animal populations. For now, and until there are more studies of corridor effects on population persistence (see later), corridor design, siting, and restoration should proceed with the recognition that focal species are embedded within food webs that include antagonistic species.

When considering population synchronization, microcosm experiments have most strongly demonstrated how corridors can synchronize such fluctuations (Holyoak 2000*a*; Cooper et al. 2012). Yet, even microcosm studies produce contradictory evidence because these studies show that corridors may (Holyoak 2000*a*) or may not (Cooper et al. 2012) stabilize prey populations in the presence of predators. Furthermore, models show that effects caused by corridors in synchronizing populations are unlikely for slow-growing, poorly dispersing species that are often targets of conservation (Hudgens & Haddad 2003). Especially given the observed differences in positive effects of corridors between microcosm experiments and other systems (Gilbert-Norton et al. 2010), more research is needed to understand the conditions under which corridors will increase spatial synchrony of populations and increase local extinctions.

Our review has additional implications for the types of studies that are needed to better understand the potential negative effects of corridors for conservation. We found no consistent negative effects of corridors, yet our meta-analysis has its own limitations. Our sample size in terms of the number of studies was relatively low, and some studies had low sample size and power to detect negative effects. Scientists do not appear to be biased toward publication of positive or negative effects because we found nearly identical numbers of studies in this review as in the most recent review that examined positive effects (Gilbert-Norton et al. 2010). Still, studies that showed no effect may be under-reported because such studies are often viewed as uninteresting or suspect. Stronger meta-analysis will only be possible through continued research and better designed studies of corridors.

We found more experimental studies than observations of restored or conserved corridors in natural landscapes. These experiments fulfilled reasonably strict criteria, especially with regard to comparisons between treatments and controls. Yet most experimental study sites are necessarily smaller than most conservation corridors. Experimental studies can provide reasonable models to test corridor responses and provide data comparable to data from observational studies conducted at larger scales (Gilbert-Norton et al. 2010). Still, more and larger scale studies are needed to evaluate the negative (and positive) effects of conservation corridors. Observational studies that met our review criteria clearly identified comparison groups that were connected and unconnected. Beier and Gregory (2012) provide a helpful list of criteria that specify how this can be done. New studies at larger scales might take advantage of planned restoration or other land use changes that could be paired with appropriate unconnected comparison landscapes to create experiment-like contexts in landscapes that are slated to be manipulated.

We found few studies have assessed either the negative or positive effects of corridors on population persistence (or related metrics such as occupancy or species richness, Gregory & Beier 2014). Because corridors are ultimately designed to increase population persistence for target species, the conspicuous lack of population studies is likely impeding progress in understanding how and when corridors have negative (or positive) effects. Although we have strong evidence for positive community-level impacts of connectivity (e.g., Damschen et al. 2006), we have limited capacity to predict the impact of corridors on populations of most individual species. Population-level studies of corridors are thus critically needed to assess both the negative and positive effects of corridors on persistence (Haddad & Tewksbury 2006; Gregory & Beier 2014), and longer term studies are needed that track population dynamics and extinction in the context of corridors (Beier & Gregory 2012).

Looking ahead, it will be important to ask how interactions between corridors and other global changes may lead to negative effects of corridors. Corridors have been identified as the most popular landscape strategy for mitigating the effects of climate change (Heller & Zavaleta 2009). However, it is unclear, for example, whether corridors will favor climate-driven range shifts differentially for invasive over native species or whether corridors will have greater effects on the dispersal of predators or their prey. New studies will need to address the potential for a mismatch in corridor effectiveness across communities of species as climate changes.

Some of the negative effects of corridors proposed by Simberloff and colleagues (Simberloff & Cox 1987; Simberloff et al. 1992), particularly effects of corridors in creating edges and perhaps their effects on antagonists, merit focused consideration in conservation and restoration. Others, such as the effects of corridors on invasions and synchronization appear limited to special cases or seem inconsequential. The potential negative effects of corridors acting through changes in disturbance will require context-dependent evaluation because the value of disturbance itself varies across landscapes. Most important, there is no evidence that corridors are consistently detrimental in a way that overcomes their established benefits. In sum, the weight of existing empirical evidence continues to show that the potential costs of corridors are outweighed substantially by their conservation benefits.

Acknowledgments

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Supporting Information

A list of studies identified through systematic review of potential negative effects of corridors (Appendix S1) is available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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