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Impacts of corridors on populations and communities

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36 **Introduction**

37 This chapter focuses specifically on the most popular approach to maintain
38 connectivity in conservation and management, which is to create or maintain habitat
39 corridors. The popularity of corridors in conservation derives from the direct and
40 intuitive relationship to their purported function: by physically connecting otherwise
41 isolated fragments, corridors should increase the movement of both individuals and
42 genes. In doing so, corridors provide sources of immigrants to offset local extinction,
43 and sources of genetic diversity to reduce harmful effects of inbreeding and drift. The
44 most fundamental spatial models in ecology, including island biogeographic models
45 (MacArthur & Wilson 1967) and metapopulation models (Levins 1969; Hanski 1999),
46 predict that movement between patches will increase population size and persistence
47 (Moilanen and Hanski, Chapter 3) and, through the rescue of declining populations
48 (Brown & Kodric-Brown 1977), maintain local species richness. We recognize that
49 studies focusing on corridors represent only a small fraction of studies on connectivity,
50 and the large literature examining effects of patch isolation on colonization and
51 occupancy in metapopulations has been reviewed elsewhere (see table 9.1 in Hanski
52 1999; Moilanen & Nieminen 2002). The goal of this chapter is to assess existing
53 evidence for corridor effects on populations and communities, and to discuss future
54 directions that would permit more rigorous evaluation of their use in conservation.

55 We focus on population and community impacts of corridors because evidence
56 for the necessary prerequisite – that corridors increase movement and gene flow – has
57 been growing and has also been reviewed elsewhere. In a review by Beier and Noss
58 (1998) of 32 published studies as of 1997, 21 studied some aspect of animal movement

59 through or within corridors, and many supported the role of corridors in increasing
60 movement. Since that review, a number of other studies have demonstrated that corridors
61 enhance movement rates of plants and animals between otherwise isolated patches (e.g.,
62 Coffman et al. 2001; Berggren et al. 2002; Tewksbury et al. 2002; Haddad et al. 2003).
63 Still other recent studies have documented the role of connectivity in enhancing gene
64 flow (Aars & Ims 1999; Hale et al. 2001; Mech & Hallett 2001; Kirchner et al. 2003).
65 While some studies have not found evidence for corridor effects (Rosenberg et al. 1998;
66 Bowne et al. 1999; Danielson & Hubbard 2000), no studies have shown that corridors
67 decrease movement rates.

68 The growing number of studies that show how corridors affect movement
69 between patches provide a critical base of support for the idea that corridors should
70 enhance population viability. From this work, it follows that corridors will reduce
71 stochastic temporal variation in local and regional population sizes by increasing the rates
72 of immigration from high density to lower density patches. Another possibility that has
73 emerged from theoretical results is that corridors may have a negative effect by
74 synchronizing dynamics and causing simultaneous extinction (Petchey et al. 1997; Earn
75 et al. 2000; Hudgens & Haddad 2003). However, in cases most typical in conservation
76 where small populations have rare dispersal and low growth rates, corridors should
77 reduce local extinctions and allow individual patches to maintain a larger number of
78 species with stable population dynamics (Brown & Kodric-Brown 1977; Gonzalez &
79 Chaneton 2002). Other potential negative effects of corridors that have been discussed
80 extensively in the literature are reviewed elsewhere in this volume (Crooks and Sanjayan,
81 Chapter 1; Crooks and Suarez, Chapter 19; Dobson and McCallum, Chapter 20).

82 The link between corridor effects on movement and their effects on the
83 demography and persistence of populations, and ultimately, the maintenance of local and
84 regional biodiversity, is critical for the appropriate use of corridors in management. Yet,
85 there is currently a paucity of studies addressing population or community effects of
86 corridors. Consistent empirical evidence regarding population and community effects of
87 corridors would support their expanded implementation in conservation. In this chapter,
88 we first review empirical corridor studies that focus on population and community
89 effects, seeking synthesis across studies. We highlight deficiencies in the existing
90 literature, describe conditions under which corridor effects are expected, and discuss
91 problems with study scale and design. We then go on to detail how new research could
92 more effectively test the case for conservation benefits of corridors on populations and
93 communities.

94

95 **A review of corridor effects on populations and communities**

96 *I. The literature*

97 We reviewed all empirical studies that examined terrestrial and microcosm
98 corridor effects on population size or persistence, or on species diversity. Ideally for
99 conservation, population studies would focus on how corridors affect population
100 viability, and would thus measure persistence. Population growth can also be a strong
101 indicator of persistence, especially when corridors may tip the balance between
102 decreasing and increasing population trends. However, these measures are often difficult
103 to obtain as they require long-term studies for meaningful estimates. Other population-
104 level responses to corridors, such as size and survivorship, are less useful in assessing

105 conservation value, but are still correlated with population viability. Regarding diversity,
106 the most relevant response variables for conservation are often those that describe change
107 in community composition after fragmentation, such as the rate of species loss,
108 particularly with regard to species of management concern. One commonly measured
109 community response, species richness, could be used to assess loss. In our review, we
110 list response variables measured in existing corridor studies.

111 In our analysis, we included studies of corridor effects within patches relative to
112 similar, isolated areas. Although a number of studies have shown that corridors affect
113 population sizes by providing habitat for plants or animals within corridors, (e.g.,
114 Machtans et al. 1996; Laurance & Laurance 1999; Perault 2000; Pryke & Samways 2001;
115 Mönkkönen & Mutanen 2003) we are interested in the effects of corridors on population
116 or communities within patches they connect. We also did not include corridor studies
117 where different numbers and configurations of corridors were added (Holyoak 2000),
118 unless there were also treatments of unconnected fragments.

119 We searched the following journals using ISI Web of Science: *Biological*
120 *Conservation*, *Conservation Biology*, *Ecological Applications*, *Ecological Monographs*,
121 *Ecology*, *Ecology Letters*, *Ecography*, *Journal of Animal Ecology*, *Journal of Applied*
122 *Ecology*, *Journal of Ecology*, *Nature*, *Oikos*, and *Science*. We searched using the
123 following terms: (corridor*) and (population* or communit* or biodiversity). Our
124 search extended from 1977-2003, and was conducted on 15 December 2003.

125 We found 15 studies that tested for corridor effects on populations and 5 studies
126 that tested for corridor effects on diversity (Table 1). Some studies were included in both
127 categories, as they analyzed both population and community responses. Studies covered

128 a variety of species, including population studies on mammals, insects, microorganisms,
129 birds, and a lizard (in order of decreasing frequency), and diversity studies on arthropods
130 and birds. No studies focused on plants. Most studies (15/19) were experimental, as they
131 manipulated and replicated landscape pattern.

132 At first glance, support for the idea that corridors affect population size or
133 persistence appears strong. Of the fifteen studies focusing on population responses to
134 corridors, thirteen demonstrated some corridor effect. Yet there were often caveats along
135 with observed effects. Some studies (Fahrig & Merriam 1985; Mansergh & Scotts 1989;
136 Dunning et al. 1995) were unreplicated and others (Burkey 1997; Schmiegelow et al.
137 1997; Haddad & Baum 1999; Schmiegelow & Monkkonen 2002) observed corridor
138 effects that may have been caused by patch shapes, edges, or habitat types that were
139 confounded with corridor effects (see below, *III. Designing corridor studies in variable*
140 *environments*). Regarding corridor effects on diversity, all measured species richness and
141 only two microcosm experiments showed convincing positive effects (Gilbert et al. 1998;
142 Gonzalez & Chaneton 2002). The only other study to report evidence for corridor effects
143 on diversity had no replication (MacClintock et al. 1977).

144 We conclude that the empirical literature to date shows ambiguous support for
145 corridor effects on populations or communities. In support of corridors, most studies
146 reported some positive effect. These effects are apparent even above many other local
147 factors that are known to impact populations (like effects of local environments and other
148 landscape-level effects) and that might obscure corridor effects. Despite these results,
149 evidence remains weak because of confounding effects, and because some species
150 performed more poorly in patches connected by corridors (Holyoak & Lawler 1996;

151 Burkey 1997). At this time, current evidence offers tentative support for corridors, and
152 much more work on population and community responses is needed.

153 *II. When to expect positive corridor effects*

154 In considering why our review did not strongly support corridor effects, it is
155 important to be clear about the mechanisms or conditions under which we expect
156 corridors to impact populations. Certain species in any community will perceive corridor
157 habitat as being of equal or lesser quality than other surrounding habitat. It should be
158 clear that these species, often habitat generalists, will not respond to corridors. Thus even
159 when corridor experiments are conducted at the appropriate scale and are well controlled
160 and replicated, we do not expect all species to respond positively. Thus corridor research
161 and application should focus on species that are either specialists for the habitats and
162 corridors of interest, or are likely to exhibit reduced survival when traveling through
163 matrix habitat. Even for habitat specialists, patches must be separated by distances large
164 enough to restrict movement to the rate of few or no individuals per generation without
165 corridors. If movement rates between unconnected patches are high, then immigration
166 does not limit population size or diversity, and corridor utility for increasing population
167 viability depends on their capacity to reduce mortality risk relative to matrix habitat
168 (Hudgens & Haddad 2003).

169 Finally, corridor effects are likely to be highly scale-specific, both in terms of the
170 scale of the landscape relative to an organism's size or movement distances, and in terms
171 of the time scale of study relative to an organism's movement rate and generation time.
172 Our literature review points directly to this issue of scale. Studies focusing on smaller
173 organisms were generally more likely to find corridor effects than studies focusing on

174 larger organisms (Table 1). While just over half of the studies focusing on mammals or
175 birds found corridor effects for a majority of species, all studies focusing on insects and
176 on microcosms found such effects (Table 1). One reason for more consistent responses
177 with smaller species is that the landscape size can be better matched to the organism's
178 home range or ambit. Although this could be a strength of model systems, we found that
179 researchers tended to adjust their corridor length to the size of the organism, and that the
180 length of organisms in microcosm studies was not significantly longer relative to corridor
181 length (Fig. 1a). Though again not significant, microcosm studies were conducted for
182 many more generations (and include the four right-most points on Fig. 1b), allowing a
183 greater time for population dynamics to respond to corridors. Focus on scale should not
184 become overly restrictive in the study or implementation of corridors, in that any corridor
185 is likely to benefit many organisms, and likewise any organism is likely to respond to
186 corridors at many scales. For example, our work with colleagues on one experiment with
187 1 ha patches and 150 m long corridors that was initially designed with a focus on
188 butterflies has demonstrated corridor effects on birds, small mammals, insects, and plants
189 (Tewksbury et al. 2002; Haddad et al. 2003). Still, more attention should be devoted to
190 matching the scales of organisms and landscapes.

191 **[Table 1 and Figure 1]**

192 *III. Designing corridor studies in variable environments*

193 It is evident from our review that, in addition to issues of scale, issues of
194 landscape variability also need more attention in the design of future studies. Corridor
195 effects are only likely under a certain set of limited conditions, as their role is to increase
196 the likelihood of rare events. Thus, corridors may have no effect on populations in years

197 where dispersal is high (under density-dependant dispersal, these may be at times when
198 populations are growing), but these same corridors may be critical in years when
199 reproduction is lower, and dispersal is limited. Corridors may also have no effects when
200 habitats in the landscape are stable, but be essential in the face of disturbance (Shirley &
201 Sibly 2001). Thus, studies are needed that address the variability of effects rather than
202 simply mean effects. These studies would be conducted for longer time periods and
203 would more explicitly link corridor effects with population stresses.

204 Our review also makes clear that a critical aspect of study design is to assure that
205 corridor effects are not confounded by other factors. These are not simply factors
206 determined by the local environment, but rather are factors intrinsic to the landscape
207 design. Adding a corridor affects not only connectivity, but patch size and shape, which
208 can also affect population sizes and diversity (Harrison & Bruna 1999; Orrock et al.
209 2003). Haddad and Baum (1999) showed how the addition of a corridor changes edge
210 effects within patches, increasing the area available to edge avoiding butterflies, and thus
211 increasing their abundances. Schmiegelow (1997) and Collinge (2000) both discuss how
212 adding corridors affected the size of their experimental patches by adding the area of a
213 corridor, and thus influencing population size and diversity. Only four experiments have
214 controlled for the added area and change in shape caused by corridors in testing for their
215 effects (Gonzalez et al. 1998; Boudjemadi et al. 1999; Gonzalez & Chaneton 2002;
216 Tewksbury et al. 2002). Perhaps it is because of the difficulty in separating effects of
217 these uncontrolled variables that most studies in our review were experimental rather than
218 observational. Of critical importance in future studies is to account for environmental
219 and landscape variability in the design of experimental and observational studies.

220

221 **Future directions linking theory, model systems, and management**

222 The next decade in corridor research should include an explicit focus on how
223 corridors, and the movement they facilitate, affect populations and communities. Unlike
224 studies of movement alone, which can usually be conducted over short time periods and
225 at a variety of scales, studies of population and community consequences will have to
226 more carefully incorporate into their design an understanding of isolation's impact, both
227 in time and space. Because corridors often have their effects on extinction and on the
228 recolonization that follows, the role of corridors is likely to be observed only after long-
229 term studies or in particularly stressful years.

230 Theoretical predictions as well as some microcosm studies point to strong effects
231 of corridors on population and community dynamics, yet studies on macro-invertebrates
232 and vertebrates show weaker and inconsistent effects. Why is this? While corridors may
233 influence movement in many organisms, theory predicts stronger corridor effects on
234 populations linked by rare events – either because the patches are sufficiently distant that
235 migration is rare, or because the organisms are relatively sedentary. Microcosm studies
236 appear to back this claim, with clear population effects in moss microcosm systems
237 (patch area = 79 cm²) where the microinvertebrates in the moss are specialists on moss
238 habitat (Gilbert et al. 1998; Gonzalez et al. 1998; Gonzalez & Chaneton 2002). In those
239 studies, fragmentation created a matrix of completely unsuitable habitat, maximizing the
240 barriers to dispersal between isolated patches and the benefits incurred by corridors that
241 promote exchange. Larger scale studies are typically leaky systems – corridors may
242 increase movement between patches, but the degree of influence relative to movement

243 through the matrix is often hard to determine and variable between and within species. In
244 the following sections, we outline several research approaches to address corridor effects
245 on populations and communities of species of management concern.

246 *I. Corridors as conduits for rare events*

247 Most corridor studies to date are small in scale, typically covering centimeters to
248 hundreds of meters. These studies have provided a great deal of insight into how
249 corridors function. Yet their mismatch with scales of landscape conservation is striking.
250 This mismatch is further compounded by typical study species, which are usually
251 common and mobile. These characteristics are convenient for obtaining results in short-
252 term studies. Unlike species of conservation concern, common, mobile species are likely
253 to move through inhospitable matrix, especially when distances between patches are
254 relatively short. Higher movement rates between connected patches may not have
255 population consequences for these species, particularly over short time periods, as
256 movement rates between isolated patches are often sufficient to offset extinction in most
257 years (Hudgens & Haddad 2003).

258 When movement events are rare and corridors buffer populations against local
259 extinctions during stressful periods, corridors are likely to be most valuable in
260 conservation. Perhaps that is why microcosm studies show such consistently strong
261 effects. Gonzalez and colleagues (1998) examined microarthropod communities on moss
262 patches for only six months, and demonstrated some of the strongest effects of corridors
263 to date. While the study appears short in duration, it spanned at least several generations
264 for all species, much greater than typical studies of corridors.

265 Organisms of management concern that disperse over smaller areas and have
266 generation times of a year or less are much more likely to benefit from empirical studies
267 of corridor effects, because small-scale studies are applicable. There are many species of
268 plants, insects, small mammals, amphibians, and reptiles with relatively short generation
269 times that make up much of total biodiversity and that are likely to benefit from small-
270 scale corridors. Still, full accounting of the spatial and temporal dynamics that mediate
271 corridor effects in these species will require studies lasting multiple generations.

272 For many rare species with short generation times, local extinctions and
273 colonization dynamics are imposed by natural disturbances, and elucidating the role of
274 corridors requires long-term studies of movement and population sizes to determine
275 population viability. For example, our work with collaborators on an endangered
276 butterfly, the St. Francis Satyr (*Neonympha mitchellii francisci*), is designed to determine
277 the role of corridors in facilitating colonization and maintaining viable populations. This
278 sedentary subspecies occurs in small (0.1 – 0.6 ha), wetland openings along streams (Fig.
279 2) that are maintained by disturbances caused by beavers and by fire, without which
280 vegetation quickly succeeds to unsuitable riparian forest. Butterflies can survive neither
281 the disturbance nor the succession. We believe that riparian habitats serve as corridors to
282 promote colonization of new sites. Yet, in two years of research encompassing four
283 butterfly generations, we've marked 450 butterflies and observed just three movements
284 between patches, all between the closest (separated by 300m), connected patches.

285 **[Figure 2]**

286 The St. Francis Satyr case study highlights an important role of corridors: their
287 effects may be particularly important under stress or disturbance. Successional habitat

288 dynamics for St. Francis Satyr occur over many years or decades. The creation of new
289 openings by disturbance generates the opportunity for natural experiments. We've
290 already observed colonization of two sites that had been flooded and then abandoned by
291 beavers (both within a couple hundred meters of existing sites). It will take many years
292 to observe a sample size of openings that permits conclusions that will affect landscape-
293 level habitat restoration. Although studies of the interaction between corridors and
294 disturbance are rare, Shirley and Sibly (2001) created a microcosm experiment with fruit
295 flies that demonstrated the important interactions between corridors and environmental
296 disturbance. They investigated metapopulation response under unpolluted and polluted
297 conditions, and found that corridors increased population persistence in patches disturbed
298 with pollution (Shirley & Sibly 2001). An important area of future research will be to
299 further understand how the interrelationship between corridors and disturbance affects
300 populations and communities.

301 *II. Thinking big: large scale manipulations*

302 Conservation at the landscape scale usually involves corridors that may extend
303 kilometers to hundreds of kilometers. At these scales, there have been only a few
304 successful studies of movement (Beier 1995), gene flow (Hale et al. 2001; Mech &
305 Hallett 2001), or population sizes (Dunning et al. 1995). One response variable that is
306 not included in the corridor studies we reviewed, but is typical of connectivity studies in
307 metapopulations, is patch occupancy (Moilanen & Nieminen 2002). One approach to
308 expand the number of corridor studies at larger scales may be to focus more specifically
309 on patch occupancy in landscapes with and without natural corridors.

310 The primary constraint on studies at large scales is the difficulty in finding
311 replication and in controlling for variables that may confound corridor effects. In
312 addition to the confounding factors discussed above, connected patches tend to be larger
313 than unconnected patches (Villard et al. 1999; Fahrig 2003). Overcoming confounding
314 effects of other variables will likely require a great deal of replication and/or judicious
315 pairing of control and treatment sites, which can be difficult to find and sample at large
316 spatial scales.

317 Ideally, larger-scale, longer-term studies will involve some level of controlled
318 experimentation. Experimental manipulation of both habitat and disturbance levels
319 allows isolation of mechanisms and greater time-efficiency by eliminating confounding
320 variables. Long-term studies where landscapes are manipulated over large areas are
321 much more likely to yield definitive results regarding corridor effects, and collaborative
322 teams of researchers working at large scales may be much more effective than individual
323 researchers working separately at smaller scales. Evidence from one long-term, large-
324 scale fragmentation experiment, the Biological Dynamics of Forest Fragments Project in
325 Brazil, suggests that responses accumulate over time. This experiment was created
326 starting in 1980 in Manaus, Brazil to test the effects of fragmentation and patch size on
327 tropical ecosystems. It is only recently, after nearly 20 years of study, that major
328 community and ecosystem impacts of fragmentation have been documented (e.g.
329 Laurance et al. 1997; Bierregaard & Gaston 2001; Laurance et al. 2001; Ferraz et al.
330 2003). Given the critical roles of habitat loss and fragmentation as the most important
331 factors impacting the loss of biodiversity (Wilcove et al. 1998), more such studies are
332 needed.

333 One approach to studying effects of connectivity at large scales is to take
334 advantage of landscape manipulations that occur as part of landscape management. Such
335 manipulations occur every day through forestry, development, agriculture, and other
336 changes in land use. Although many alterations come through habitat loss, habitat
337 restoration should also provide opportunities for experimental assessment of responses to
338 connectivity. Because large-scale habitat modification for scientific research alone can
339 create serious ethical concerns, we recommend coordinating research plans along with
340 planned habitat modifications (destruction or restoration), so that useful information can
341 be gained in the context of adaptive management. Unfortunately, land use manipulations
342 are typically uncontrolled with respect to landscape factors like connectivity and other
343 important environmental factors that might obscure landscape-level responses, thus
344 limiting their usefulness in guiding future management. As pointed out by Beier and
345 Noss (1998), a good example of how a study can be designed around landscape
346 management was conducted by Mansergh and Scotts (1989). By measuring responses
347 before and after corridor restoration at a ski resort, they demonstrated positive effects of
348 corridors on Mountain Pygmy-possum survivorship.

349 In lieu of controlled experimentation, new research will have to be creative in
350 identifying opportunities for replicated large-scale manipulations allowing isolation of
351 corridor effects. In our own work, we have found that academic partnerships and close
352 collaboration with land-management agencies are critical for the success of these
353 projects. With investigators from three additional academic institutions, we have been
354 working closely with the U.S. Forest Service at the Savannah River Site in South
355 Carolina to assess large-scale effects of corridors. The Savannah River Site is an 80,000

356 ha site managed for plantation pine forest and as native habitat for wildlife. The Forest
357 Service employs clearcut forestry, and creates clearings that range in size from 5-50 ha.
358 These clearings vary in their connectivity, as some of the clearings are connected to
359 others by long, straight utility right-of-ways and roads (Fig. 3). Because these right-of-
360 ways are subjected to frequent, thorough disturbance (by herbicide and mowing), they are
361 unlikely to be long-term sources of butterflies, but instead serve as corridors between
362 suitable habitats.

363 **[Figure 3]**

364 To test the effects of large scale, open corridors in landscapes managed for
365 forestry, we have studied butterfly species that thrive in early successional habitats for up
366 to 8 years after forest harvest, when the pine canopy starts to close. After extensive
367 studies of two of these species, the buckeye (*Junonia coenia*) and the variegated fritillary
368 (*Euptoieta claudia*) using large, replicated, experimental landscapes, we have shown that
369 both are more likely to move between connected patches separated by up to 400 m
370 (Haddad 1999a; Tewksbury et al. 2002). To test these corridor effects at the much larger
371 scales of operational forestry, we conducted repeated surveys for both species in all (n =
372 137) clearcut openings on the Savannah River Site (some connected by utility right-of-
373 way corridors, others not). After controlling for potentially confounding effects such as
374 stand type, area, and age, very preliminary analyses from the first year of a multi-year
375 study indicate that the presence of a corridor increases population sizes of fritillaries, but
376 not buckeyes (B. Danielson and N. Haddad, unpublished data). Thus, at least for the
377 fritillary, results from small-scale studies appear to ‘scale up’ to larger areas. It is worth
378 noting that the one species whose responses did scale-up – the fritillary – is more

379 sedentary than the species whose responses did not show corridor effects at the largest
380 scale, the buckeye (Haddad 1999a). While far from conclusive, this supports the
381 theoretical prediction that corridor effects are more likely in situations in which migration
382 between patches is relatively rare. This work highlights a challenge in ecology and
383 conservation, which is to reconcile often smaller-scale experimental with often larger-
384 scale observational data.

385 *III. Linkage across life-history and trophic levels*

386 Population- and community-level responses to corridors are potentially caused by
387 many different mechanisms spanning trophic levels and acting on different life-history
388 stages. This diversity of corridor effects could magnify or dampen the observed response
389 for any particular population or community. Most often, researchers consider the effects
390 of corridors on movement or gene flow within an individual species. Considered more
391 deeply, however, there can be multiple stages at which movement can be important, and
392 multiple interactions that can result in positive or negative effects of corridors on
393 individual species. For even a single species, these may include a diversity of
394 interactions with different groups – predators, competitors, mutualists, parasites – all of
395 which may respond to fragmentation and corridors. For many plants, the initial effect of
396 corridors on movement rates will be a direct function of corridor effects on pollinators
397 and seed dispersers, and plant establishment will additionally be influenced by the
398 response of seed-predators, parasites, and herbivores. This diversity of interactions may
399 cause contrasting responses and can make detection of net population responses difficult.
400 The positive effects of corridors may be dampened or reversed by negative effects (Fig.

401 4; see also Crooks and Sanjayan, Chapter 1), and more work is needed to assess the
402 balance of positive and negative effects on population and community structure.

403 **[Figure 4]**

404 At both small and large scales, assessing net corridor effects on populations will
405 most likely be done through long-term studies. In studies of short duration (i.e., the
406 typical duration of a grant funding cycle or of a dissertation program), approaches that
407 focus on aspects of population demography might provide more rapid assessment of
408 corridor effects on survivorship and reproduction at key life-history stages (see Mansergh
409 & Scotts 1989; Beier & Noss 1998; Coffman et al. 2001). This approach may
410 occasionally allow researchers to model corridor effects on populations, especially if key
411 life-history attributes and developmental stages are easily identified. With structured
412 data, population models can be used to assess population dynamics and viability in the
413 presence or absence of corridors (discussed below). Yet conclusions from demographic
414 models must be approached with caution, as parameters estimated over relatively short
415 time intervals may fail to capture corridor impacts in extreme years (catastrophes or
416 bonanzas, Morris & Doak 2002) when corridors may be most important.

417 We have conducted an experimental study over the past decade where we have
418 had some success at determining corridor effects on aspects of population demography
419 (Tewksbury et al. 2002; Haddad et al. 2003). These experiments at Savannah River Site,
420 South Carolina have involved 1 ha experimental patches that are separated by 100+
421 meters. The patches are open, early-successional habitat surrounded by plantation pine
422 forest. Here, the openings are suitable for many species of plants, insects, mammals, and
423 birds, while the pine forest is not. Our work has focused mainly on movement of insects,

424 small mammals, birds, and plants, but we have made some inroads into understanding
425 effects on population demography. For example, we have found that corridors increase
426 plant pollination rates and dispersal of fruiting plants (Tewksbury et al. 2002; Haddad et
427 al. 2003). Both of these factors should lead to higher seed numbers in connected patches,
428 leading to predictions of higher population sizes (Tewksbury et al. 2002). Yet corridor
429 effects on plant demography are complex, and effects at one life-stage may be modified
430 or reversed by effects on other life-history stages. Studies with our collaborators, for
431 example, have shown that the same corridors that increase pollination and seed dispersal
432 (Tewksbury et al. 2002) also lead to increases in seed predation by mammals that use
433 corridors as foraging conduits (J. Brinkerhoff, unpublished data; Orrock et al. 2003). The
434 net impact of these corridor-related effects on whole plant population demography is
435 unclear (Fig. 4). Further research should focus on integrating landscape effects across
436 life-history stages.

437 *IV. Model-directed experimental research*

438 Empirical approaches will benefit from informed models that guide targeted
439 experiments. Three types of modeling exercises may be effective at informing future
440 research: individual-based models, numerical models, such as demographic models
441 linking effects at different life-stages, and analytical models that determine the types of
442 organisms most likely to respond to corridors. Models will serve to assess impacts of
443 empirically-measured responses at one life history stage on total population size. They
444 will also be important in determining which demographic characteristics and behaviors
445 should be the focus of further empirical study.

446 Individual-based models, often spatially-explicit, have the advantage of linking
447 some of the most available data on corridor use – movement data – to impacts on
448 populations and communities. To date, such models have had some success at linking
449 local behavior to larger-scale distribution (Tracey, Chapter 13; Tilman et al. 1997;
450 Tischendorf & Wissel 1997; Haddad 1999b). Individual-based models can incorporate
451 understanding of fine-scale decision rules that link dispersal to landscape structure.
452 Habitat-specific data on movement distances and turning can be used to predict corridor
453 effects on patch colonization. Of specific interest is the role of habitat boundaries, as
454 they define corridor structure and function (Cadenasso et al. 2003), and vary in their
455 permeability across species (Haddad 1999b). Other decision rules, such as the effects of
456 density or presence of related individuals (as in Le Galliard et al. 2003), may also be
457 included. One advantage to such models is that landscape characteristics can be easily
458 varied to generate predictions about corridor impacts. For example, three different
459 models have predicted that there is an asymptote to the effect of corridor width on
460 movement rates (Tilman et al. 1997; Tischendorf & Wissel 1997; Haddad 1999b).
461 Although this prediction has received some empirical support (Andreassen et al. 1996),
462 more is needed. A disadvantage of this approach is that adapting such models to
463 population-level questions involves a large and often intractable number of parameters.
464 Such individual-based models may be most effective in predicting corridor effects on
465 species with large ranges and long generation times, for which population trends are very
466 difficult to obtain. In these circumstances, individual-based models of movement in
467 relation to habitat boundaries, coupled with spatially explicit, habitat-specific data on

468 reproduction and survival, may provide much needed insight into the probable
469 effectiveness of proposed changes in land management.

470 Two other types of models may have greater practical applicability in determining
471 corridor effects on population size and community structure. Numerical models, such as
472 matrix models and structural equation modeling (Grace & Pugsek 1998; Caswell 2001),
473 can be used to project population trends and assess population viability. The primary
474 advantage to these approaches is that they integrate empirical estimates from research
475 targeted at specific life-history stages. Rather than ignore all corridor effects but those on
476 movement and on population sizes, a model-based approach integrates the impacts of
477 corridors on species and interactions across life-history stages. In addition to determining
478 the contribution of each stage to population growth, sensitivity analyses can be used to
479 determine how management targeted at a specific stage might be used to increase
480 population sizes in connected landscapes. To date, the use of these approaches has been
481 limited, primarily because researchers have yet to gather data on the effects of corridors
482 across life-history stages.

483 Another approach that can be used to predict responses to corridors is analytical
484 modeling. Analytical models can have a closed form solution, such that the equations
485 that describe the effects of corridors on populations can be expressed as a mathematical
486 function. These are often much simpler than the real-world corridors they represent, but
487 they can provide guidance about which characteristics are in need of targeted research,
488 and which species are in need of conservation. Metapopulation models have become
489 increasingly common in assessing effects of connectivity, including corridors (Henein &
490 Merriam 1990; Hess 1996; Anderson & Danielson 1997; McCallum & Dobson 2002;

491 Moilanen and Hanski, Chapter 2). Furthermore, these models have provided some of the
492 few analyses of how species interactions in fragmented landscapes with or without
493 corridors may affect host populations in the context of disease dynamics (Hess 1996;
494 McCallum & Dobson 2002; Dobson and McCallum, Chapter 20).

495 Analytical models that assess the role of corridors on population size are less
496 common. In simple population growth models, Earn and colleagues (2000) showed how
497 corridors can synchronize population dynamics and lead to metapopulation extinction.
498 Hudgens and Haddad (2003) used simple logistic population growth models to determine
499 for what types of species and situations corridors were likely to affect populations. They
500 modeled a two patch system that accounted for corridor effects by including terms for
501 corridor and matrix migration and mortality. Their results generated a number of
502 implications for further research and future conservation. First, their results suggest that
503 corridors are likely to benefit species with high population growth rates in the short term,
504 whereas they are likely to benefit species with low population growth rate in the long
505 term. Since most species of conservation concern have low growth rates, this result
506 further reinforces the need for studies of long-term population responses to corridors.
507 Second, their results suggest that the type of population dynamics exhibited by a species
508 will determine corridor effectiveness. Species that have large population oscillations
509 with years of low population size are likely to be harmed by corridors, as corridors are
510 likely to synchronize population dynamics among patches. Corridors are likely to benefit
511 species of conservation concern that are experiencing sustained population decline.
512 Third, they showed that it is usually not just dispersal through corridor and matrix
513 habitats, but also corridor and matrix mortality that determine corridor benefits. Only

514 when species have extremely low matrix migration are corridors likely to benefit
515 populations through their role in increasing migration. With higher matrix migration,
516 corridors are likely to increase population viability by reducing mortality during
517 dispersal. These results emphasize the need for demographic studies not only in patches,
518 but in corridor and matrix habitats as well.

519

520 **Conclusion**

521 Over the past decade, empirical research has generated broad support for the
522 hypothesis that habitat corridors increase movement through fragmented landscapes for
523 many species. The effects of corridors on population viability, however, are less well
524 studied, and the empirical understanding of corridor effects on community structure and
525 diversity is still in its infancy. In our review of the existing evidence, we find that
526 support for corridor effects on populations is growing, though with many caveats. There
527 is more support for corridor effects in smaller taxa with shorter generation times. This
528 result reflects greater ease in matching temporal and spatial scales of experiments with
529 smaller species. Although corridors are intended to promote movement, their ultimate
530 effectiveness in conservation must be measured by their population and community level
531 effects in promoting colonization, reducing extinction, and increasing population
532 viability.

533 Empirical support for corridors at the population and community level would
534 strengthen arguments to maintain or construct corridors, rather than to allocate resources
535 toward other conservation strategies. Empirical tests of corridor effects on populations
536 and communities will require long-term experiments conducted at large spatial scales,

537 coupled with creative approaches to obtaining difficult to observe events, such as rare,
538 long-distance dispersal. While such studies require careful coordination, we believe there
539 are opportunities for such large-scale studies in conjunction with planned habitat
540 restoration or destruction. For rare species, purely observational studies may be the only
541 ones that are possible to inform conservation decisions. However, they rarely can
542 overcome the many inter-correlated factors confounding the effects of connectivity.
543 Rather than focusing only on population abundance or species numbers, successful
544 studies are likely to integrate research on movement, habitat-specific demography, and
545 density-dependent interactions between species in an assessment of corridor effects on
546 population viability. Empirical studies would be aided by insights from analytical,
547 demographic, and individual-based models that help to focus research on specific life-
548 history characteristics and life-cycle stages that link corridor effects to population
549 dynamics. We are hopeful that such approaches will help stimulate more rapid progress
550 in understanding the impacts of corridors on populations and communities, and, thus,
551 their value in conservation.

552

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564 **Literature Cited**

- 565 Aars, J., and R. A. Ims. 1999. The effect of habitat corridors on rates of transfer and
566 interbreeding between vole demes. *Ecology* **80**:1648-1655.
- 567 Anderson, G. S., and B. J. Danielson. 1997. The effects of landscape composition and
568 physiognomy on metapopulation size: the role of corridors. *Landscape Ecology*
569 **12**:261-271.
- 570 Andreassen, H. P., S. Halle, and R. A. Ims. 1996. Optimal width of movement corridors
571 for root voles: not too narrow and not too wide. *Journal of Applied Ecology*
572 **33**:63-70.
- 573 Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. *Journal of Wildlife*
574 *Management* **59**:228-237.
- 575 Beier, P., and R. F. Noss. 1998. Do habitat corridors really provide connectivity?
576 *Conservation Biology* **12**:1241-1252.
- 577 Berggren, A., B. Birath, and O. Kindvall. 2002. Effects of corridors and habitat edges on
578 dispersal behavior, movement rates, and movement angles in Roesel's bush-
579 cricket (*Metrioptera roeseli*). *Conservation Biology* **16**:1562-1569.
- 580 Bierregaard, R. O., Jr., and C. Gaston. 2001. The Biological Dynamics of Forest
581 Fragments project: overview and history of a long-term conservation project in R.
582 O. Bierregaard, Jr., C. Gascon, T. E. Lovejoy, and R. C. G. Mesquita, editors.
583 Lessons from Amazonia: the ecology and conservation of a fragmented forest.
584 Yale University Press, New Haven, Connecticut, USA.

- 585 Boudjemadi, K., J. Lecomte, and J. Clobert. 1999. Influence of connectivity on
586 demography and dispersal in two contrasting habitats: an experimental approach.
587 *Journal of Animal Ecology* **68**:1207-1224.
- 588 Bowne, D. R., J. D. Peles, and G. W. Barrett. 1999. Effects of landscape spatial structure
589 on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). *Landscape*
590 *Ecology* **14**:53-65.
- 591 Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect
592 of immigration on extinction. *Ecology* **58**:445-449.
- 593 Burkey, T. V. 1997. Metapopulation extinction in fragmented landscapes: using bacteria
594 and protozoa communities as model ecosystems. *The American Naturalist*
595 **150**:568-591.
- 596 Cadenasso, M. L., S. T. A. Pickett, K. C. Weathers, S. S. Bell, T. L. Benning, M. M.
597 Carreiro, and T. E. Dawson. 2003. An interdisciplinary and synthetic approach to
598 ecological boundaries. *Bioscience* **53**:717-722.
- 599 Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*,
600 second edition. Sinauer Associates, Inc., Sunderland, Massachusetts.
- 601 Coffman, C. J., J. D. Nichols, and K. H. Pollock. 2001. Population dynamics of *Microtus*
602 *pennsylvanicus* in corridor-linked patches. *Oikos* **93**:3-21.
- 603 Collinge, S. K. 2000. Effects of grassland fragmentation on insect species loss,
604 colonization, and movement patterns. *Ecology* **81**:2211-2226.
- 605 Danielson, B. J., and M. W. Hubbard. 2000. The influence of corridors on the movement
606 behavior of individual *Peromyscus polionotus* in experimental landscapes.
607 *Landscape Ecology* **15**:323-331.

- 608 Dunning, J. B., Jr, J. R. Borgella, K. Clements, and G. K. Meffe. 1995. Patch isolation,
609 corridor effects, and colonization by a resident sparrow in a managed pine
610 woodland. *Conservation Biology* **9**:542-550.
- 611 Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. *Science*
612 **290**:1360-1364.
- 613 Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of*
614 *Ecology and Systematics* **34**:487-515.
- 615 Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival.
616 *Ecology* **66**:1762-1768.
- 617 Ferraz, G., G. J. Russell, P. C. Stouffer, R. O. Bierregaard, Jr., S. L. Pimm, and T. E.
618 Lovejoy. 2003. Rates of species loss from Amazonian forest fragments.
619 *Proceedings of the National Academy of Sciences* **100**:14069-14073.
- 620 Forney, K. A., and M. E. Gilpin. 1989. Spatial structure and population extinction: a
621 study with *Drosophila* flies. *Conservation Biology* **3**:45-51.
- 622 Gilbert, F., A. Gonzalez, and I. Evans-Freke. 1998. Corridors maintain species richness in
623 the fragmented landscape of a microecosystem. *Proceedings of the Royal Society*
624 *of London, Series B* **265**:577-582.
- 625 Gonzalez, A., and E. J. Chaneton. 2002. Heterotroph species extinction, abundance and
626 biomass dynamics in an experimentally fragmented microecosystem. *Journal of*
627 *Animal Ecology* **71**:594-602.
- 628 Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998.
629 Metapopulation dynamics, abundance, and distribution in a microecosystem.
630 *Science* **281**:2045-2047.

- 631 Grace, J. B., and B. H. Pugsek. 1998. On the use of path analysis and related procedures
632 for the investigation of ecological problems. *The American Naturalist* **152**:151-
633 159.
- 634 Haddad, N. M. 1999a. Corridor and distance effects on interpatch movements: a
635 landscape experiment with butterflies. *Ecological Applications* **9**:612-622.
- 636 Haddad, N. M. 1999b. Corridor use predicted from behaviors at habitat boundaries. *The*
637 *American Naturalist* **153**:215-227.
- 638 Haddad, N. M., and K. A. Baum. 1999. An experimental test of corridor effects on
639 butterfly densities. *Ecological Applications* **9**:623-633.
- 640 Haddad, N. M., D. R. Bowne, A. Cunningham, B. J. Danielson, D. J. Levey, S. Sargent,
641 and T. Spira. 2003. Corridor use by diverse taxa. *Ecology* **84**:609-615.
- 642 Hale, M. L., P. W. W. Lurz, M. D. F. Shirley, S. Rushton, R. M. Fuller, and K. Wolff.
643 2001. Impact of landscape management on the genetic structure of red squirrel
644 populations. *Science* **293**:2246-2248.
- 645 Hannon, S. J., and F. K. A. Schmiegelow. 2002. Corridors may not improve the
646 conservation value of small reserves for most boreal birds. *Ecological*
647 *Applications* **12**:1457-1468.
- 648 Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, England.
- 649 Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation:
650 what do we know for sure? *Ecography* **22**:225-232.
- 651 Henein, K., and G. Merriam. 1990. The elements of connectivity where corridor quality
652 is variable. *Landscape Ecology* **4**:157-170.

- 653 Hess, G. R. 1996. Linking extinction to connectivity and habitat destruction in
654 metapopulation models. *The American Naturalist* **148**:226-236.
- 655 Holyoak, M. 2000. Habitat patch arrangement and metapopulation persistence of
656 predators and prey. *American Naturalist* **156**:378-389.
- 657 Holyoak, M., and S. P. Lawler. 1996. The role of dispersal in predator-prey
658 metapopulation dynamics. *Journal of Animal Ecology* **65**:640-652.
- 659 Hudgens, B. R., and N. M. Haddad. 2003. Predicting which species will benefit from
660 corridors in fragmented landscapes from population growth models. *The*
661 *American Naturalist* **161**:808-820.
- 662 Ims, R. A., and H. P. Andreassen. 1999. Effects of experimental habitat fragmentation
663 and connectivity on root vole demography. *Journal of Animal Ecology* **68**:839-
664 852.
- 665 Kirchner, F., J. Ferdy, C. Andalo, B. Colas, and J. Moret. 2003. Role of corridors in plant
666 dispersal: an example with the endangered *Ranunculus nodiflorus*. *Conservation*
667 *Biology* **17**:401-410.
- 668 La Polla, V. N., and G. W. Barrett. 1993. Effects of corridor width and presence on the
669 population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape*
670 *Ecology* **8**:25-37.
- 671 Laurance, S. G., and W. F. Laurance. 1999. Tropical wildlife corridors: use of linear
672 rainforest remnants by arboreal mammals. *Biological Conservation* **91**:231-239.
- 673 Laurance, W. F., S. G. Laurance, L. V. Ferreira, J. M. Rankin- de Merona, C. Gascon,
674 and T. E. Lovejoy. 1997. Biomass collapse in Amazonian forest fragments.
675 *Science* **278**:1117-1118.

- 676 Laurance, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'angelo, A.
677 Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the
678 structure of Amazonian liana communities. *Ecology* **82**:105-116.
- 679 Le Galliard, J., R. Ferrière, and J. Clobert. 2003. Mother-offspring interactions affect
680 natal dispersal in a lizard. *Proceedings of the Royal Society of London Series B-*
681 *Biological Sciences* **270**:1163-1169.
- 682 Levins, R. 1969. Some demographic and genetic consequences of environmental
683 heterogeneity for biological control. *Bulletin of the Entomological Society of*
684 *America* **15**:237-240.
- 685 MacArthur, R. H., and E. O. Wilson 1967. *The theory of island biogeography*. Princeton
686 University Press, Princeton, New Jersey, USA.
- 687 MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb. 1977. Island biogeography and
688 the "habitat islands" of eastern forest. II. Evidence for the value of corridors and
689 minimization of isolation in preservation of biotic diversity. *American Birds* **31**:6-
690 12.
- 691 Machtans, C. S., M. Villard, and S. J. Hannon. 1996. Use of riparian buffer strips as
692 movement corridors by forest birds. *Conservation Biology* **10**:1366-1379.
- 693 Mansergh, I. M., and D. J. Scotts. 1989. Habitat continuity and social organization of the
694 mountain pygmy-possum restored by tunnel. *Journal of Wildlife Management*
695 **53**:701-707.
- 696 McCallum, H., and A. Dobson. 2002. Disease, habitat fragmentation and conservation.
697 *Proceedings of the Royal Society of London Series B-Biological Sciences*
698 **269**:2041-2049.

- 699 Mech, S. G., and J. G. Hallett. 2001. Evaluating the effectiveness of corridors: a genetic
700 approach. *Conservation Biology* **15**:467-474.
- 701 Moilanen, A., and M. Nieminen. 2002. Simple connectivity measures in spatial ecology.
702 *Ecology* **83**:1131-1145.
- 703 Mönkkönen, M., and M. Mutanen. 2003. Occurrence of moths in boreal forest corridors.
704 *Conservation Biology* **17**:468-475.
- 705 Morris, W. F., and D. F. Doak 2002. Quantitative conservation biology: theory and
706 practice of population viability analysis. Sinauer Associates, Inc., Sunderland,
707 Massachusetts.
- 708 Orrock, J. L., B. J. Danielson, M. J. Burns, and D. J. Levey. 2003. Spatial ecology of
709 predator-prey interactions: corridors and patch shape influence seed predation.
710 *Ecology* **84**:2589-2599.
- 711 Perault, D. R. 2000. Corridors and mammal community structure across a fragmented,
712 old-growth forest landscape. *Ecological Monographs* **70**:401-422.
- 713 Petchey, O. L., A. Gonzalez, and H. B. Wilson. 1997. Effects on population persistence:
714 the interaction between environmental noise colour, intraspecific competition and
715 space. *Proceedings of the Royal Society of London Series B-Biological Sciences*
716 **264**:1841-1847.
- 717 Pryke, S. R., and M. J. Samways. 2001. Width of grassland linkages for the conservation
718 of butterflies in South African afforested areas. *Biological Conservation* **101**:85-
719 96.

- 720 Rosenberg, D. K., B. R. Noon, J. W. Megahan, and E. C. Meslow. 1998. Compensatory
721 behavior of *Ensatina eschscholtzii* in biological corridors: a field experiment.
722 Canadian Journal of Zoology **76**:117-133.
- 723 Schmiegelow, F. K. A., C. S. Machtans, and S. J. Hannon. 1997. Are boreal birds
724 resilient to forest fragmentation? An experimental study of short-term community
725 responses. Ecology **78**:1914-1932.
- 726 Schmiegelow, F. K. A., and M. Monkkonen. 2002. Habitat loss and fragmentation in
727 dynamic landscapes: Avian perspectives from the boreal forest. Ecological
728 Applications **12**:375-389.
- 729 Shirley, M. D. F., and R. M. Sibly. 2001. Metapopulation dynamics of fruit flies
730 undergoing evolutionary change in patchy environments. Ecology **82**:3257-3262.
- 731 Tewksbury, J. J., D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J.
732 Danielson, J. Brinkerhoff, E. I. Damschen, and P. Townsend. 2002. Corridors
733 affect plants, animals, and their interactions in fragmented landscapes.
734 Proceedings of the National Academy of Sciences **99**:12923-12926.
- 735 Tilman, D., C. L. Lehman, and P. Kareiva. 1997. Population dynamics in spatial habitats.
736 Pages 3-20 in D. Tilman, and P. Kareiva, editors. Spatial ecology: the role of
737 space in population dynamics and interspecific interactions. Princeton University
738 Press, Princeton, NJ, USA.
- 739 Tischendorf, L., and C. Wissel. 1997. Corridors as conduits for small animals: attainable
740 distances depending on movement pattern, boundary reaction, and corridor width.
741 Oikos **79**:603-611.

742 Villard, M., M. K. Trzcinski, and G. Merriam. 1999. Fragmentation effects on forest
743 birds: relative influence of woodland cover and configuration on landscape
744 occupancy. *Conservation Biology* **13**:774-783.

745 Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying
746 threats to imperiled species in the United States. *Bioscience* **48**:607-615.

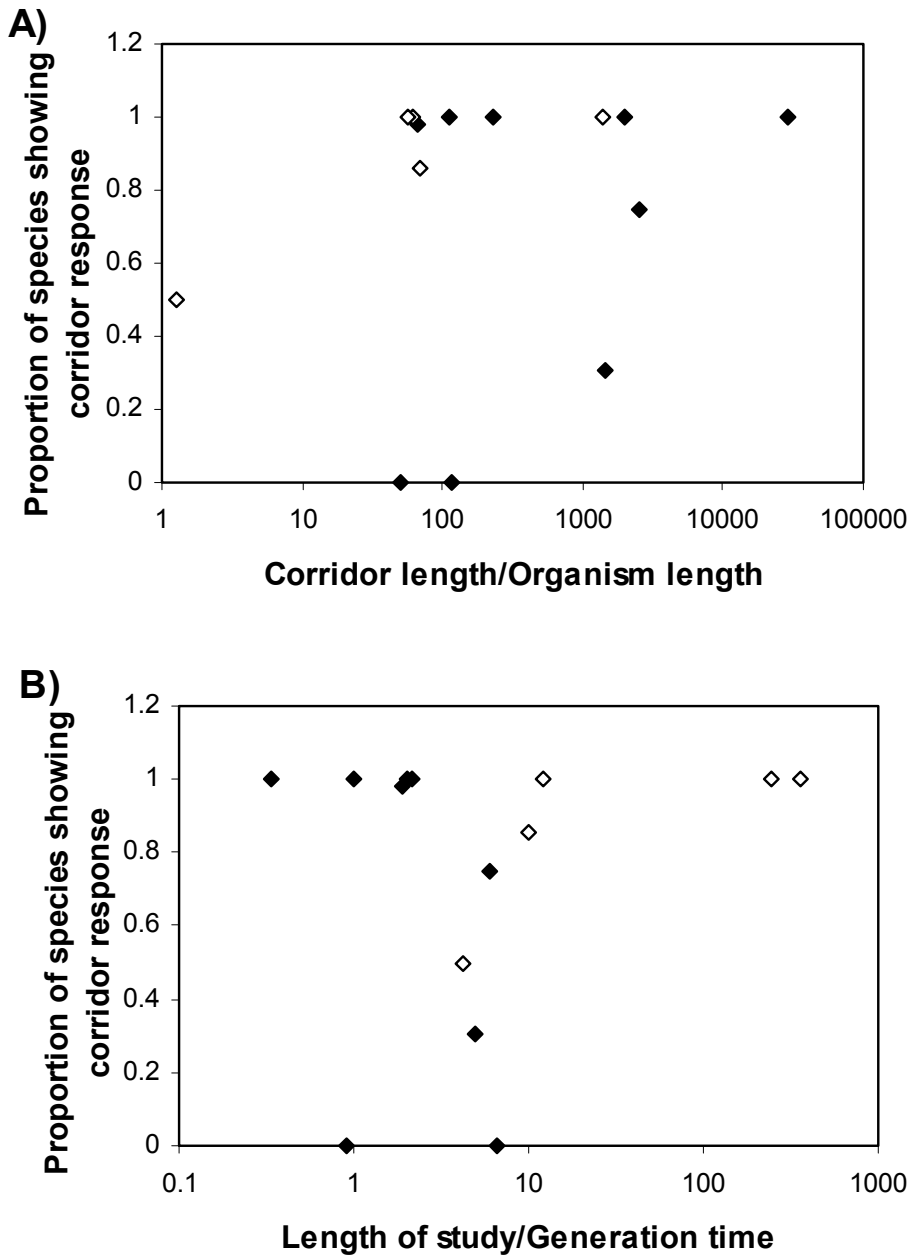
747 **Table 1.** Studies reporting responses of populations or communities within patches that are either connected by corridors or isolated.

Study	Species	Scientific Name	Study Type	Corridor Effect	Measured Population Response
<i>On Populations</i>					
Fahrig & Merriam 1985	Mammal: white-footed mouse	<i>Peromyscus leucopus</i>	Observational	Yes	Size
Mansergh & Scotts 1989	Mammal: mountain pygmy-possum	<i>Burramys parvus</i>	Observational	Yes	Survivorship
La Polla & Barrett 1993	Mammal: meadow vole	<i>Microtus pennsylvanicus</i>	Experimental	Yes	Size
Ims & Andreassen 1999	Mammal: Townsend's vole	<i>Microtus townsendii</i>	Experimental	No	Growth
Coffman et al. 2001	Mammal: meadow vole	<i>M. pennsylvanicus</i>	Experimental	No Yes	Size Survivorship
Hannon & Schmiegelow 2002; Schmiegelow et al. 1997	Birds		Experimental	Yes for 7 of 23 species	Size
(Dunning et al. 1995)	Bird: bachman sparrow	<i>Aimophila aestivalis</i>	Observational	Yes	Size
Boudjemadi et al. 1999	Herpetile: common lizard	<i>Lacerta vivipara</i>	Experimental	Yes in rich habitats No in poor habitats	Survivorship and Fecundity
Haddad & Baum 1999	Insects: butterflies		Experimental	Yes for 3 of 4 species	Size
Forney & Gilpin 1989	Insects: fruit fly	<i>Drosophila hydei</i> <i>D. pseudoobscura</i>	Experimental ¹	Yes for 1 of 2 species	Persistence
Shirley & Sibly 2001	Insect: fruit fly	<i>D. melanogaster</i>	Experimental ¹	Yes in polluted areas No in non-polluted areas	Persistence
(Gonzalez et al. 1998)	Microarthropods		Experimental ¹	Yes for 18 of 21 species	Persistence and Size

Burkey 1997	Microorganisms	Experimental ¹	Yes	Persistence
Holyoak & Lawler 1996	Microorganisms	Experimental ¹	Yes for 2 of 2 species	Persistence and Size
<i>On Diversity</i>				
(MacClintock et al. 1977)	Birds	Observational	Yes	Species Richness
Schmiegelow et al. 1997	Birds	Experimental	No	Species Richness, Log Series α , Jaccard Similarity
Collinge 2000	Insects	Experimental	No	Species Richness
(Gilbert et al. 1998)	Microarthropods	Experimental ¹	Yes	Species Richness
(Gonzalez & Chaneton 2002)	Microarthropods	Experimental ¹	Yes	Species Richness

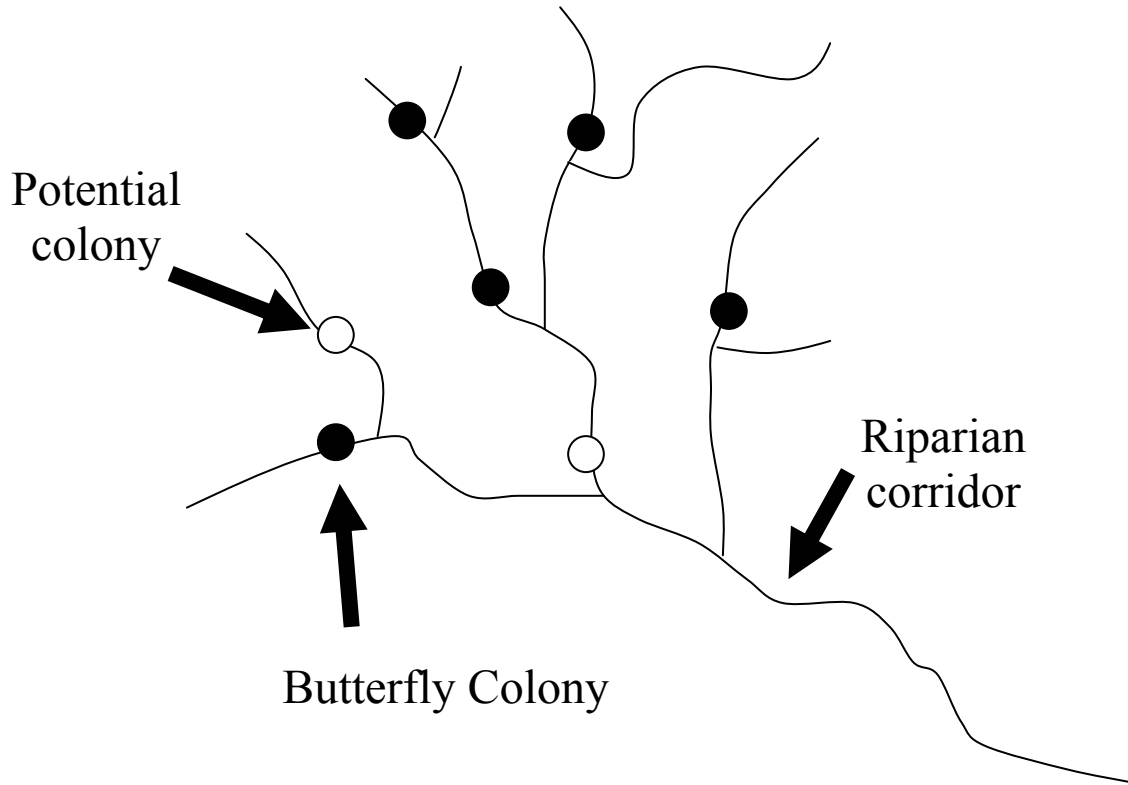
749 **Figure 1.** Effects of spatial and temporal scale on population responses to corridors.
 750 Each data point represents one population study in Table 1, and shows the proportion of
 751 species that demonstrated population response to corridors (that is, populations
 752 performed significantly differently in connected relative to unconnected patches; n = 14
 753 studies), as a function of A) the ratio of corridor length to average organism length within
 754 a study, and B) the ratio of study duration to the average generation time within a study.
 755 Neither relationship was significant in analyses with all studies, or excluding microcosm
 756 studies (white diamonds).

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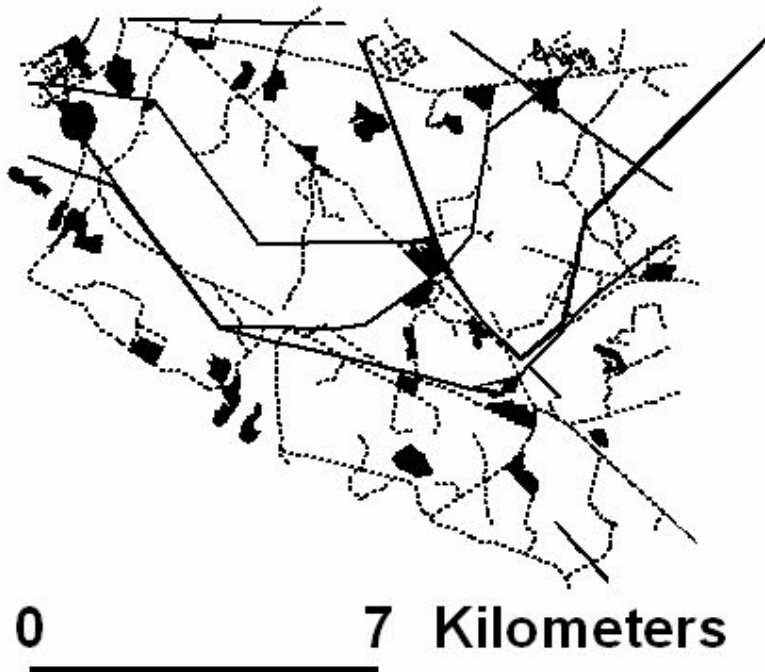
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777 **Figure 2.** Metapopulation structure of the St. Francis Satyr. Riparian corridors may
778 serve as movement corridors to promote colonization of habitats created by disturbance.
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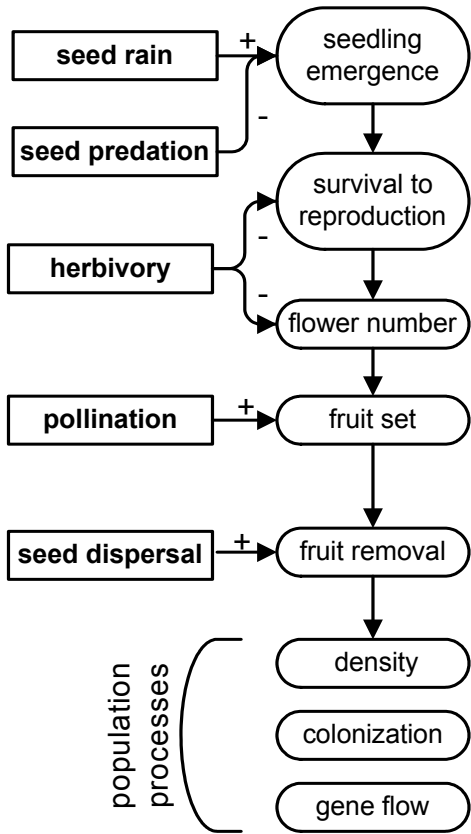
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781 **Figure 3.** Fragmentation of cleared patches caused by forest management at the
782 Savannah River Site, SC. Black areas are clearings 1-7 years of age. Solid black lines
783 are utility right-of-ways that may serve as corridors for dispersing butterflies and other
784 organisms. Dashed lines are roads, primarily small, forest roads, that are less likely to
785 serve as corridors. Cleared patches vary in isolation, both in their distance to other
786 patches and in their connection to other patches utility right-of-ways.
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790 **Figure 4.** Effects of corridors on various life stages of plants. Multiple plant-animal
 791 interactions could cancel or enhance corridor effects on a single plant species.
 792 Interactions are in square boxes, with arrows pointing to life-history stage affected (in
 793 ovals) with positive and negative signs indicating the most likely effect on plant
 794 demography. Density dependent linkages between interactions (seed-rain and seed
 795 predation, pollination and herbivory), and feedbacks onto animal counterparts of the
 796 plants (seed predators, herbivores, pollinators etc.) further increase the complexity of
 797 effects that may be influenced by patch isolation and connectivity.
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