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Meta-analysis on a Decade of Testing Corridor Efficacy: What New Have we Learned?

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Abstract

Purpose of Review Corridors are widely considered as a strategy to mitigate effects of habitat fragmentation on biodiversity. There are, however, lingering concerns about whether corridors work as intended and whether managing for connectivity in fragmented landscapes is even important for biodiversity conservation. In response, numerous manipulative and natural experiments have been conducted to test the effectiveness of corridors. Gilbert-Norton et al. Conserv Biol. 2010;24(3):660-8 (2010) reviewed such studies published between 1985 and 2008 and concluded that corridors are generally effective at increasing interpatch movement. The authors noted a lack of studies measuring responses at the population and community levels, responses that would better approximate corridor effects on population persistence and aspects of biodiversity. Here I explored what new insights can be gained on corridor effectiveness from studies published in the last decade, particularly with an eye toward insights going beyond effects on inter-patch movement.

Recent Findings Following the same selection criteria as Gilbert-Norton et al. Conserv Biol. 2010;24(3):660-8 (2010), I reviewed studies published between 2008 and 2018 that tested corridor effectiveness by comparing ecological response variables from patches connected and not connected by corridors. Analysis of effect sizes showed that corridors increase response variables, reinforcing earlier conclusions that corridors function as intended. Whereas the previous review mainly included corridor effects on dispersal, recent research shows support for corridor efficacy at a variety of levels of organization, from individuals to communities.

Summary These findings provide further support for the conclusion that efforts spent creating and maintaining corridors are worthwhile for biodiversity conservation.

Keywords Corridor experiment · Habitat fragmentation · Conservation · Landscape ecology · Connectivity · Biodiversity

Introduction

The reduction of connectivity from habitat loss and fragmentation can restrict movement of organisms between sub-populations, which can result in decreased gene flow, local extinctions, and loss of biodiversity

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Julian Resasco jresasco@colorado.edu [1, 2]. One method to maintain connectivity is through the conservation or restoration of landscape corridors, strips of habitat that connect otherwise isolated habitat fragments. Despite their intuitive appeal, however, there are long-standing doubts about whether corridors work as intended [3–5]. Assessing the effectiveness of corridors is often challenging due to the difficulty of attaining replication and appropriate controls in landscapes to deal with potentially confounding factors like habitat area and inter-patch distance. Indeed, doubts that took hold about the effectiveness of corridors were in part due to a lack of empirical evidence [4, 6]. In response, a large number of studies have tested corridor function, often controlling for confounding factors.

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In a meta-analytic review, Gilbert-Norton et al. [7] synthesized studies (both manipulative and natural experiments) that tested the efficacy of corridors. Reviewing studies from 1985 to 2008, the authors found that: (1) corridors tended to increase movement between habitat patches, (2) the efficacy of corridors varied among taxa, and (3) studies with natural corridors showed greater movement than experimentally manipulated corridors. Given these results, the authors concluded that corridors generally increase movement in fragmented landscapes and therefore corridors are a worthwhile conservation strategy. Gilbert-Norton et al. [7] made significant progress toward addressing the concern about whether corridors function as intended. In addition, concerns of possible negative effects of corridors, such as the spread of disturbance, invasive species, and disease, were addressed in another metaanalysis by Haddad et al. [8]. Yet, Gilbert-Norton et al. [7] also noted that most studies did not test whether inter-patch movement was sufficient to maintain population viability. Moreover, few studies examined population or community level effects. This gap is important because conservation efforts and debates on the effects of landscape structure [9, 10] often focus on the level of populations and communities.

I conducted a meta-analysis on studies testing the effects of corridors to determine whether the past decade of research supports the efficacy of corridors and what new insights can be gained, in particular insights beyond effects on inter-patch movement.

Methods

I searched for relevant studies on Web of Science (ISI) using the same search terms used by Gilbert-Norton et al. [7]: corridor, movement, effectiveness, connectivity, and habitat connectivity (TS = [corridor AND movement] OR [corridor AND effectiveness] OR [corridor AND connectivity] OR [corridor AND habitat connectivity]). I refined the search results to categories that could include relevant studies: ecology OR environmental sciences OR biodiversity conservation OR zoology OR biology OR behavioral sciences OR soil science OR entomology OR parasitology OR plant sciences OR agronomy. Search results were restricted from 2008 to 2018, allowing me to review the literature since Gilbert-Norton et al. [7]. I also searched the EBSCO Wildlife & Ecology Studies Worldwide database and ProQuest for theses and dissertations.

The Web of Science search resulted in over 1200 results but as in Gilbert-Norton et al. [7], I only included studies if they had replicated corridor and control (unconnected) treatments. Also, as in the previous review, I used the following rules: (1) for studies conducted over multiple time periods, I used the last time period; (2) for studies with multiple types of isolated fragments, I used fragments with a shape that best approximated that of the connected patch; (3) for studies in which data were presented in multiple publications, I used the study that provided the clearest comparison between corridor and control treatments; (4) for studies testing corridors of different widths or lengths, I used the narrowest or longest corridor reasoning that these likely best approximate corridors used in conservation. Similarly, if a study contained treatments with multiple corridors, I used the treatment with the fewest connections. I did not include studies if they were based solely on modeling. I excluded any studies published in 2008 that were already included in Gilbert-Norton et al. [7]. I did not include studies measuring negative interspecific interactions where effects could be ambiguously interpreted as positive for one species and negative for another (e.g., herbivory, [11]). Response variables had to be biotic and included measures like proportion of individuals moved, abundance, and species richness. In cases where multiple closely-related response variables were reported, I selected the variable that I believed to be most meaningful.

For each response variable, I calculated the effect size d, sometimes referred to as the standardized mean difference or Hedges' d [12], as in Gilbert-Norton et al. [7]. Values of d > 0 indicate positive effects of corridor treatments compared to unconnected control treatments on ecological response variables. For further interpretation of effect sizes, I use the convention of referring to effect sizes of d = 0.2 as small, d = 0.5 as medium, and d = 0.8 as large [13]. The calculation of d uses the mean, standard deviation, and sample sizes for corridor-connected and unconnected control groups. In most cases, I was able to extract these values (or data from which these values can be calculated) from the text or figures (using WebPlotDigitizer; https:// automeris.io/WebPlotDigitizer/) in the paper or by contacting the corresponding author. I was not able to include five studies which did not include the necessary information and for which authors did not respond to requests for data or the values necessary to calculate d. As in Gilbert-Norton et al. [7], I noted variables of interest for each study. These were: taxon (invertebrates, birds, non-avian vertebrates, and plants); whether studies controlled for area; whether studies controlled for distance between source and recipient patches; whether studies were manipulative (corridors were created for the experiment) or natural experiments (corridors already present, and if created by humans, not for the purposes of the experiment), and finally whether studies were done at the Savannah River Site Corridor Experiment (South Carolina, USA), a site where many studies meeting the previously stated criteria have been done. I also recorded the level of organization of each response variable as movement, genetic, individual fitness, population, or community.

I analyzed the data using the function "metahdep.HBLM", hierarchical Bayes linear models allowing for hierarchical dependence, in the R package "metahdep" like in [14], Gilbert-Norton et al. [7]. Gilbert-Norton et al. [7] controlled for sampling dependence which can occur when one control group is compared to multiple experimental groups and hierarchical dependence which can occur when many response variables are measured as a part of a single study. I assumed independence in specifying the model's dependence structure because all studies analyzed included only a single experimental treatment and most studies had one associated response variable. Differences in effect sizes within studies measuring multiple response variables did not differ from differences among studies measuring single response variables (0.86 ± 0.85 SD and 1.03 ± 0.78 SD respectively; Welch 2 sample test: t = -1.56, df = 112.85, P = 0.12). I checked that effect sizes conformed to a normal distribution using a Kolmogorov-Smirnov test. I checked that there was not problematic evidence of potential publication bias graphically with a funnel plot and with a normal quantile plot (Wang and Bushman 1998).

Results

The number of publications from the Web of Science search in the last decade was more than twice those of the previous two decades combined. However, the number of publications that tested the efficacy of corridors in a way that met the criteria for inclusion similar in number to those in Gilbert-Norton et al. [7], 32 here compared to 35 publications for Gilbert-Norton et al. [7]. From these 32 studies, I calculated 56 effect sizes compared to 78 in Gilbert-Norton et al. [7] (Fig. 1a; Appendix Table 1). There were 30 response variables for invertebrates, 13 for non-avian vertebrates (only mammals), 7 for birds, and 6 for plants. There were 11 response variables from 10 papers that examined



Fig. 1) Effect size (*d*) summaries for studies assessing corridor effectiveness. Values of d > 0 indicate positive effects of corridor treatments on ecological response variables compared to unconnected control treatments. The dashed vertical lines demarcate d = 0. The top panel (A) is a histogram representing the 56 *d* values from this meta-analysis. The bottom panel (B) shows estimates of *d* from meta-analysis models for different levels of organization as well as for all levels of organization combined ("overall") in filled gray dots. Error bars represent \pm SE values from meta-analysis models. Note that the "genetic" category has no error bars because there is a single value of *d* associated with it. Colored dots represent corresponding individual *d* values with colors representing taxonomic groups. These dots are jittered along the *y*-axis to reduce overlap. Vertical gray lines indicate benchmarks of small (d = 0.2), medium (d = 0.5), and large (d = 0.8) effect sizes [13]

movement [16, 20, 23, 27, 28, 32, 37, 39–41], 1 response variable from 1 paper that examined population genetics [45], 4 response variables from 4 papers that examined fitness of individuals [18, 24, 25, 29], 26 response variables from 10 papers that were at the population level [17, 19, 22, 26, 29–31, 42, 43, 46], and 14 responses from 12 papers that were at the community level [15, 21, 26, 31, 33–36, 38, 42, 44, 46] (Appendix Table 1). Manipulated corridors were used to generate 29% of these response variables while natural corridors were used in 71%. Most studies controlled for distance (89%) and area (82%) either experimentally or in site selection. Most responses (88%) did not come from the Savannah River Site Corridor Experiment.

Across all types of response variables, corridors showed an overall positive effect of medium strength (d = 0.49, P < 0.001; Fig 1b). For comparison, the mean value of d for Gilbert-Norton et al. [7] was 0.48. Mean d values for all levels of organization (movement, genetic, fitness, population, and community) were positive (Fig. 1b). For the movement level, d was medium-large (d = 0.74, P < 0.001). For the genetic level, d was large (d = 1.09) but there was only one value of d. For the fitness level, d was medium-large (d = 0.77, P = 0.01). For the population level response variables, d was medium (d = 0.46, P < 0.001). For the community level, d was small (d = 0.19, P = 0.002).

Discussion

Results from this meta-analysis reinforce finding that corridors are effective at increasing movement and further extend those conclusions by showing positive effects at a variety of levels of organization, including at the organizational levels of populations and communities. These levels were previously deficiently represented in Gilbert-Norton et al.'s meta-analysis and are more closely aligned with those of conservation goals [47].

While results show that corridors were generally effective, they were not universally effective across studies (e.g., [30, 33, 34] (Fig. 1). Species vary in how they use landscapes and consequently how they respond to fragmentation and corridors [48]. Appropriate tests of corridor effectiveness require appropriate consideration of life history of study organisms and spatial and temporal scale. Most studies reviewed here were surely designed using prior knowledge or intuition about organisms' responses to landscape structure. At the community level, species richness was usually the response variable. Variation in responses to fragmentation among constituent species in species pools may account for the small effect size. That is, species may respond to corridors, but if winners are balanced by losers, then net richness may change little. This is more generally an important consideration in assessments of fragmentation or connectivity effects that consider only species richness [10]. Moreover, timescales could be an important consideration as effects of fragmentation and connectivity can increase with time [2, 49]. Studies reviewed here, as in Gilbert-Norton et al. [7], tended to be short in duration and small in spatial scale compared to typical management activities for biodiversity conservation. Manipulative experiments that are long-term and at the scale of management activities offer unique opportunities to control confounding variables while having high real-world applicability, however, they face strong logistical limitations and so are rare [2, 50, 51].

While manipulative experiments or carefully designed observational studies like those reviewed here offer powerful ways to test the effectiveness of corridors by controlling for confounding factors, other approaches, such as mapping habitat connectivity, simulation studies, animal movement analysis, and behavioral studies can be used to gain system-specific insight as well as contribute to general understanding on effectiveness of corridors. For example, Fletcher et al. [52] broadly reviewed the literature on effects of landscape connectivity and found that, similarly to here, effects of connectivity are frequently observed across levels of organization and are usually positive.

Overall, these findings suggest that to best conserve biodiversity, we need to not only conserve what remains of fragments but conserve and restore their connectivity. This review also points to areas where tests of corridor function were sparse which could guide future studies. As stated previously, studies conducted over large spatial and long temporal scales remain rare but are particularly valuable. While studies at the population and community levels increased in representation, few studies measured responses beyond abundance and species richness to better assess whether corridors reduce extinction risk. There was a surprising lack of studies that tested for effects on gene flow or genetic diversity. There are often mismatches between foci of ecological studies on fragmentation and issues of interest to conservation practitioners, for example, community-based human dimensions, ecosystem services, and interactions of multiple threats to biodiversity [50]. Some of these echo emerging foci for studying fragmentation [2]. Development of research (particularly in coproduction with conservation practitioners) in these areas will increase understanding in ecology and in applications for conservation. In closing, current interest in the ecology of corridors in strong; future studies will help reveal mechanisms and contexts for understanding how biodiversity responds to landscape change [9, 10] and allow for increasingly nuanced synthesis.

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Compliance with Ethical Standards

Conflict of Interest Julian Resasco declares that he has no conflict of interest.

Human and Animal Rights and Informed Consent This article does not contain any studies with human or animal subjects performed by any of the authors.

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Citation	Organisms	Taxonomic category	Response variable	Level of organization	Ne Nc	: Xe	Xc	Se	Sc Sc	p o	I
Araujo Calçada et al. (2013) [15]	Forest herbs	Plant	Species richness	Community	8 24	56.770	28.520	14.451	56.770	50.195	0.549
Awade and Metzger	Variable antshrike (Thamnophilus	Bird	Probability of crossing	Movement	38 38	0.813	0.500	0.403	0.509	0.459	0.674
Awade and Metzger	Golden-crowned warbler	Bird	Probability of crossing	Movement	38 38	0.889	0.560	0.323	0.507	0.425	0.766
Bowler and Benton	(pussitenter us cuticivorus) Mites	Invertebrate	Fecundity	Population	5 5	2.720	1.650	1.160	0.570	0.914	1.057
Cranmer et al. (2012)	Plants	Plant	Percent seedset	Fitness	34	60.587	55.488	4.376	4.317	4.341	0.989
Evans et al. (2012)	Grasshoppers	Invertebrate	Abundance	Population	8	43.750	40.000	6.250	6.000	6.126	0.579
Fletcher et al. (2014)	Cactus bug (Chelinidea vittiger)	Invertebrate	Colonization probability	Movement	10 10	0.049	0.060	0.018	0.021	0.019	- 0.585
Galanes and Thomlinson (2011)	Millipede	Invertebrate	Species richness	Community	9 9	6.667	6.500	1.211	1.378	1.297	0.119
Grainger and Gilbert	Aphid (Aphis nerii)	Invertebrate	Max abundance	Population	7 7	65.600	26.600	152.500	33.500	110.405	0.331
Grainger and Gilbert	Aphid (Aphis asclepiadis)	Invertebrate	Max abundance	Population	7 7	47.500	10.000	120.700	6.600	85.475	0.411
Hadley and Betts	Green hermit (Phaethornis guy)	Bird	Homing	Movement	10 9	0.007	0.002	0.045	0.023	0.037	0.123
Hawn et al. (2018)	Green Lynx Spiders (Peucetia viridans)	Invertebrate	Lipids	Fitness	8	1.380	0.930	0.460	0.160	0.344	1.235
Herrmann et al. (2017) [25]	Bumble bee (Bombus impatiens)	Invertebrate	Abundance (individuals)	Fitness	8	390.700	387.100	167.600	157.900	162.822	0.021
Holzschuh et al. (2009) [26]	Wasps	Invertebrate	Species richness	Community	11 9	2.636	1.667	1.502	1.500	1.501	0.619
Holzschuh et al. (2009) [26]	Wasps	Invertebrate	Occupied broodcells	Population	11 9	41.273	16.000	34.523	17.937	28.375	0.853
Ibarra-Macias et al. (2011) [27]	Birds	Bird	Proportion recaptured after translocation	Movement	5 5	0.390	0.061	0.179	0.031	0.128	2.314
Jesus et al. (2012)	Plants	Plant	Seed rain	Movement	3	19,296.000	10,164.000	1562.000	5437.000 4	683.739	1.560
Kormann et al. (2016) [29]	Heliconia (Heliconia tortuosa)	Plant	Proportion pollinated flowers	Fitness	13 13	0.190	0.080	0.110	0.110	0.110	0.965
Kormann et al. (2016) r201	Green hermit (Phaetornis guy)	Bird	Occupancy probability	Population	26 26	0.520	0.130	0.598	1.197	0.946	0.406

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Table 1 (continued)												
Citation	Organisms	Taxonomic category	Response variable	Level of organization	Ne N	Jc Xe	Xc	Se	S	S	0	di
Krewenka et al. (2011)	Solitary bees	Invertebrate	Abundance	Population	13	8 1.3	300	1.900	0.071	0.145	0.105	-0.918
(2011) [30] (2011) [30]	Bumble bees	Invertebrate	Abundance	Population	13	8 0.3	380	0.750	0.031	0.045	0.037	3.365
Kuykendall and Keller (2011) [31]	Rodents	Mammal	Species richness	Community	3	3 7.	000	8.000	1.732	0.000	1.225	- 0.653
Kuykendall and Kaller (2011) [21]	Western harvest mouse	Mammal	Abundance	Population	б	3 75.	000 4	.2.000	46.592	38.105	42.561	0.620
Kuykendall and	(neuro outonomy) meganous) Plains harvest mouse	Mammal	Abundance	Population	Э	3 35.	000 4	.8.700	4.503	54.040	38.344	- 0.286
Kuykendall and Valler (2011) [21]	(North American deermouse) (Domensions maniford of the	Mammal	Abundance	Population	З	3 25.	500 1	7.000	20.958	12.124	17.121	0.402
Kuykendall and	(Leventyscus municutuus) Hispid cotton rat (Sigmodon hispidus)	Mammal	Abundance	Population	б	3 32.0	000 1	1.300	17.321	20.611	19.037	0.870
Kuykendall and Value (2011) [31]	Hispid pocket mouse (<i>Chaetodipus</i>	Mammal	Abundance	Population	З	3 13.	300 1	4.700	11.258	12.124	11.699	- 0.096
Kuykendall and	Northern grasshopper mouse	Mammal	Abundance	Population	б	3 2.	200	5.700	7.967	14.030	11.409	-0.210
Kuykendall and	(Unycriomys teucogaster) Thirteen-lined ground squirrel	Mammal	Abundance	Population	3	3 1.	700	5.000	2.598	10.739	7.812	-0.338
Kuykendall and	(Spermophilus tridecernimeatus) House mouse (Mus musculus)	Mammal	Abundance	Population	3	3 3.	000	1.300	7.448	1.039	5.317	0.256
Kuykendall and Vollor (2011) [31]	Ord's kangaroo rat (Dipodomys ordii)	Mammal	Abundance	Population	3	3 1.	000	0.700	2.944	1.905	2.480	0.097
Leidner and Haddad	Crystal skipper (Atrytonopsis sp1)	Invertebrate	Proportion moved	Movement	З	6 0.	320	0.098	0.185	0.120	0.142	1.388
Orrock et al. (2011) [33]	Arthropods	Invertebrate	Species richness	Community	Г	7 49.	5 000	1.000	4.050	2.700	3.442	-0.544
Paolucci et al. (2012) [34]	Ants	Invertebrate	Species richness	Community	Ś	5 5.2	200	9.400	2.316	2.009	2.168	- 1.750
Resasco et al. (2012) [35]	Red fire ant (Solenopsis invicta)	Invertebrate	Trophic position	Community	10 1	0 1.3	367	1.686	0.271	0.541	0.428	0.405
Resasco et al. (2014) [36]	Ants	Invertebrate	Species richness	Community	~	8 10.	500 1	3.000	4.986	4.690	4.840	-0.488
Riva et al. (2018) [37]	Arctic fritillary butterfly (Boloria chariclea)	Invertebrate	Probability of persisting in directional movement	Movement	9	3 0.3	260	0.110	0.087	0.053	0.079	1.684
Seaman and Schultze	Forest-specialist bird	Bird	Estimated species richness	Community	4	4 13.	700	9.500	4.400	9.500	7.403	0.493
(2016) [20] (2016) [39]	Forest birds	Bird	Probability of crossing	Movement	16 1	2 0.	798	0.472	0.228	0.243	0.235	1.349
Van Geert et al. (2010) [40]	Common primrose (Primula vulgaris)	Plant	Proportion individuals with pollen dye moved	Movement	13 1	1 0.0	090	0.000	0.112	0.000	0.083	0.703

(continued)	
Table 1	

Citation	Organisms	Taxonomic category	Response variable	Level of organization	Ne	Vc Xe	X	0	Se	Sc	Sp	di
Van Rossum and	True oxlip (Primula elatior)	Plant	Proportion individuals with	Movement	ю	2	0.098	0.000	0.061	0.000	0.050	1.433
Vergnes et al. (2012) [42]	Spiders	Invertebrate	ponen ayo moved Species richness	Community	4	4	4.940	4.090	2.260	2.280	2.270	0.326
Vergnes et al. (2012) [42]	Carabid beetles	Invertebrate	Species richness	Community	4	4	1.580	1.160	2.440	2.480	2.460	0.148
Vergnes et al. (2012) [42]	Staphylinid beetles	Invertebrate	Species richness	Community	4	4	3.320	1.290	2.320	2.420	2.371	0.745
Vergnes et al. (2012) [42]	Spiders	Invertebrate	Abundance	Population	4	4	10.960	6.500	2.300	2.320	2.310	1.679
Vergnes et al. (2012) [42]	Carabid beetles	Invertebrate	Abundance	Population	4	4	2.190	1.840	2.840	2.860	2.850	0.107
Vergnes et al. (2012) [42]	Staphylinid beetles	Invertebrate	Abundance	Population	4	4	11.160	3.870	2.480	2.520	2.500	2.536
Vergnes et al. (2013) [43]	Greater white-toothed shrew (Crocidura russula)	Mammal	Occupancy	Population	4	4	1.750	1.670	0.850	0.630	0.748	0.093
Vergnes et al. (2013) [43]	Crowned shrew (Sorex coronatus)	Mammal	Occupancy	Population	4	4	1.500	0.500	1.500	0.500	1.118	0.778
Vergnes et al. (2013) [43]	Eurasian pygmy shrew (Sorex minutus)	Mammal	Occupancy	Population	4	4	0.750	2.500	0.750	2.170	1.623	-0.937
Viljur et al. (2018) [44]	Open habitat Butterflies	Invertebrate	Species richness	Community	18	8	13.100	11.800	3.100	2.700	2.907	0.437
Wells et al. (2009) [45]	Buckeye butterfly (Junonia coenia)	Invertebrate	Heterozygosity (observed)	Genetic	9	9	0.193	0.155	0.043	0.015	0.032	1.086
Zaitsev et al. (2014) [46]	Soil Macrofauna	Invertebrate	Taxon richness	Community	ю	3	18.000	13.000	1.039	1.559	1.325	3.019
Zaitsev et al. (2014) [46]	Soil Macrofauna	Invertebrate	Abundance	Population	3	3 25	73.000	2040.000	478.046	1290.378	973.037	0.438
Zaitsev et al. (2014) [46]	Oribatid mites	Invertebrate	Abundance	Population	ŝ	3 30,2	50.000 19),533.000	7996.879	6283.880	7191.565	1.192
Zaitsev et al. (2014) [46]	Mesostigmatid mites	Invertebrate	Abundance	Population	\mathfrak{c}	3 26	33.000	2067.000	1357.928	923.183	1161.085	0.390

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