ECOGRAPHY

Research

Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape

Sean R. Griffin and Nick M. Haddad

S. R. Griffin (https://orcid.org/0000-0003-4398-9202) ✉ (srgriffin108@gmail.com) and N. M. Haddad, Dept of Integrative Biology, Michigan State Univ., East Lansing, MI, USA, and: W. K. Kellogg Biological Station, Michigan State Univ., Hickory Corners, MI, USA.

Ecography
44: 919–927, 2021
doi: 10.1111/ecog.05299

Subject Editor: Michel Baguette
Editor-in-Chief: Miguel Araújo
Accepted 22 January 2021

Though landscape corridors increase dispersal of many animals and plants, it remains unknown whether these positive effects extend to the process of colonization and establishment of new populations in fragments. Working in experimentally fragmented landscapes, we tested how two aspects of habitat fragments altered by corridors – connectivity and edge-to-area ratio – determine patterns of colonization by a solitary, cavity-nesting bee *Megachile rotundata*. We found that though connectivity initially affected rates of nest-site occupation, edge-to-area ratio ultimately determined the final patterns of patch occupation and nest building, likely due to habitat selection by our focal species. Bee colonization was also higher in patches with higher abundances of their preferred food resources, flowers from the Fabaceae family. Our results show the importance of considering the effects of both connectivity and edge on population dynamics in habitat-based conservation.

Keywords: habitat loss, habitat patch, isolation, landscape conservation, landscape corridors

Introduction

Habitat fragmentation, which decreases habitat amount and simultaneously increases habitat isolation, is among the most serious threats to animal and plant populations worldwide (Haddad et al. 2015, Hanski 2015). At a landscape scale, fragmentation causes declines in metapopulation persistence by reducing the survival of local populations and providing a significant barrier to immigration between habitat patches (Gonzalez et al. 1998). Colonization is a key driver of these metapopulation dynamics; increasing rates of recolonization in habitats where local populations have been lost can increase metapopulation viability across fragmented landscapes (Hanski 1998). Theory predicts that colonization rates may be affected by spatial aspects of fragments such as connectivity to other habitat patches, patch shape and patch area (Weins 1997, Klok and DeRoos 1998, Moilanen and Hanski 1998, Moilanen and Nieminen 2002, Ewers and Didham 2007). However, there has been little study of how habitat-focused conservation practices, like corridors, alter the ability of dispersing organisms to establish local populations.

NORDIC SOCIETY OIKOS

www.ecography.org

One justification for the use of landscape corridors (thin strips of habitat used to connect isolated habitat fragment) is that they are expected to promote colonization of fragments and thereby increase population viability. Increased connectivity due to corridors has been shown to effectively increase the movement of plants and animals across landscapes (Gilbert-Norton et al. 2010, Resasco 2019). In turn, increased movement caused by corridors increases abundance (Haddad and Baum 1999, Resasco et al. 2014) and species richness in connected fragments (Gilbert et al. 1998, Damschen et al. 2006, 2019). It is unclear whether the positive effects of corridors on abundance and species richness are due to increased population persistence within connected habitats, or to increased rates of colonization and establishment by dispersing organisms. Although the higher dispersal caused by corridors is expected to positively affect rates of colonization, few studies have explicitly studied the effects of corridors on population-level processes like establishment (Beier and Gregory 2012).

In addition to their primary function of restoring connectivity, corridors can have an unintended consequence: they increase edge-to-area ratio of fragments (Haddad and Baum 1999, Tewksbury et al. 2002). Higher edge-to-area ratio due to the long, thin shape of corridors may alter abiotic conditions within connected patches (Menz et al. 2011, Evans et al. 2012, Damschen et al. 2014) and increase the amount of suitable habitat for edge-associated species (Ewers and Didham 2007, Haddad et al. 2014). The addition of edgy habitat may also raise the probability that dispersing organisms will encounter the habitat when moving through the landscape (Ewers and Didham 2006, 2007). Though both connectivity and edge effects of landscape corridors have been found to affect movement of organisms between fragmented habitats, their relative impacts on colonization are unknown.

Habitat-based conservation is commonly used for one group, the wild bees, with little understanding of how spatial factors may affect the ability of bees to establish new populations. Wild bee populations have been devastated by the destruction of natural habitat and other human activities (Potts et al. 2010, Winfree 2010, Goulson et al. 2015), causing these important pollinators to become a major focus of conservation efforts worldwide (Byrne and Fitzpatrick 2009, Wilson et al. 2017). Conservation practices generally center on the creation of high-flowering habitats (Winfree 2010, Scheper et al. 2015, Vaudo et al. 2015, Williams et al. 2015), with the hope that bees will quickly colonize these new habitats and diverse bee communities will persist over time. Thus, strategies that increase the likelihood and success of bee colonization may be vital for meeting conservation goals.

Bees are mobile organisms with relatively strong flight ability, but female bees are central-place foragers limited in their movement by the energetic costs of traveling back and forth from their nests (Murray et al. 2009, Zurbuchen et al. 2010). In addition, bee flight ability is related to body size, with smaller bees exhibiting smaller flight distances (Greenleaf et al. 2007). Thus, many bees forage relatively close to their nests (Gathmann and Tscharntke 2002, Greenleaf et al. 2007) and exhibit reduced reproductive success (Peterson and Roitberg 2006, Zurbuchen et al. 2010) and lower abundance with increasing distance from natural, resource-rich areas (Garibaldi et al. 2011, Kennedy et al. 2013). Landscape corridors may benefit bees in isolated and fragmented habitats by increasing bee movement and their ability to access resources (Haddad et al. 2003, Townsend and Levey 2005, Cranmer et al. 2012). Foraging bumblebees follow hedgerows and other linear habitat elements through agricultural fields, essentially using them as corridors (Cranmer et al. 2012). In addition, higher connectivity between habitats leads to higher pollen transfer, indicating longer travel distances and increased movement by foraging bees and other pollinators (Tewksbury et al. 2002, Townsend and Levey 2005, Geert et al. 2010, Cranmer et al. 2012, Kormann et al. 2016). However, these and other studies of bee response to landscape fragmentation generally measure foraging bees rather than dispersers (Pyke 1984, Palladini and Maron 2014). It is unknown whether the positive effects of landscape corridors on bee movement extend to population-level processes such as dispersal and colonization.

To test the effects of connectivity and edge-to-area ratio on habitat colonization by bees, we conducted a large-scale release experiment with solitary, cavity-nesting bees within a set of experimentally fragmented landscapes. This bee species was not previously found in our landscapes, so any bees we observed originated from the location of our releases. This allowed us to examine patterns of colonization without the confounding effects of pre-existing populations. We tested for effects of patch connectivity and edge-to-area ratio on three aspects of solitary bee colonization: initial bee occupation of nests, nest-building and reproductive output. We also included floral availability as a covariate in our analysis based on the known, positive relationship between bee abundance and floral abundance (Potts et al. 2003, Roulston and Goodell 2011, Hopwood et al. 2015, Herrmann et al. 2017). Due to previous findings that corridors increase pollinator movement (Tewksbury et al. 2002, Haddad et al. 2003, Townsend and Levey 2005), we hypothesized that corridors would increase bee colonization across our fragmented landscapes and that these effects would be primarily driven by connectivity rather than edge effects.

Methods

Experimental landscapes

To test the effects of corridors and habitat edges on patterns of bee colonization, we used a long-established set of experimentally fragmented landscapes: the Savannah River Site Corridor Project. These experimental landscapes were created in winter 2000 and 2007 and are maintained by the USDA Forest Service at Savannah River Site (SRS; Fig. 1A), a National Environmental Research Park in Aiken and Barnwell Counties in South Carolina, USA (33°20'N, 81°40'W). Within this experiment, each of seven replicate

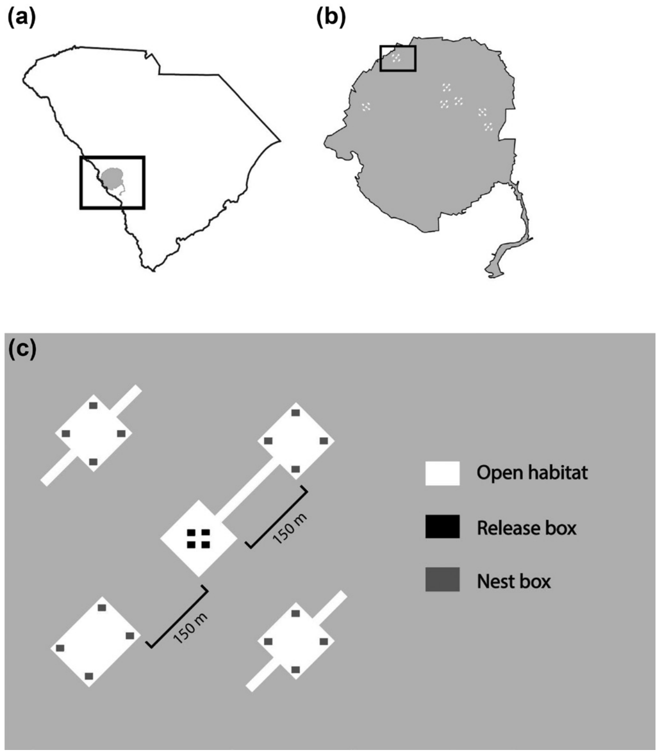

Figure 1. (a) Savannah River Site (SRS) in South Carolina; (b) location of experimental landscape blocks within SRS; (c) diagram of one of seven experimental blocks. Four bee release boxes were placed in the center patch of each block (36.77 m from two near edges), and four nest boxes were placed in the corners (14.85 m from two near edges) of each peripheral habitat patch.

landscapes (hereafter 'blocks') (Fig. 1B) is composed of five patches of open longleaf pine savanna habitat within a surrounding matrix of pine forest. Each block has one, 1-ha center patch surrounded by four, 1.375-ha peripheral patches. A single peripheral patch is connected to the center patch by a 150 m long by 25 m wide habitat corridor of open longleaf pine savanna habitat ('connected' patch). Three unconnected patches in each block are also separated from the center by 150 m and are the size of the connected patch plus the corridor. The additional area is added either as a blind-ended corridor ('winged' patches) or an extended footprint ('rectangular' patches), to control for the added area of the corridor (Fig. 1C). Within each block, one unconnected patch is winged, one is rectangular and the third is either winged or rectangular. The relative position of all patches within each block is randomized to control for any effect of directionality and patch orientation. All habitat patches are actively restored to longleaf pine savanna through prescribed burning and hardwood removal, and contain a diversity of flowering forbs that serve as floral resources for bees. In contrast, the matrix around the habitat patches is predominantly composed of dense plantations of pine trees and is largely devoid of flowering resources.

Our experimental design lets us separate out the effects of connectivity and edge-to-area ratio. Comparison between connected and winged patches provides a test of the effect of connectivity because the two patch types have similar shapes and edge-to-area ratios but differ in connectivity. Comparison between winged and rectangular patches provides a test of the effect of edges, because both patch types are disconnected, but winged patches have ~50% more edge than rectangular patches. Finally, comparison between connected and rectangular patches provides a test of the additive effects of connectivity and edge, because connected patches have more edge and connectivity than rectangular patches.

Experimental bee release

We studied the alfalfa leafcutting bee *Megachile rotundata*, a small solitary bee commonly managed as a pollinator of alfalfa and other commercial crops. Although this bee originated in Europe, its current range extends throughout the entire United States (Strange et al. 2017). *Megachile rotundata* was an ideal model organism for our landscape-level experiment for several reasons. First, because this bee species is commercially available and overwinters as larvae within cocoons made from leaves, it was possible to obtain sufficient numbers of bees and carefully control their emergence timing for our experiment (Pitts-Singer and Cane 2011). Second, as *M. rotundata* is a cavity-nesting species, we were able to manipulate nesting resources across each block to study patterns of dispersal and fragment colonization (McCorquodale and Owen 1997). Third, though this bee is widespread and found in the region surrounding SRS, it has not been previously found in our experimental landscapes, giving us confidence that any *M. rotundata* found within our sites originated from our release points. Finally, because body size predicts foraging range and dispersal ability in bees (Greenleaf et al. 2007), *M. rotundata* is a relevant model for the dispersal and colonization behavior of other small-bodied, solitary bees. *Megachile rotundata* also exhibits similar cavity-nesting behaviors to native Megachilids, a common group in our study region (Horn and Hanula 2004).

In early April 2018, we obtained *M. rotundata* cocoons from a commercial bee provider, JWM Leafcutters Inc. (Nampa, ID, USA). We stored all cocoons at 4°C until late April when spring temperatures and floral resources at the experimental blocks were approaching suitable levels for *M. rotundata*. We then incubated the cocoons at 30°C for ~17 days until the first of the male bees started emerging, after which we placed 40 g of cocoons (approximately 500 individuals) into each release box. Release boxes consisted of white cardboard boxes (10.16 by 10.16 by 5.08 cm) with small holes cut in one side, placed inside empty wooden nest boxes and mounted on heavy metal fenceposts one meter above the ground. Wooden boxes were built using 1.5 cm pine plywood, and were 36 cm tall, 24 cm wide and 18 cm deep, with an extra 6 cm overhang to protect bee nests from rain and direct sun. Four of these wooden nest boxes were placed in the center patch of each experimental block (36.77 m from the two closest edges), for a total of approximately 2000 *M. rotundata* individuals released per block. Because female bees generally make up about 1/3 of all *M. rotundata* (Pitts-Singer and James 2005), our releases constituted approximately 667 reproductive female bees released per experimental block. All cocoons in release boxes were placed in the field on 10 and 11 May, and full emergence likely occurred within one to two weeks following this initial placement.

Prior to bee release, we placed standardized nesting resources in all peripheral patches to allow observation of bee colonization and brood rearing. Within nest boxes (identical to the wooden boxes described above), we used two types of nesting resources: bundles of *Phragmites* reeds ~0.8 cm diameter and 15.24 cm long, and polystyrene blocks with holes 0.6 cm diameter and 7.62 cm long. Two bundles of 30 reeds were zip-tied to the sides of each nest box, and one 15.24 by 15.24 cm polystyrene nesting block with approximately 210 holes was glued to the back of each nest box (Supporting information). Nest boxes were provisioned with this overabundance of nesting resources to increase our chances of colonization and so remove nesting resource availability as a factor that could limit bee colonization. We placed four nest boxes in each peripheral patch, positioned in every corner 14.85 m from the two closest edges. Nest boxes were mounted on heavy metal fence posts approximately one meter from the ground and placed facing the south-east to standardize directionality and allow for morning sun exposure. Chicken wire was also attached to the front of all nest boxes as protection from disturbance by birds and mammals.

Bee dispersal and colonization

To study initial *M. rotundata* occupation of habitat patches, we counted individual bees within nest boxes soon after release. To do this, we visited nest boxes at night when all occupying bees were present in their nests. Shining a bright flashlight into the reeds and nest blocks, we counted every female bee present in nests. We were able to reliably distinguish *M. rotundata* from other species of wood nesting *Megachile* by their small size and white scopa. We started our first round of observation on 20 May, 10 days after release, to give female bees adequate time to emerge, mate and search for nests. We continued to visit all nests until no additional nesting *M. rotundata* were found in nest boxes (13 June, 34 days after release), at which time we removed all nest materials from the field.

In the lab, we dissected all reeds and occupied nesting blocks to count total number of nests and brood cells produced. As a measure of nests produced by *M. rotundata*, we counted all nesting resources (individual reeds or holes in polystyrene blocks) that had one or more fully formed brood cells. To measure the number of cells per nest, we counted the number of fully formed cells within each individual reed or hole, pulling apart attached cells to gain an accurate count. Brood cells were reared to adulthood and all emerged bees were confirmed as *M. rotundata* with a dissecting microscope.

Floral resources

To measure floral resources available to nesting bees during our experiment, we counted flowers within all peripheral patches of each experimental block. We created 50 m transects within each peripheral patch at three distances from the nearest edge (1, 14.85 and 36.77 m). The mid-point of each transect was measured from a randomly selected corner toward the center of the patch. The transect formed a right angle, with each extending 25 m parallel to the nearest patch edge (see the Supporting information for diagram of floral transects). Within 1 m of each side of the transect, we counted all flowering plant individuals per species. For ten individual plants of each species, we counted the number of inflorescences per plant. We then multiplied the average inflorescences for these 10 individuals by the number of individuals of that species to obtain an estimated number of inflorescences per species per transect. We then added together the estimated number of inflorescences in a patch to obtain a relative count of inflorescences per species per patch. Because our focal species *M. rotundata* is known to prefer legume flowers from the plant family Fabaceae, we added together the estimated counts per plant species to create two measures of floral abundance for our analyses: the relative count of Fabaceae inflorescences per patch and the relative count of all non-Fabaceae inflorescences per patch. We conducted two rounds of floral sampling, with the first round between 25 and 29 May and the second between 10 and 13 June. Over these two sample rounds, we identified and counted 11 Fabaceae species and 42 other species of flowering plants. There was no correlation between Fabaceae and non-Fabaceae abundances ($r = 0.1$, $p = 0.63$), and patch type did not affect either Fabaceae abundance ($\chi^2 = 0.82$, $df = 2$, $p = 0.66$) or the abundance of non-Fabaceae flowering plants ($\chi^2 = 0.62$, $df = 2$, $p = 0.73$) over the two rounds of sampling.

Analysis

We used generalized linear mixed models to test for the effects of patch type and floral resources on three measures of *M. rotundata* colonization: initial nest occupation after 10 days since release, final number of nests created and final number of cells per nest. Due to the large distances between patches and the few points with experimental nest boxes, we expected an overall low rate of nest-site occupation. Therefore, we calculated all response variables per patch by combining counts from both types of nesting materials (reeds and nest blocks) and each of the four nest boxes within a patch. This gave us a total sample size equivalent to the number of peripheral patches in our study ($n = 28$) per response variable. For each of our three models, we used patch type (connected, winged and rectangular) and floral abundance as our main effects and included block as a random effect. We only used floral abundances from the first round of sampling for the initial nest occupation model to better match the timing of floral counts to the response variable. We summed floral abundances from both rounds of floral sampling for the other two models. For the cells per nest response variable, we removed one block from the model because bees did not build any nests in that block. We used GLMMs with Poisson distribution for initial nest occupation and number of nests, and a normal distribution for the number of cells per nest (package lme4, Bates et al. 2014). Test statistic (χ^2 value) and significance for fixed effects in all models were estimated using type III ANOVAs. We then conducted Tukey–Kramer contrasts (package lsmeans, Lenth 2016) to determine the effect of patch type. All analyses were performed in R (<www.r-project.org>).

Results

In our first survey starting 10 days after bee release, we observed 88 nesting female *Megachile rotundata*. We found an effect of patch type ($\chi^2=7.8$, df=2, p=0.02) on initial occupation rates. Connected patches had higher, albeit non-significant, initial occupation than winged patches (35% more bees, Fig. 2) and significantly higher initial occupation than rectangular patches (111% more bees, Fig. 2), indicating an additive effect of connectivity and edge-to-area ratio. We also found a significant positive effect of Fabaceae abundance ($\chi^2=4.19$, df=1, p=0.04, Fig. 3A) but no effect of overall non-Fabaceae floral resources ($\chi^2=0.85$, df=1, p=0.36, Supporting information) on initial patch occupation.

After the nest tubes were removed from the field at the end of the flight period, we counted a total of 168 *M. rotundata* nests containing 494 sealed brood cells. We found that the number of nests in patches was strongly affected by patch type ($\chi^2=20.05$, df=2, $p < 0.0001$), as bees in connected and winged patches produced similar numbers of nests, but those patch types had 122–159% more nests than rectangular patches (Fig. 4A). The number of bee nests was higher in patches with more Fabaceae flowers ($\chi^2=8.46$, df=1, p=0.004, Fig. 3B), but unrelated to the abundance of non-Fabaceae flowers ($\chi^2=2.00$, df=1, p=0.16, Supporting information). The number of cells per nest was not affected by patch type ($\chi^2=0.69$, df=2, p=0.71, Fig. 4B) or non-Fabaceae floral resources ($\chi^2=1.54$, df=1, p=0.22, Supporting information), but positively affected by increased Fabaceae abundance ($\chi^2=7.44$, df=1, p=0.006, Fig. 3C).

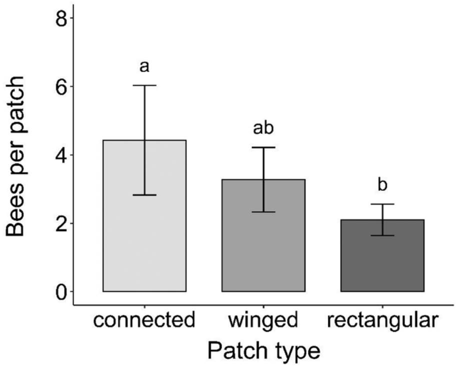

Figure 2. Arithmetic means (± SE) of counts of *M. rotundata* bees initially occupying nesting resources in each patch type, measured during the first round of observation started 10 days after bee release. Letters denote significant differences ($p < 0.05$) between patch types, calculated using Tukey–Kramer contrasts on generalized linear mixed models.

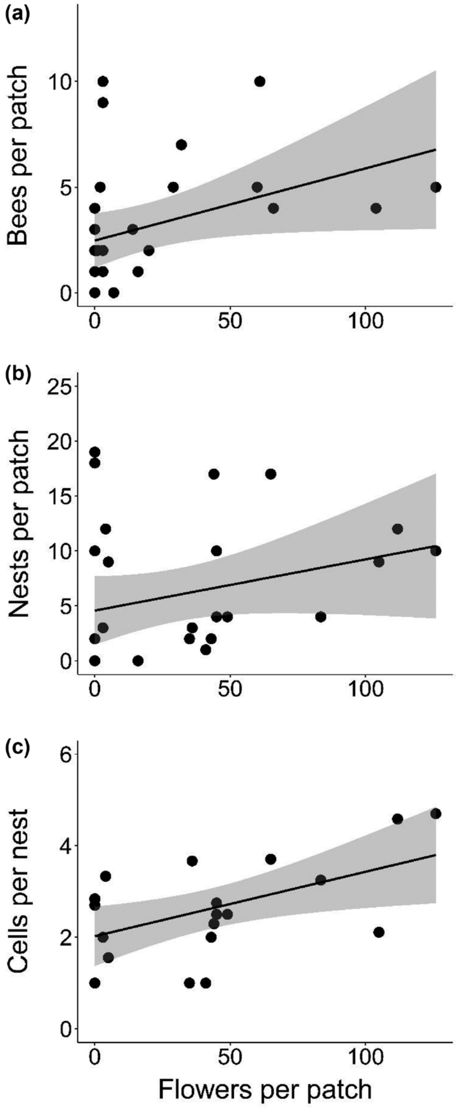

Figure 3. Higher abundances of Fabaceae flowers increased *M. rotundata* colonization of peripheral patches. (a) Initial nest site occupation versus Fabaceae flowers at each patch (peripheral patches only; 1st round of floral resource surveys). (b) Total number of nests created per patch versus Fabaceae flowers at each patch (peripheral patches only; sum of 2 rounds of floral resource surveys). (c) Cells created per nest versus Fabaceae flowers at each patch (peripheral patches only; sum of 2 rounds of floral resource surveys).

Discussion

By introducing a new species to experimentally fragmented landscapes and studying its occupation of empty habitat

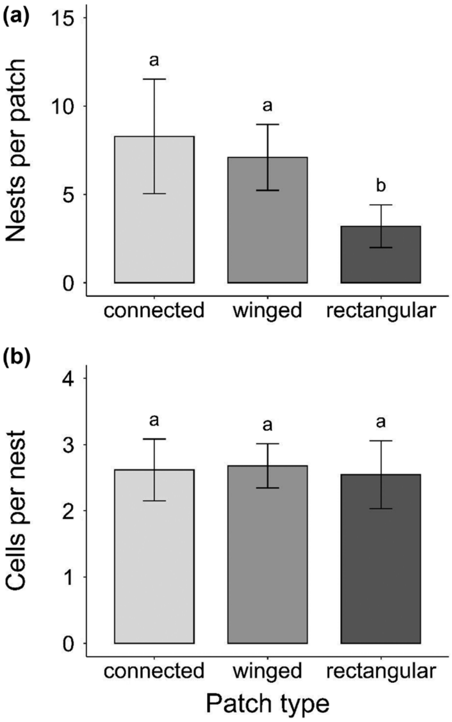

Figure 4. The effect of patch type on *M. rotundata* nesting and brood production, measured through nest dissection at the end of the flight period. Arithmetic means (± SE) of (a) *M. rotundata* nests produced in each patch type and (b) *M. rotundata* cells created per nest. Letters denote significant differences ($p < 0.05$) between patch types, calculated using Tukey–Kramer contrasts on generalized linear mixed models.

patches, we show that landscape corridors increase patch colonization and likely increase metapopulation viability. Bee colonization of fragmented habitats responded strongly to both spatial aspects altered in our experimental design by corridors, increased connectivity and increased edge-to-area ratio. There was a temporal component to these effects: landscape corridors increased initial bee occupation of nest boxes in connected habitats due to the additive effects of increased connectivity and increased edge-to-area ratio, whereas higher edge-to-area ratio was the ultimate determinant of nest establishment across habitat fragments. Thus, landscape corridors affect not only individuals' movement and dispersal behaviors as previously shown (Resasco 2019), but also population-level processes within fragmented habitats.

The effects of corridors on colonization observed in our study may have important consequences for metapopulation dynamics. Because viability in the long-term depends on the overall size of the metapopulation and its ability to replace extirpated local populations, metapopulation persistence across landscapes is a function of both local population viability and colonization rates of unoccupied habitats (Hanski 1998). To date, population-focused work with corridors has largely focused on local population viability. Previous studies have shown that higher connectivity can increase dispersal between habitat fragments (Gilbert-Norton et al. 2010, Resasco 2019) and increase population sizes (Gonzalez et al. 1998, Hudgens and Haddad 2003, Resasco 2019). Our study instead focused on the second factor that affects metapopulation viability, colonization, and found positive effects of both increased connectivity and edge. Thus, higher rates of metapopulation survival in landscapes connected by corridors (Gonzalez et al. 1998) may be attributable to both increased local population viability and higher rates of recolonization. Further, these population-level responses can be expected to scale up to affect entire communities, providing a possible mechanism for increased species richness in habitat fragments connected by landscape corridors (Damschen et al. 2006, 2019).

Our study shows that increases in insect movement that have been observed in response to corridors (Townsend and Levey 2005) result in more rapid colonization of patches. Connectivity had an additive effect on initial rates of nest-site occupation, with the highest initial occupation of nest boxes occurring in patches connected by a landscape corridor. Corridors likely channeled dispersing bees from the center patches of the experimental blocks towards connected patches, allowing them to quickly find suitable nesting habitats and establish new populations. Such behavior may have been due to edge-following from release patches into the corridors (Haddad 1999, Joyce et al. 1999, Berggren et al. 2002, Holzschuh et al. 2009, Cranmer et al. 2012) and a preference for flying through the open habitat of the corridors rather than through the forest matrix. An effect of connectivity was evident in our fragmented habitats separated by only 150 m; differences in colonization rates may be even more pronounced when fragments are more isolated or smaller in size (Haddad 1999).

Although connectivity initially affected occupation of nest-sites, edge-to-area ratio had an additive effect on these occupation rates and ultimately drove patterns of nest building. Almost double the number of nests were produced in high-edge connected and winged patches than in low-edge rectangular patches. Because most nests were incomplete during the final count, we believe that most female bees only produced one nest each within our study; thus, patterns of nest building were likely driven by dispersal by individuals rather than differences in reproductive success between patches. One explanation for our findings is that dispersing bees may have eventually been able to fly anywhere at the scale of our experimental blocks, and preferentially settled in high-edge patches. Such habitat selection for high edge habitat seems likely given that the bee used in our experiment, *Megachile rotundata*, is a cavity-nesting species that would naturally nest in holes in trees (Pitts-Singer and Cane 2011). Dispersing bees may also prefer the abiotic conditions of high-edge habitats, which are cooler than rectangular patches (Evans et al. 2012). Bees are known to be sensitive to temperature in terms of their foraging (Rader et al. 2013) and nesting (Potts and Willmer 1997, Weissel et al. 2006), so differences in temperature between patches differing in edge:area ratio could affect bee brood production and nesting. Another explanation for these patterns is that the corridors in connected patches and blind-ended corridors (wings) of the winged patches may have functioned to intercept and channel dispersing bees towards the interior of the habitat patches (Fried et al. 2005). High-edge habitats are known to have higher rates of colonization than more compact, low-edge fragments due to the increased chance of encounters by dispersing organisms (Hamazaki 1996, Bevers and Flather 1999, Collinge and Palmer 2002, Ewers and Didham 2006, 2007), but this effect has rarely been shown in relation to habitat corridors (Tewksbury et al. 2002, Levey et al. 2005, Townsend and Levey 2005, but see Fried et al. 2005).

Megachile rotundata colonization was higher in patches with more Fabaceae flowers. This is unsurprising, given this species' well-known preference for alfalfa and other species of legumes (Horne 1995). Patches with more Fabaceae flowers had higher initial occupation, nest building and even cell production, indicating that the availability of their preferred food resources affected not only female bees' decision to nest but also their ultimate reproductive success. In fact, once bees settled in patches, female fecundity was affected only by Fabaceae availability, not by patch connectivity or edge. *Megachile rotundata* are small bees with limited foraging ranges (Greenleaf et al. 2007), meaning that they may have foraged solely in the patch in which they nested. Thus, connectivity with other patches may have been irrelevant from a foraging perspective.

In our study, the released *M. rotundata* only produced an average of fewer than three cells per nest, which represents low brood production for this species (Peterson 2006). Floral abundance is known to strongly affect both *M. rotundata* nesting success and brood production (Peterson 2006, Pitts-Singer and Bosch 2010), and previous studies have found similarly low numbers of cells per nest when *M. rotundata* are placed in fields with insufficient floral resources (Peterson 2006). Though the longleaf savannah system contains high plant diversity, floral abundance was generally low throughout the study season, especially for legume species. Therefore, it is likely that bees were seriously limited by floral abundance across our experimental landscapes. In addition, the highly variable, harsh environmental conditions of our study sites in South Carolina may have further impacted the ability of bees to establish and provision nests. Regardless, despite low establishment across our study, our experimental design allowed us to compare colonization between replicated treatments in an ecologically-relevant system.

Conservation efforts for bees generally focus on improving the quality of food and nesting resources within new and restored habitat patches (Winfree 2010, Scheper et al. 2015, Vaudo et al. 2015, Williams et al. 2015). Our results show that while these factors are essential, spatial aspects of habitats should also be an important consideration for bee conservation. We show that bee colonization of pollinator habitats may be facilitated through increases in habitat connectivity and edge. Given the importance of colonization for metapopulation persistence, habitat-based conservation practices such as landscape corridors that increase these qualities should be implemented widely to support bee populations in fragmented landscapes.

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.76hdr7svq> (Griffin and Haddad 2021).

Acknowledgements – We thank our collaborators and the USDA Forest Service-Savannah River for creating and maintaining our experimental landscapes, especially J. Blake, M. Burt, E. Damschen, D. Levey, J. Orrock, J. Resasco and L. Brudvig. We thank M. Burt, S. Breland, J. Herrmann, L. Brudvig and G. Pardee for their advice and support during this project, and A. McCutcheon and M. Burt for assistance with fieldwork.

Funding – This work was funded through the Dept of Agriculture's US Forest Service under Interagency Agreement DE-EM0003622 with the Dept of Energy, Aiken, SC, and through the NSF Long-term Research in Environmental Biology Program DEB-1913501.

Author contributions

Sean R. Griffin: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Nick M. Haddad**: Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (lead); Writing – review and editing (equal).

References

Bates, D. et al. 2014. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Beier, P. and Gregory, A. J. 2012. Desperately seeking stable 50-year-old landscapes with patches and long, wide corridors. – PLoS Biol. 10: e1001253.

Berggren, Å. et al. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates and movement angles in Roesel's bush-cricket *Metrioptera roeseli*. – Conserv. Biol. 16: 1562–1569.

Bevers, M. and Flather, C. H. 1999. Numerically exploring habitat fragmentation effects on populations using cell-based coupled map lattices. – Theor. Popul. Biol. 55: 61–76.

Byrne, A. and Fitzpatrick, U. 2009. Bee conservation policy at the global, regional and national levels. – Apidologie 40: 194–210.

Collinge, S. K. and Palmer, T. M. 2002. The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. – Landscape Ecol. 17: 647–656.

Cranmer, L. et al. 2012. Landscape structure influences pollinator movements and directly affects plant reproductive success. – Oikos 121: 562–568.

Damschen, E. I. et al. 2006. Corridors increase plant species richness at large scales. – Science 313: 1284–1286.

Damschen, E. I. et al. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. – Proc. Natl Acad. Sci. USA 111: 3484–3489.

Damschen, E. I. et al. 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. – Science 1480: 1478–1480.

Evans, D. M. et al. 2012. Habitat patch shape, not corridors, determines herbivory and fruit production of an annual plant. – Ecology 93: 1016–1025.

Ewers, R. M. and Didham, R. K. 2006. Confounding factors in the detection of species responses to habitat fragmentation. – Biol. Rev. Camb. Phil. Soc. 81: 117–142.

Ewers, R. M. and Didham, R. K. 2007. The effect of fragment shape and species' sensitivity to habitat edges on animal population size: contributed papers. – Conserv. Biol. 21: 926–936.

Fried, J. H. et al. 2005. Habitat corridors function as both drift fences and movement conduits for dispersing flies. – Oecologia 143: 645–651.

Garibaldi, L. A. et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. – Ecol. Lett. 14: 1062–1072.

Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. – J. Anim. Ecol. 71: 757–764.

Geert, A. Van et al. 2010. Do linear landscape elements in farmland act as biological corridors for pollen dispersal? – J. Ecol. 98: 178–187.

Gilbert, F. et al. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. – Proc. R. Soc. B 265: 577–582.

Gilbert-Norton, A. L. et al. 2010. A meta-analytic review of corridor effectiveness. – Conserv. Biol. 24: 660–668.

Gonzalez, A. et al. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. – Science 281: 2045–2047.

Goulson, D. et al. 2015. Bee declines driven by combined stress from parasites, pesticides and lack of flowers. – Science 347: 1255957.

Greenleaf, S. S. et al. 2007. Bee foraging ranges and their relationship to body size. – Oecologia 153: 589–596.

Griffin, S. R. and Haddad, N. 2021. Data from: Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.76hdr7svq>.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. – Am. Nat. 153: 215–227.

Haddad, N. M. and Baum, K. A. 1999. An experimental test of corridor effects on butterfly densities. – Ecol. Appl. 9: 623–633.

Haddad, N. M. et al. 2003. Corridor use by diverse taxa. – Ecology 84: 609–615.

Haddad, N. M. et al. 2014. Potential negative ecological effects of corridors. – Conserv. Biol. 28: 1178–1187.

Haddad, N. M. et al. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. – Sci. Adv. 1: E1500052.

Hamazaki, T. 1996. Effects of patch shape on the number of organisms. – Landscape Ecol. 11: 299–306.

Hanski, I. 1998. Metapopulation dynamics. – Nature 396: 41–49.

Hanski, I. 2015. Habitat fragmentation and species richness. – J. Biogeogr. 42: 989–993.

Herrmann, J. D. et al. 2017. Testing the relative importance of local resources and landscape connectivity on *Bombus impatiens* (Hymenoptera, Apidae) colonies. – Apidologie 48: 545–555.

Holzschuh, A. et al. 2009. Grass strip corridors in agricultural landscapes enhance nest-site colonization by solitary wasps. – Ecol. Appl. 19: 123–132.

Hopwood, J. et al. 2015. Literature review: pollinator habitat enhancement and best management practices in highway rights-of-way. – Federal Highway Admin.

Horn, S. and Hanula, J. L. 2004. A survey of cavity-nesting bees and wasps in loblolly pine stands of the Savannah River Site, Aiken County, South Carolina. – J. Entomol. Sci. 39: 464–469.

Horne, M. 1995. Pollen preference and its relationship to nesting success of *Megachile rotundata* (Hymenoptera: Megachilidae). – Ann. Entomol. Soc. Am. 88: 862–867.

Hudgens, B. R. and Haddad, N. M. 2003. Predicting which species will benefit from corridors in fragmented landscapes from population growth models. – Am. Nat. 161: 808–820.

Joyce, K. A. et al. 1999. Influences of hedgerow intersections and gaps on the movement of carabid beetles. – Bull. Entomol. Res. 89: 523–531.

Kennedy, C. M. et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. – Ecol. Lett. 16: 584–599.

Klok, C. and DeRoos, A. M. 1998. Effects of habitat size and quality on equilibrium density and extinction time of *Sorex araneus* populations. – J. Anim. Ecol. 67: 195–209.

Kormann, U. et al. 2016. Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. – Proc. R. Soc. B 283: 20152347.

Lenth, R. V. 2016. Least-squares means: the R package lsmeans. – J. Stat. Softw. 69: 1–33.

,Levey, D. J. et al. 2005. Effects of landscape corridors on seed dispersal by birds. – Science 309: 146–148.

McCorquodale, D. B. and Owen, R. E. 1997. Allozyme variation, relatedness among progeny in a nest, and sex ratio in the leafcutter bee, *Megachile rotundata* (Fabricius) (Hymenoptera: Megachilidae). – Can. Entomol. 129: 211–219.

Menz, M. H. M. et al. 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. – Trends Plant Sci. 16: 4–12.

Moilanen, A. and Hanski, I. 1998. Metapopulation dynamics: effects of habitat quality and landscape structure. – Ecology 79: 2503–2515.

Moilanen, A. and Nieminen, M. 2002. Simple connectivity measures in spatial ecology. – Ecology 83: 1131–1145.

Murray, T. E. et al. 2009. Conservation ecology of bees: populations, species and communities. – Apidologie 40: 211–236.

Palladini, J. D. and Maron, J. L. 2014. Reproduction and survival of a solitary bee along native and exotic floral resource gradients. – Oecologia 176: 789–798.

Peterson, J. H. 2006. Impact of resource levels on sex ratio and resource allocation in the solitary bee, *Megachile rotundata*. – Behavior 35: 1404–1410.

Peterson, J. H. and Roitberg, B. D. 2006. Impacts of flight distance on sex ratio and resource allocation to offspring in the leafcutter bee, *Megachile rotundata*. – Behav. Ecol. Sociobiol. 59: 589–596.

Pitts-Singer, T. L. and Bosch, J. 2010. Nest establishment, pollination efficiency and reproductive success of *Megachile rotundata* (Hymenoptera: Megachilidae) in relation to resource availability in field enclosures. – Environ. Entomol. 39: 149–158.

Pitts-Singer, T. L. and Cane, J. H. 2011. The alfalfa leafcutting bee, *Megachile rotundata*: the world's most intensively managed solitary bee. – Annu. Rev. Entomol. 56: 221–237.

Pitts-singer, T. L. and James, R. R. 2005. Emergence success and sex ratio of commercial alfalfa leafcutting bees from the united states and canada emergence success and sex ratio of commercial alfalfa leafcutting bees from the United States and Canada. – J. Econ. Entomol. 98: 1785–1790.

Potts, S. G. and Willmer, P. 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. – Ecol. Entomol. 22: 319–328.

Potts, S. G. et al. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? – Ecology 84: 2628–2642.

Potts, S. G. et al. 2010. Global pollinator declines: trends, impacts and drivers. – Trends Ecol. Evol. 25: 345–353.

Pyke, G. H. 1984. Optimal foraging theory: a critial review. – Annu. Rev. Ecol. Syst. 15: 523–575.

Rader, R. et al. 2013. Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. – Global Change Biol. 19: 3103–3110.

Resasco, J. 2019. Meta-analysis on a decade of testing corridor efficacy: what new have we learned? – Curr. Landscape Ecol. Rep. 4: 61–69.

Resasco, J. et al. 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. – Ecology 95: 2033–2039.

Roulston, T. H. and Goodell, K. 2011. The role of resources and risks in regulating wild bee populations. – Annu. Rev. Entomol. 56: 293–312.

Scheper, J. et al. 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. – J. Appl. Ecol. 52: 1165–1175.

Strange, J. P. et al. 2017. Novel microsatellite loci reveal high genetic diversity yet low population structure for alfalfa leafcutting bees in North America. – Conserv. Genet. 18: 679–687.

Tewksbury, J. J. et al. 2002. Corridors affect plants, animals and their interactions in fragmented landscapes. – Proc. Natl Acad. Sci. USA 99: 12923–12926.

Townsend, P. A. and Levey, D. J. 2005. An experimental test of whether habitat corridors affect pollen transfer. – Ecology 86: 466–475.

Vaudo, A. D. et al. 2015. Bee nutrition and floral resource restoration. – Curr. Opin. Insect Sci. 10: 133–141.

Weins, J. 1997. The emerging role of patchiness in conservation biology. – In: Pickett, S. T. A. et al. (eds), The ecological basis of conservation: heterogeneity, ecosystems and biodiversity. Springer, pp. 93–107.

Weissel, N. et al. 2006. The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*. – Insectes Soc. 53: 390–398.

Williams, N. M. et al. 2015. Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. – Ecol. Appl. 25: 2119–2131.

Wilson, J. S. et al. 2017. Interest exceeds understanding in public support of bee conservation. – Front. Ecol. Environ. 15: 460–466.

Winfree, R. 2010. The conservation and restoration of wild bees. – Ann. N. Y. Acad. Sci. 1195: 169–197.

Zurbuchen, A. et al. 2010. Long foraging distances impose high costs on offspring production in solitary bees. – J. Anim. Ecol. 79: 674–681.