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Corridors restore animal-mediated pollination in fragmented tropical forest landscapes

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Tropical biodiversity and associated ecosystem functions have become heavily eroded through habitat loss. Animal-mediated pollination is required in more than 94% of higher tropical plant species and 75% of the world's leading food crops, but it remains unclear if corridors avert deforestation-driven pollination breakdown in fragmented tropical landscapes. Here, we used manipulative resource experiments and field observations to show that corridors functionally connect neotropical forest fragments for forest-associated hummingbirds and increase pollen transfer. Further, corridors boosted forest-associated pollinator availability in fragments by 14.3 times compared with unconnected equivalents, increasing overall pollination success. Plants in patches without corridors showed pollination rates equal to bagged control flowers, indicating pollination failure in isolated fragments. This indicates, for the first time, that corridors benefit tropical forest ecosystems beyond boosting local species richness, by functionally connecting mutualistic network partners. We conclude that small-scale adjustments to landscape configuration safeguard native pollinators and associated pollination services in tropical forest landscapes.

1. Introduction

In an era of rocketing human-driven habitat modification, biodiversity and ecosystem functions are at risk and maintaining them may be a challenge [1,2]. Animal-mediated pollination is such a crucial ecosystem function, required in 87% of higher terrestrial plant species and 75% of the world's leading food crops [3,4]. Critically, loss of pollinator function through increased habitat conversion is of global concern [2,5,6], particularly in the tropics, where high rates of habitat loss and fragmentation coincide with an above-average proportion of angiosperms dependent on animal-mediated pollination (more than 94% of species; [3,7,8]).

Breakdown of pollination mutualisms through habitat modification (i.e. habitat loss and fragmentation) result from reduced availability of suitable pollen donors, degraded pollinator pools, restricted movement of pollinators and subsequently reduced pollen flow between habitat fragments (the 'pollinator-movement-hypothesis' *sensu* [9]). In turn, many animal-pollinated plants suffer from impaired sexual reproduction as a consequence of pollination limitation after habitat loss and fragmentation [6,10], filtering plant communities towards non-animal-pollinated species [6,11].

Corridors may benefit pollination services by facilitating pollinator movement among habitat fragments, pollinator demography and higher availability of pollinators and outcross pollen [10,12–15]. To date, however, whether corridors affect animal-mediated pollination in highly biodiverse tropical systems, which are of global conservation importance, remains unexplored [7,16].

Narrow wooded elements such as living fencerows and narrow riparian buffers (less than 15 m; figure 1c) often constitute the only abundant wooded structures outside forest remnants in tropical agricultural landscapes worldwide
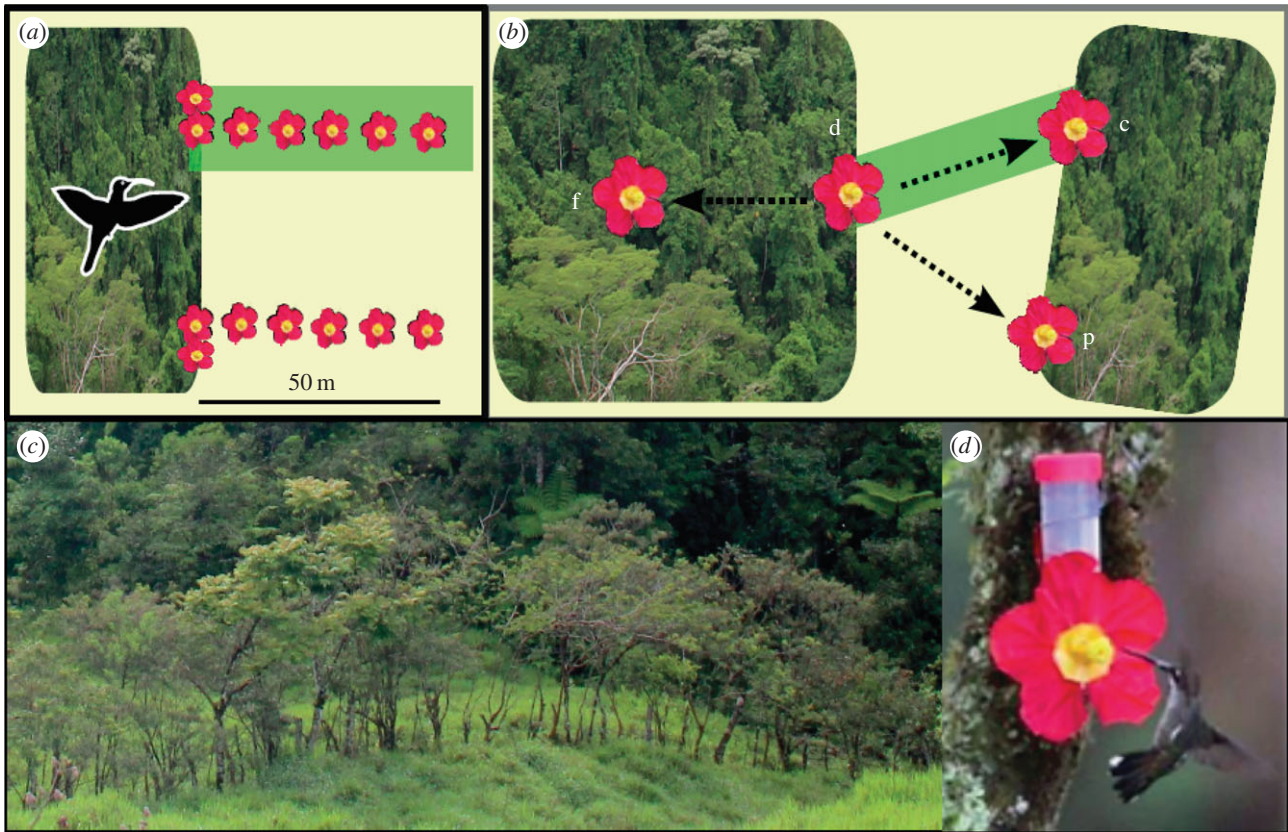
Figure 1. Experiments used to test hummingbird and pollen movement. (*a*) Experimental design to test the effects of narrow wooded corridors on hummingbird movement through pasture. Sites consisted of forest patches surrounded by pasture and a living fencerow ('corridor', light green bar). Experimental food resources (artificial flowers or live *H. tortuosa* plants) were placed at 0–50 m distance from the forest edge, at 10 m intervals, along pasture or along the corridor. (*b*) Experimental design used to assess hummingbird-mediated pollen transfer between forest fragments. Sites had two neighbouring forest patches surrounded by pasture, connected by a living fencerow ('corridor', light green bar). A central artificial flower treated with pollen analogue ('pollen donor', d) was encircled by three 'pollen receiver' flowers placed at equal distances (arrows, distance range 40–120 m). 'Pollen receivers' differed in the type of intervening land cover to the 'pollen donor': forest (f), corridor (c) or pasture (p). (*c*) Narrow woody corridor (living fencerow) used in this study. (*d*) Hummingbird (*Heliomaster longirostris*) visiting an artificial flower. (Online version in colour.)

[17]. In Latin America these structures are often retained by small-scale farmers, mostly for agricultural purposes, and recent studies highlight their capacity to harbour a substantial proportion of tropical biodiversity [17,18]. To date, however, it remains unclear if such elements increase connectivity for species associated with remaining tropical forest and whether this ultimately translates into the provision of ecosystem processes such as pollination [19].

Here, we tested whether linear wooded corridors between tropical forest remnants enhance functional connectivity [20] for pollinators and subsequently, animal-mediated pollination. In our Southern Costa Rican study area, only approximately 30% of the original forest cover persists—mostly in scattered fragments surrounded by pasture and coffee plantations [21]. However, narrow wooded corridors are common in the study region, and one-third of forest fragments are interconnected by narrow wooded corridors [21]. Previous work in the study region has reported that forest loss and fragmentation erode insect and avian pollinator communities [22–24]. We used hummingbird-mediated pollination as a model system, as hummingbirds may be powerful agents for connecting fragmented plant populations, given their extensive daily foraging distances of up to 1300 m in our study region [25]. Between 18% and 34% of neotropical understory flowering plants show adaptations for hummingbird pollination [26,27]; however, the species richness of hummingbird pollinated flowers may be reduced in highly disturbed landscapes

[11]. Further, forest gaps appear to limit hummingbird movement [28], resulting in pollen limitation of the understory herb *Heliconia tortuosa*, the most common and highly linked floral resource in the regional hummingbird–plant pollination network [24,29,30].

We tested if narrow woody corridors affect animal-mediated pollination by using four complementary approaches: first, we conducted a titration experiment to test whether movement of whole hummingbird communities was greater along corridors than across open pasture with the same resource availability, expecting that a corridor effect is more accentuated for habitat specialists to habitat generalist species. Second, we tested if pollen flow is greater between neighbouring forest fragments when they are connected by corridors. Third, we tested if corridors boost the occupancy of the most abundant habitat specialist and habitat generalist hummingbird species in small forest fragments. Finally, we evaluated whether corridors increase pollination in *H. tortuosa* in small, pollination-depressed forest fragments.

2. Methods

We conducted the study in Southern Costa Rica around the Las Cruces Biological Station (8°47′ N, 82°57′ W, electronic supplementary material, figure S1*a*–*d*). The region was originally characterized by contiguous Pacific premontane humid forest,

but massive deforestation since the 1950s resulted in a patchwork of forest fragments (900–1500 m.a.s.l.), ranging from less than 1 to more than 1000 ha in size surrounded by pastures (more than 90%), coffee plantations and human settlements. Details are given in [21].

(a) Pollinator movement

We tested the corridor effect on hummingbird foraging movement by measuring foraging visits in two replicated, standardized food titration experiments between April and June 2012 (figure 1). Food titration experiments are a method for measuring the motivation of organisms to move through a given habitat type under standardized conditions. Standardization is accomplished by experimentally supplementing resources (e.g. food) across a suite of land cover types differing in hypothesized functional connectivity [31]. First, we measured rates of hummingbird visits to artificial flowers placed according to two experimental titration treatments replicated 16 times at spatially discrete sites (electronic supplementary material, figure S1a). All sites were composed of a central forest fragment (size range 2.7–180 ha) surrounded by pasture and an adjacent living fencerow. Fencerows consisted of rows of remnant or planted trees (length: 182 ± 35 m; width: 1.2 ± 0.2 m; height: 7.5 ± 0.6 m, mean $\pm$ s.e., figure 1c). Within each site, we applied two treatments (figure 1a): seven artificial flowers were placed along the wooded fencerow (treatment: corridor) and seven directly in pasture (treatment: no corridor). In both treatments, the first two flowers were placed at the forest edge, followed by five consecutive flowers placed in a line 10 m apart, thus representing a crossed 'treatment × distance' design. Treatments within sites were more than 150 m apart. To limit potential confounds, existing flowers along the treatments were removed or covered with mesh bags to render them unavailable during the experiments.

Artificial flowers consisted of 50 ml Falcon tubes equipped with a red plastic flower and a straight tubular 'corolla', mimicking a highly attractive ornithophilous flower with constant nectar supply. Although of high resource quality, these flowers are assumed not to substantially alter hummingbird foraging behaviour; that is, hummingbirds maintain typical behaviours such as traplining despite feeder presence (U.K., A.S.H., M.G.B. 2012–2014, personal observation).

Feeders were constantly available during five successive days per site, and daily refilled with 10% saccharose nectar. After 3 days of habituation, two observers visited each site on days 4 and 5 of exposure to visually quantify hummingbird visits during peak hummingbird activity (between 05.30–10.00 and 14.30–18.00) for a total of 40 min per feeder. Treatments were randomly assigned to observers on day 4 and assignment changed on day 5. We statistically analysed the six most common species (more than 30 observations), four forest-associated hummingbird species and two habitat generalist species that also occur in open habitats (table 1). Habitat affiliation was determined based on previous work in the region [30,32], field guides [33] and personal observations (U.K., A.S.H., M.G.B., February–April 2011, 2012 and 2013, personal observations).

Further, we conducted a second experiment at seven additional sites using the same design as above, but with experimental, live plants of H. tortuosa in lieu of artificial flowers. H. tortuosa requires visits of long-distance traplining hummingbird species with specialized bills for successful sexual reproduction [24,34], but pollen tubes can be initiated both by self- and outcross pollen (partial self-compatibility; [34]). Individual H. tortuosa plants bloom for several months, but individual flowers are only open and pollen receptive for a single day before abscising, after which an indicative colour change occurs. Although H. tortuosa is mostly found in forest, it can thrive in open areas such as pastures and readily sets seed given sufficient pollination (e.g. [34] and U.K., April

Table 1. Linear effects (intercept and corridor) on predictors for visits of six hummingbird species at artificial flowers, based on the best-fitting Bayesian model. Shown are posterior means (β), lower 2.5% credible interval (2.5CI) and upper 97.5% credible interval (97.5CI). Significance (p) indicates if the 95% credible interval includes 0 or not.

	β	2.5CI	97.5CI	p
Phaetornis guy ($n = 159$)				
intercept	−2.040	−2.989	−1.255	0
corridor	1.380	0.448	2.384	0.005
Campylopterus hemileucurus ($n = 40$)				
intercept	−10.945	−20.791	−5.324	0
corridor	7.851	2.185	17.736	0.002
Heliodoxa jacula ($n = 72$)				
intercept	−3.528	−4.990	−2.284	0
corridor	1.002	−0.588	2.629	0.208
Lampornis castaneoventris ($n = 37$)				
intercept	−4.240	−6.177	−2.698	0
corridor	1.650	0.699	2.674	0.005
Amazilia tzacatl ($n = 431$)				
intercept	0.036	−0.487	0.467	0.240
Heliomaster longirostris ($n = 75$)				
intercept	−2.168	−3.509	−1.004	0.005

and May 2012, personal observation). For each site, we selected 14 plants with four to six flowers in the central forest patch, and transplanted them into the adjacent pasture. Importantly, nectar volume and sucrose concentration of bagged control flowers did not differ between transplanted corridor and pasture flowers (volume two-way ANOVA, $F_{1,26} = 0.052$, $p = 0.822$; sucrose two-way ANOVA: $F_{1,26} = 0.462$, $p = 0.503$).

To quantify pollinator visits, we visited treatments on days 4 and 5 after plant transplantation between 05.30 and 09.30, for a total of 40 min of observation per plant (2×20 min). In addition, we collected day-old styles ($n = 280$) from the exposed plants (mean $= 3.42$ styles per plant collected during at least 2 days) identified by indicative colour change according to [34] and [24]. We determined pollen tube growth (i.e. the number of pollen tubes observed per style) with epifluorescent microscopy (*sensu* [34], electronic supplementary material, SI 2 for details).

We provide a statistical overview with methodological details in the electronic supplementary material, table S1. We analysed hummingbird visits at artificial and planted flowers, and the number of pollen tubes observed per style with mixed Bayesian, generalized additive models for location, scale and shape [35] implemented in BAYESX [36]. This method allowed us to (i) take into account the hierarchical data structure, (ii) incorporate the spatial dependency of neighbouring flowers (serial autocorrelation), (iii) model the nonlinear effect of distance to forest via a non-parametric function for distance and to (iv) model the detected zero-inflation and/or overdispersion in the dependent variable. We first selected the adequate response distribution by choosing among Poisson, zero-inflated Poisson, negative binomial and zero-inflated negative binomial, based on quantile residual-plots of the full model. Full models included corridor (linear), distance to forest (non-parametric) and their interactions as fixed factors, as well as treatment nested within site as random factor (further details on predictor specifications and the modelling approach are given in the electronic supplementary material, S1). Second, we followed [35] to identify the relevant predictors by

comparing models with all possible variable combinations, using the deviance information criterion (DIC, a Bayesian analogue of the Akaike information criterion (AIC)) and significance values of parameters to determine the top candidate models (ΔDIC < 5). More details on model specifications and selection are given in the electronic supplementary material, S1 and table S1.

(b) Pollen movement

To test if corridors facilitate hummingbird-mediated pollen flow between neighbouring forest fragments, we tracked pollen transfer among artificial flowers using fluorescent dye as a pollen substitute [37]. Fluorescent dyes have been shown to accurately mirror pollen movement by hummingbirds [38] and plant gene flow [37]. In April and May 2013, we established a pollen tracking experiment in 14 replicated landscapes (see electronic supplementary material, figure S1b), each with two neighbouring forest fragments surrounded by pasture (figure 1b). Both fragments were connected by a wooded fencerow (corridor), ranging in length from 40 to 120 m. A central artificial flower (the 'pollen donor') was placed in the first fragment at the beginning of the corridor. Three 'pollen receiver' flowers encircled the donor at equal distances (i.e. the length of the corridor): the 'corridor flower' at the corridor end in the second fragment, the 'pasture flower' also at the edge of the second fragment, but isolated from the donor by pasture and the 'forest flower' at equidistant position inside the first forest fragment. Pastures were virtually free of floral resources. All feeders remained operative for approximately 96 h, and were equipped on day three with filaments and, in the case of the donor, yellow fluorescent dye (RadgloR, Radiant Color, Belgium). After 24 h of exposure, filaments were collected, replaced with clean filaments for 24 h and dye reapplied. We then photographed the collected filaments under UV light and used automated image analysis to count the number of pollen particles on filaments (function 'AnalyzeParticle' in IMAGEJ, [39], following [40]). We used generalized linear-mixed models [41] with a negative-binomial distribution in R (v. 3.0.3 beta) and stepwise backwards model selection based on AICc to identify the best-fitting model (electronic supplementary material, table S1). The full model contained the number of deposited pollen particles as a function of distance to the dye source, intervening cover type (treatment) and their interaction. Flower position was nested within 'site' as a random factor. Multiple comparisons among treatments types were done using Tukey's pairwise comparisons (glht function [42]).

(c) Pollinator presence in forest fragments

To test if corridors increase pollinator availability in pollinator-depauperate forest fragments, we assessed the presence of the two most common hummingbird species, the highly mobile, but forest-restricted *Phaetornis guy* (habitat specialist) and the habitat generalist *Amazilia tzacatl*. For this, we selected 26 small forest patches (2.23 ha $\pm$ 1.29 s.e., electronic supplementary material, figure S1c), as previous studies in the region indicated strongly reduced hummingbird communities and abundances in small forest fragments [24]. Patches represented a gradient in the number of corridor connections to other forest patches ([0–3], CORRIDOR). Corridors were 1–2 trees wide, and either living fencerows or slender riparian buffers. Fragments were not connected to other forest fragments by any additional riparian strips, that is, all connecting corridors per patch were included in the design. Patches were selected based on aerial images and corridor integrity later verified in the field. For each patch, we measured patch size (SIZE), proportion of forest within a 250 m radius of the patch centroid (PROPFOR) and altitude (ALT) based on existing digital forest cover maps [24].

In 2012, we visited each forest fragment and assessed presence/absence of both hummingbird species visually and acoustically at three haphazardly placed point count locations inside the forest (radius 25 m, count duration 12 min). We detected *P. guy* and *A. tzacatl* during 35% and 60% of all point counts, respectively ($n = 78$), corresponding to 15 (58%) and 21 (80%) of all patches, respectively. We then used an occupancy modelling approach [43] to evaluate the effect of the explanatory variables (CORRIDOR, SIZE, PROPFOREST and ALTITUDE) on patch use by each species while simultaneously accounting for imperfect detection. Points within-patches were treated as spatial subsamples of the patch; this sampling approach should yield unbiased occupancy parameter estimates for highly mobile species such as hummingbirds [44]. All covariates were standardized by subtracting the mean and dividing by the standard deviation before inclusion in models. We selected the single best combination of explanatory variables for each species by starting with a full model and using backwards variable selection based on AICc (electronic supplementary material, table S1). To account for the potential biases in detectability as a function of patch size, we include this variable as a covariate for detection probability in all models.

(d) Pollination success

To test if enhanced hummingbird movement afforded by corridors subsequently boosted pollination, we assessed pollination rates in naturally occurring *H. tortuosa* in fragments differing in their connectivity. We selected 13 small forest fragments (AREA: 1.03 ha $\pm$ 0.43, electronic supplementary material, figure S1d and table S8) that were surrounded by pasture but connected to neighbouring forest fragments by either zero, one or two corridors (CORRIDOR). Again, corridors were either living fencerows or slender riparian buffers, ranging from one to two trees in width. In May 2013, we sampled approximately 20 1-day-old flowers per fragment (mean per fragment $\pm$ s.d. = 18.58 $\pm$ 2.39, following [24]) and systematically recorded *H. tortuosa* density per patch (FLOWER). We then determined the distance to the next forest more than 5 ha (DISTANCE) and proportion of forest as described above (PROPFOREST). Pollination was then assessed for every flower by the presence of pollen tubes (see electronic supplementary material, Methods S2). Of 238 collected *H. tortuosa* styles, 59 were pollinated (mean per fragment $\pm$ s.d. = 26.46% $\pm$ 16.32). As a pollinator exclusion control, we also bagged five to six inflorescences in four sites with mesh bags and subsequently collected two 1-day-old flowers from each inflorescence (42 flowers in total). We then analysed the proportion of styles with pollen tubes per patch using logistic regression with a binomial error structure in R (glm, [45]), including CORRIDOR, AREA, FLOWER, DISTANCE and PROPFOREST as explanatory variables. Here, we used stepwise model selection based on AICc to identify the best-fitting model (electronic supplementary material, table S1).

3. Results

(a) Pollinator movement

We quantified hummingbird visits at artificial flowers for a total of 1280 min. We analysed the six most common species ($n > 30$ observations/species) that accounted for 98.5% of all observations. While the best-fitting additive model indicated that all four habitat specialists visited more flowers along corridors (figure 2, effect significant in three of four species, $p \leq 0.005$; table 1; electronic supplementary material, tables S1 and S2), we detected no corridor effect for the two habitat generalists (figure 2 and table 1; electronic supplementary material, tables S1 and S2). Further, visitation rates for all species showed significant and strong decays with increasing distance
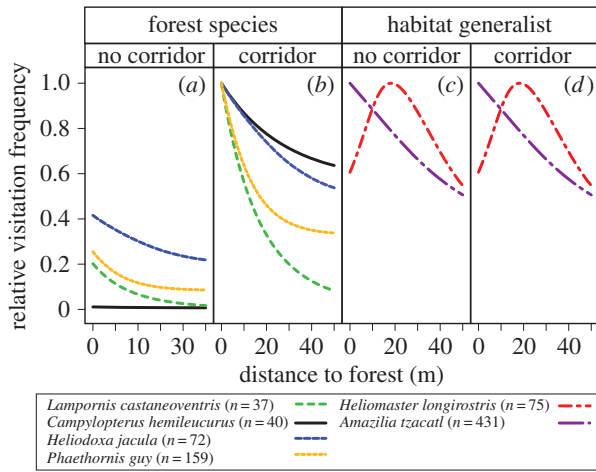
Figure 2. Effect of corridors and habitat preferences on hummingbird foraging movement through deforested habitat, to visit artificial resources placed at increasing distances to the forest edge. Shown are predicted visitation rates for four forest specialist species without corridors (a) and along corridors (b), and for two habitat generalists along corridors (d) and without corridor (c). Visitation rates are scaled to [0, 1] per species and based on the best-fitting models. Numbers in the legend show the number of observed visits per species. (Online version in colour.)

Figure 3. Pollen transfer between artificial flowers within forest, corridor or pasture. Shown is the mean number of artificial pollen particles as a function of the distance to the pollen source and intervening cover type. Pollen transport decreased with increasing distance between feeders ($p = 0.04$) and was higher between feeders inside forest ($p < 0.0001$) or corridors ($p = 0.0003$) compared with pasture. Circles represent data points. (Online version in colour.)

to forest (figure 2; electronic supplementary material, tables S1 and S2). An exception was the species most strongly affiliated with open land [30,32], *Heliomaster longirostris,* which showed a unimodal activity pattern peaking at intermediate distances to forest. During observation bouts all habitat specialist individuals performed sequential foraging movement (traplining) along feeder transects; birds typically originated from the forest fragment, visited feeders sequentially and returned to the fragment. In two cases, we observed green hermits (*P. guy*) moving along the entire corridor, but starting from the opposite corridor end.

Next, in addition to counting visits to feeders, we examined hummingbird visits to experimental plants over 560 min (28 observation periods), resulting in a total of 37 visits by the primary pollinator *P. guy* and only four by *C. hemileucurus.* Therefore, we analysed only *P. guy* visits. Frequency of visits to artificial flowers was significantly greater along corridors ($p = 0.008$) and significantly decreased with increasing distance to forest (electronic supplementary material, table S2 and figure S2). In addition, the number of pollen tubes per style decayed significantly with increasing distance to forest, and tended to be higher along corridors ($p = 0.12$, $n = 280$ styles; electronic supplementary material, table S2 and figure S1).

(b) Pollen movement
The best model contained strong additive effects of pasture and distance on pollen flow. Even though pollen was transferred up to 120 m between feeders in some cases (figure 3), we found that the number of dye particles transferred decreased by a factor of 9.92 (95% CI = [1.69–57.98]) along the 40–120 m distance gradient (figure 3; GLMM: $z = -2.03$, $p = 0.042$). While corridors and forest did not significantly differ in their permeability for pollen ($p = 0.13$; electronic supplementary material, table S3), pasture strongly impeded pollen transfer relative to corridor and forest treatments (figure 3; $p < 0.001$ each; electronic supplementary material, table S3). However, this compensation effect of corridors decreased with increasing
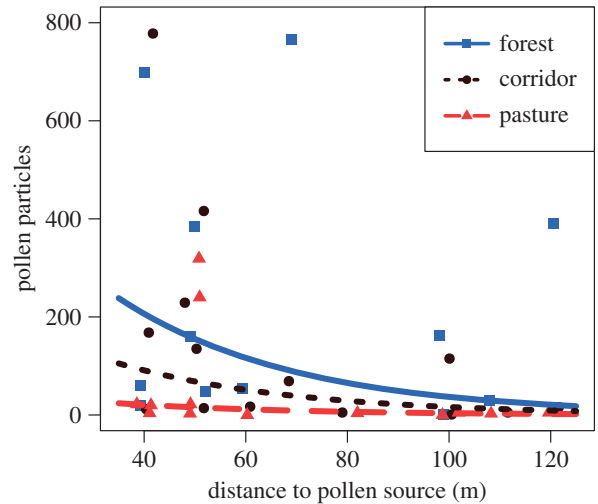
distance between fragments (figure 3; electronic supplementary material, table S3).

(c) Pollinator occupancy in forest fragments
The occupancy of the habitat-specialized *P. guy* was a strong positive function of the number of corridor connections to adjacent patches (electronic supplementary material, table S5 and figure 4); occupancy probability increased significantly by a factor 14 from nearly 0 in isolated patches (=0.14, 95% CI = [0.02–0.60]) to nearly one in patches with three corridors (=0.98, 95% CI = [0.50–1.00]). Indeed, we did not observe any *P. guy* during point counts in isolated patches ($n = 4$). These results not only suggest that corridors increase the patch use by *P. guy*, but that there may also be a threshold in connectivity below which this species does not visit fragments. In contrast, occupancy by the generalist *A. tzacatl* was not influenced by corridors (electronic supplementary material, table S5).

(d) Pollination success
Paralleling the effect on the main pollinator, *P. guy*, connectivity to forests by corridors was the only variable that determined the proportion of pollinated flowers (electronic supplementary material, table S6). Pollen tube growth, the first critical step in successful fertilization, was significantly enhanced by corridors (figure 4b, GLM: $z = 3.358$, $p < 0.0001$); the fraction of styles with pollen tubes was 5.66 times higher (95% CI = [4.32–7.01]) in patches with two corridors compared with isolated patches. Importantly, pollen tube growth rate in isolated patches was not different from bagged control flowers, suggesting a breakdown of the pollination mutualism in isolated patches (proportion of styles with tubes for isolated versus bagged: 0.091 versus 0.077, GLM: $z = -0.220$, $p = 0.826$). This indicates that connectivity via the presence of corridors not only strongly enhanced pollination rates, but also rescued plants in small patches from pollination failure.
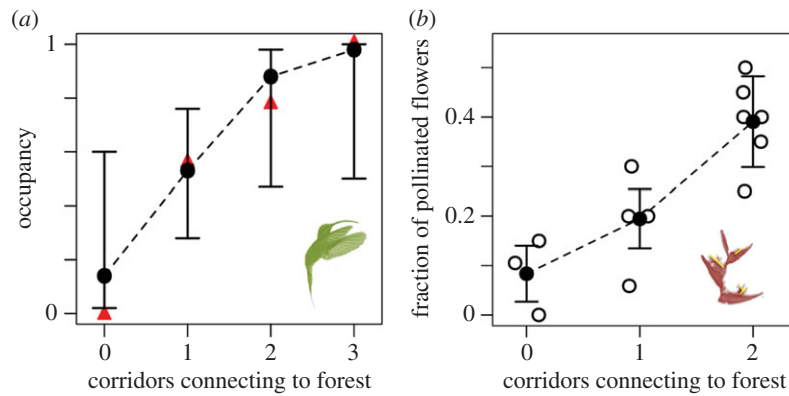
Figure 4. Corridors and their effect on pollinator occupancy (a) and subsequent pollination success (b) in small Costa Rican forest fragments (fragment size: 2.23 ha $\pm$ 1.29 s.e. for occupancy, 1.03 ha $\pm$ 0.43 for pollination success). (a) Occupancy for the most common bird pollinator—P. guy—strongly increased with increasing number of corridors connecting the fragment to a large forest ($n = 26$ fragments, $p < 0.05$). Shown are predicted occupancy values (black dots) and associated confidence intervals (bars). Triangles represent naive occupancy estimates (detection probability = 1). (b) Pollen tube growth, i.e. the proportion of flowers per forest fragment with pollen tubes, also significantly increased with the number of corridors ($n = 13$, $p < 0.000$, mean number of pollen tubes collected per fragment $\pm$ s.d. = 18.58 $\pm$ 2.39). Error bars show the 95% prediction intervals, jittered circles represent data points. (Online version in colour.)

4. Discussion

Our study provides four complementary lines of evidence for consistent and positive effects of corridors on animal-mediated pollination in tropical landscapes. Corridors strongly enhanced (i) movement of habitat specialist hummingbirds and (ii) pollen transfer through highly modified farmland, which subsequently boosted (iii) pollinator patch occupancy and (iv) pollination rates. Overall, our experiments consistently suggest that simple wooded corridors can avert the breakdown of pollination mutualisms in tropical habitat fragments by restoring functional connectivity for mobile mutualism partners.

(a) Pollinator movement

In accordance with our prediction, corridor effects on pollinator movement depended on habitat specialization: structurally contrasting vegetation (pasture) strongly impeded foraging movement for all habitat specialists but none of the generalist species. Further, the pattern seen at the experimental heliconias mirrored those seen at experimental flowers.

These results corroborate previous studies showing that habitat specialists, in contrast to habitat generalists, (i) often show a poor capacity to move between fragments [46] and are (ii) more dependent on corridors for movement through highly fragmented habitats [47]. However, to the best of our knowledge, this study provides the first experimental evidence that corridors facilitate movement of forest-dependent pollinators in tropical landscapes.

(b) Pollen movement

We found evidence that pastures strongly impede pollen transfer for hummingbird-pollinated flowers, but that corridors can substantially mitigate this detrimental effect. However, positive corridor effects on pollen transfer appear to dampen with increasing distance. That is, at high interpatch distances (e.g. more than 120 m), corridors are unlikely to maintain sufficient pollen flow to guarantee high connectivity among plant populations. The observed pollen flow pattern is consistent with the pollinator movement hypothesis [9], i.e. non-suitable habitat (matrix) significantly hampers pollen transfer by habitat-restricted pollinators, resulting in reduced plant fitness.

However, it is possible that differences in pollen transfer resulted from different hummingbird species visiting corridor versus pasture feeders. Regardless of the mechanism, our results indicate that plant gene flow through habitat-restricted pollen vectors can be substantially limited in highly modified landscapes [14,28].

(c) Pollinator presence in forest fragments

Consistent with the strong effect of corridors on specialist movement, corridors were important drivers of within-patch specialist but not generalist occupancy in forest fragments. Indeed, P. guy appeared to be virtually absent from unconnected patches. This species is thought to be a key pollinator in the local hummingbird–plant pollination network, pollinating up to 35% of all hummingbird-pollinated plant species in the region and elsewhere [30], so its absence may have potential negative consequences for the structure of the entire pollination network.

Although recent findings suggest pollinators may shift their realized niche in the absence of competing species and thus partly compensate for pollinator extinctions [48], this was not the case in our study system; apparent local extinction of P. guy in isolated patches was paralleled by a nearly complete breakdown of pollination in H. tortuosa, which was not ameliorated by the availability of the habitat generalist pollinator. Fortunately, our results show that potential perturbations to the network may be moderated by the maintenance of narrow wooded corridors.

(d) Pollination success

A striking result of this study is that small-scale landscape configuration adjustments (wooded corridors) can benefit biodiversity in highly disturbed tropical landscapes beyond simply boosting local species richness [18,49] and movement [47], but also by providing benefits to ecosystem functioning [19]. Previous empirical studies have found that various animal taxa responsible for ecosystem functions increased along narrow corridors in fragmented systems [12,15,49]. In contrast, our study is, to the best of our knowledge, the first to show that simple wooded corridors not only benefit biodiversity by enhancing movement, but that they have the

potential to functionally connect otherwise spatially isolated partners in a mutualistic network.

Although even narrow corridors enhance pollination in our study, it is important to note that pollinators with strong edge avoidance behaviour are unlikely to use narrow corridors [47]. In such cases, conserving interactions will ultimately require the conservation of large pristine habitat patches [16], or at least substantially wider corridors. Future research should focus on how corridors can be optimized to enhance pollination services (i.e. corridor width and structure, newly planted versus existing corridors), and replicate these experiments elsewhere in both tropics and temperate landscapes to determine the generality of the observed rescue effects.

5. Conclusion

The broad consistency of outcomes across our four experiments suggests that simple wooded corridors can boost landscape connectivity for pollinators and animal-pollinated plants, averting deforestation-driven breakdown of pollination services. Overall, these results highlight the need to maintain movement of mobile, 'linking' species *sensu* [1] to ensure the persistence of pollination mutualisms in spatially structured, human-modified landscapes. However, we note that our findings may also apply to other organism groups that move along corridors, potentially providing other ecosystem services. Our results therefore may have broad implications for the conservation of ecosystem services in tropical landscapes in general. So far, narrow wooded corridors have remained abundant in

many tropical farmland landscapes [50,51] and appear to be widely accepted by farmers [17].

As tropical forests are the globally most important source of new agricultural land [52], quick action is required to avert the disappearance of corridor elements between fragments. Further, connecting isolated fragments by newly established corridors may restore pollinator communities and pollination services. Complementary to large-scale conservation strategies (i.e. formally protected areas), small-scale improvements in landscape connectivity (via simple corridors) represent low-cost–big-gain tools to conserve biodiversity and ecosystem processes in tropical landscapes.

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