RESEARCH ARTICLE

Matrix composition and corridor function for austral thrushes in a fragmented temperate forest

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Abstract Although it is widely recognized that animal movement may be facilitated by corridors and hindered by the matrix, the influence of matrix composition on the use of corridors still remain poorly understood. We used translocation experiments and state-space models to assess if the movement response of the frugivorous bird, the austral thrush, to riparian forest strips varies depending on matrix composition (open pasture vs. eucalyptus plantation). In agricultural landscapes, the directions displayed by most birds when moving in the open pasture matrix were consistent with an edge-following behavior. Riparian strips also functioned as passive drift fences in agricultural landscapes, with strips being used as conduits for movements once birds entered into a riparian strip. Our results suggest that visual perception of riparian strips by birds is hampered by the complex habitat structure in the eucalyptus matrix and that the use of riparian strips as habitat is conditioned by the surrounding matrix.

Keywords Corridors · Drift fence · Edge-following behavior

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Introduction

Movement corridors offer a practical and cost-effective opportunity for providing connectivity to wildlife in fragmented forest landscapes (Naidoo and Ricketts 2006; Morrison and Boyce 2008). However, the use of narrow linear structures, such as riparian strips and fencerows, as movement corridors should be considered as a hypothesis rather than as a fact. Indeed, corridor use by animals depends on a series of different causal mechanisms linking landscape structure with the spatio-temporal response of animals to environmental heterogeneity (Soulé and Gilpin 1991;

Simberloff et al. 1992). Determining the use of narrow structures as corridors can be a complex task because the movement pattern of wildlife may vary among species, individuals and landscapes (e.g., Davies and Pullin 2007; Öckinger and Smith 2008).

The contrast in habitat quality between forest fragments and the matrix could be an important ecological condition motivating individuals to follow corridors (Ricketts 2001; Baum et al. 2004). Corridors could be effective in facilitating dispersal if they connect patches surrounded by a matrix that acts as a physical barrier to dispersal (Öckinger and Smith 2008). Low boundary permeability and high dispersal costs over the matrix should increase the likelihood of corridors being used as "movement conduits," with individuals exhibiting rapid and directional movements within corridors (Haddad 1999; Haddad and Baum 1999; Fried et al. 2005; Graves et al. 2007; Vergara 2011).

Although an increase in the quality and permeability of the matrix should result in more individuals moving through the matrix, corridors that are surrounded by a low-resistance matrix may increase the connectivity between patches to the extent that they act as a "drift fence" or serve as a functional boundary that guides the movement of animals in the matrix, hereafter defined as a "guiding edge" (see below for definitions; Ricketts 2001; Tewksbury et al. 2002; Baum et al. 2004; Levey et al. 2005; Vergara 2011). In both drift fence and guiding edge corridors, animals recognize the corridor edge, modifying their movement pattern according to the corridor's orientation (Fried et al. 2005; Levey et al. 2005). Corridors will function as drift fences when individuals are "filtered" by the corridor edge, being subsequently redirected into other patches through the corridor, i.e., individuals are first attracted to the corridor, exhibiting movements that are perpendicular to the corridor edge, and once in the corridor they use it as a movement conduit (Forman 1995; Dramstad et al. 1996; Haddad and Baum 1999; Vergara 2011; Fig. 1). Animals will use corridors as guiding edges if they exhibit an "edge-following" behavior, according to which movements through the matrix tend to be parallel to the orientation of the corridor edge (Levey et al. 2005; Fig. 1).
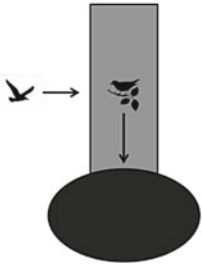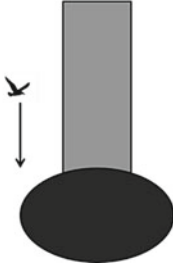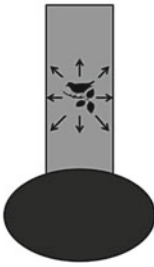
An edge response may not be the only mechanism that explains corridor function. Animal movements may be directly related to habitat characteristics rather than edge properties (Hahn et al. 2005; Nams 2011).

Thus, drift fence corridors could act as a preferred habitat for animals moving between patches, whereas guiding edges corridors themselves may not be perceived as a habitat different from the matrix (Haddad 1999; Levey et al. 2005, 2008). Nevertheless, narrow vegetation strips may offer feeding resources and provide shelter for several species, leading individuals to increase their turning rate and reduce their speed within corridors, as predicted by an "area-restricted search strategy" (Kareiva and Odell 1987; Bell 1991; Walsh 1996; Berggren et al. 2002; Fig. 1).

We studied the movement response of a frugivorous bird, the austral thrush (*Turdus falcklandii*), to riparian forest strips surrounded by two matrix types: open agricultural pasture and eucalyptus plantations. Although austral thrushes usually search for invertebrates in pastures (e.g., worms), they tend to be more abundant in riparian forest strips than in open pastures (Jaña-Prado 2007; Vergara 2011). In fact, riparian forests can support a high abundance of frugivorous birds by providing them with abundant feeding resources and nesting sites (Jaña-Prado 2007). Riparian forest strips, however, are floristically and structurally more similar to forest plantations than to open pastures, which implies that forest plantations can serve as a secondary habitat for several bird species, including thrushes (Vergara and Simonetti 2004; Silva-Rodríguez et al. 2008; Vergara 2011). Although pastures and forest plantations may represent low-resistance matrices for bird movements, the larger habitat differences between riparian strips and matrix in agricultural landscapes may result in an enhanced perception of corridor edges and strong habitat discrimination by thrushes crossing the matrix.

Animals may display a series of different behavioral modes when moving through heterogeneous landscapes (e.g., Morales et al. 2004; Schtickzelle et al. 2007), and therefore, riparian strips could function simultaneously as drift fences, guiding edges, and habitat. To assess the movement behavior of thrushes we used translocation experiments and state-space models. Based on our expectations about how birds should respond to corridor edges and habitat differences (see above), we tested whether riparian forests are used as guiding edge corridors in forest plantation landscapes and as drift fences in agricultural landscapes (see predictions in Fig. 1). We also tested for the alternative function of riparian forests as feeding or cover habitat for these species (Fig. 1).

Fig. 1 Expected movement patterns of frugivorous birds in the experimental landscapes used in this study. Three different corridor functions were tested, including drift fence, guiding edge and habitat. Parameters associated with each movement attribute are described in Table 1

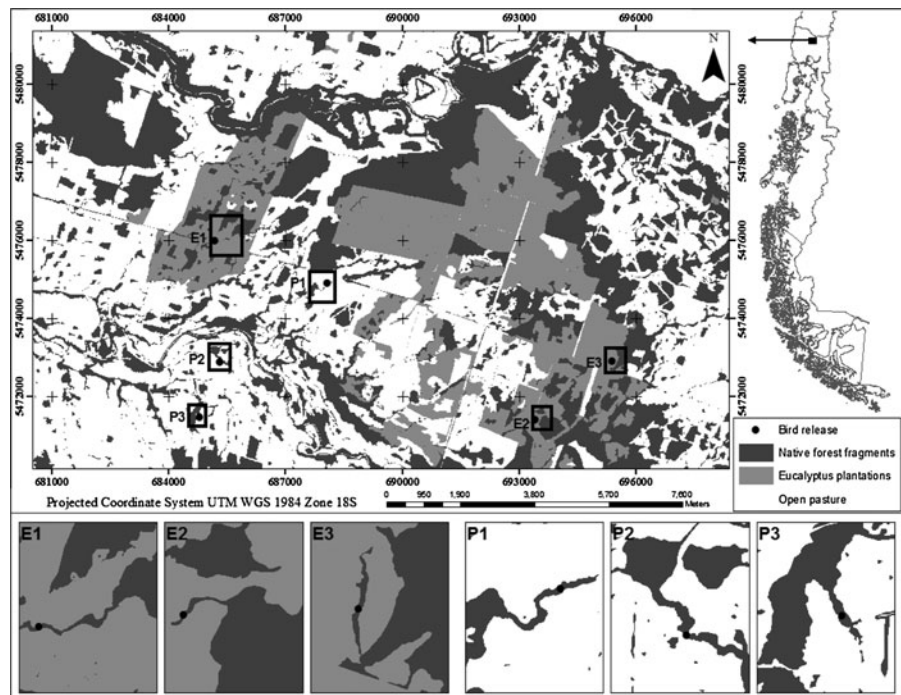| Drift fence	Guiding edge	Habitat
Speed		
No differences between the corridor and the matrix	No differences between the corridor and the matrix	Movement distances in the matrix are faster than in the corridor
Direction		
In the matrix birds move perpendicular to the corridor whereas in the corridor birds move parallel to the corridor edge	In the matrix birds move parallel to the corridor edge	Movements in the corridor are not related to the corridor edge direction
Turning rate		
No differences between the corridor and the matrix	No differences between the corridor and the matrix	Movements in the matrix are more linear than in the corridor

Methods

Study landscapes

The study was carried out west of Lake Rupanco (40.4° S, 73.0° W ca. 100 m.a.s.l.) in the Central Valley of southern Chile (Fig. 2). The Central Valley has been intensively used for raising livestock during the last two centuries and hence the dominant matrix type in such flat plains and rolling hills is open pastures (Echeverría et al. 2006, 2007). The current expansion of the forestry industry, driven by the construction of paper manufacturing plants, has promoted the replacement of pasture grasslands by exotic plantations of *Eucalyptus* spp. in the Central Valley.

Native forest remnants are scattered throughout the Central Valley landscape and a fraction of them are connected by riparian forest strips (Fig. 2). Native forest is composed by a mixture of deciduous *Nothofagus obliqua* and evergreen tree species including fleshy-fruited trees, most of them composing the intermediate canopy layer (3–15 m), such as *Aextoxicon punctatum*, *Luma apiculata*, *Persea lingue*, *Rhaphithamnus spinosus* and *Drymis winteri* (Donoso 1993). The vegetation

in riparian forest tends to be floristically similar to upland native forest, but trees are lower and support a greater proportion of species being tolerant to high soil moisture, such as *Myrtaceae* species (Donoso 1993).

We selected six different study landscapes, three of which were agricultural landscapes, with an open pasture matrix, while the other three were forest plantation landscapes, with a matrix of even-aged (9–13 years) eucalyptus plantations (Fig. 2). Each study landscape basically consisted of a riparian forest strip (17–28 m wide and 180–490 m long) connected to a single focal patch of native forest (5.2–36 ha). Focal patches were "winged" (i.e., connected to a blind riparian strip) in order to induce the birds to follow a single direction after they were released at a point adjacent to the riparian strip (see Movement data section). We used a "winged patch" design because such spatial configuration is appropriated to test for the drift-fence hypothesis (e.g., Tewksbury et al. 2002; Levey et al. 2005). In addition, this design provides a useful approach to test the "guiding edge corridor" hypothesis, which can only be verified by recording an edge-following behavior independently from the location of the focal patch.

Fig. 2 Map of the study area in southern Chile. The six study landscapes are shown at the *bottom*, including three agricultural (*P*) and three forest plantation landscapes (*E*)

Movement data

Radio-tracking experiments were conducted during the 2010 austral autumn. Each telemetry session involved the capture of a single adult austral thrush in focal patches. Birds were tagged with radio-transmitters (1.2 g; model TXB-004G, Telenax) attached to back feathers using epoxy glue and tightened with a harness made of absorbable surgical thread.

Once a transmitter was mounted on a bird, we released it at a point located in the matrix at about 150–220 m from the focal patch and adjacent (ca. 10 m) to the riparian strip edge (Fig. 2). At the release point birds were released by hand into the air in a random direction. We defined this release point in order to induce the individual to perceive the riparian strip edge. In addition, the distance between the release point and the patch was established by considering that the time taken for a bird to move between the release point and the focal patch would be less than the mean seed retention time (Vergara, unpublished). Birds were released within 15–20 min of initial capture with the exception of those that appeared stressed, which were released without being fitted with a radio-transmitter. An observer hidden near the release point recorded the bird's behavior (i.e., perching events, feeding attempts, and the height at which the bird used vegetation) by attempting to maintain visual contact while the bird moved across the landscape.

Telemetry sessions were carried out mostly during the afternoon (13:00–17:00 h), when autumn activity of frugivorous birds tends to be more pronounced (Vergara et al. 2010). Birds were radio tracked by three trained and synchronized observers, each one equipped with a 3-element Yagi antenna and a portable receiver (RX-TLNX; Telenax). Observer stations were maintained during each telemetry session and were located equidistant to the release point (ca. 180 m) forming an equilateral triangle. This design allowed us to minimize the bearing error (i.e., the angle between the actual signal location and the bearing lines). Bearings were recorded at regular 1 min intervals, a time interval short enough to capture the short-term movement patterns of birds. Therefore, a movement was defined as the displacement between two consecutive fixes. In addition, our posterior statistical analyses were robust to autocorrelation problems that are common when assessing fine-scale time-series data (see below). Transmitters were not removed after we tracked the birds.

Bearings were recorded until 180 min after a bird was released or until the telemetry signal became weak or failed. Signal locations of the birds (i.e., fixes) were triangulated using LOAS software (Ecological Software

Table 1 Parameters estimated from state-space models representing movement attributes described in Fig. 1 and used to test corridor function for austral thrushes in agricultural and eucalyptus landscapes (details in Methods section)

Movement attribute	Parameter	Symbol	Definition
Speed	Mean movement length	H_t	Mean movement distance for birds moving in habitat j
Direction	Basic movement direction	η_{ji}	Behavioral mode i, corresponding to a basic geometric angle taken by a bird in habitat j
	Angular response to the corridor edge	ω_{ji}	Primary movement direction scaled between $0°$ (moves parallel to the corridor edge) and $90°$ (moves perpendicular to the corridor edge)
	Behavioral mode probability	$P(\eta_{ij})$	Probability of an individual being in behavioral mode i in habitat j
Turning rate	Von Mises concentration	κ	Von Mises concentration parameter of turning angles for habitat j, a reciprocal measure of angle dispersion, with $\kappa = 0$ representing "pure" random walk

Solutions, Urnash, Switzerland). From this analysis we determined that fixes in agricultural and forest plantation landscapes were, respectively, within 8.1 ± 1.1 m and 7.3 ± 2.0 m from actual locations (mean $\pm$ SE). Fix accuracy was confirmed by comparing the observed and estimated locations of transmitters located on known control points. Consequently, fixes located less than 8 m from actual locations were averaged. The first fixes of each telemetry session were discarded in order to minimize possible delayed behavioral effects following animal capture and handling. We noticed such effects from visual observations as some birds tended to stay for a few minutes (4–19 min) on a perch near the release point. We also discarded the latest fixes of the tracked paths when they had large distance errors.

State-space models

State-space models were used for estimating ecological parameters describing the movement of birds (Table 1). State-space models are an efficient tool to analyze movement patterns because they estimate unobservable (hidden) states from observed locations, which are subject to sampling error (Jonsen et al. 2003, 2005; Patterson et al. 2008). We used a modified version of the Jonsen et al. (2005) model (see also Breed et al. 2009), where speed and turning angles are modeled independently in the transition equation. Our model was focused on determining if directions between locations are associated to the riparian strip orientation. The expected movement direction at time t (α_t, i.e., the angle between the longitudinal axis and the segment formed by two consecutive fixes) was modeled as a biased correlated random walk:

$$\alpha_t = p_t \eta_{ji(t)} + (1 - p_t)\eta_{ji(t-1)},$$

where $\eta_{ji(t)}$ is the basic movement direction i taken by an animal in habitat j at time t, a binary angular variable with two possible states for each habitat and time period, $i = \{1, 2\}$, each representing a particular animal's behavioral mode. Behavioral mode was allowed to switch between and within habitat type (e.g., Morales et al. 2004; Table 1). Thus, for example, in forest plantation landscapes, the model assumed two alternative behavioral modes when birds moved in the eucalyptus plantation matrix and other two modes when birds entered to the riparian strip. Parameter p_t is a time-dependent variable ranging between 0 and 1, and representing process bias in movement direction (e.g., Schultz and Crone 2001). The interpretation of the above equation is that at each time step the direction taken by an individual is the weighted average of the behavioral mode selected at time t, with probability $P(\eta_{ij})$, and the behavioral mode selected at the previous time ($\eta_{(t-1)}$; Table 1). Thus, when $p_t \to 0$ the movement approaches a standard correlated random walk, whereas if $p_t \to 1$ it will be biased in an angle that can be related to the riparian strip's orientation (Barton et al. 2009; see below). Movement length at time t was assumed to follow a negative truncated normal distribution with mean μ_t and standard deviation σ_t, with both parameters changing between successive time steps. We let μ_t be a function of the habitat type in which the birds moved:

$$\mu_{j,t} = H_j + \beta_t$$

where H_j is a parameter representing the mean movement length in habitat j (riparian strip or matrix)

and β_t a time-dependent term representing process error in speed.

State-space models were fitted to each individual's tracking data. Model fitting was examined by comparing observed fixes with the state estimates from the models (predicted locations). A good-fit state-space model produces state estimates that are both relatively close to the observed data and reasonable for extreme observations (Jonsen et al. 2005). Thus, goodness of fit of models was assessed based on the Mean Squared Prediction Error (MSPE) and the Euclidean distances, which quantify differences between the observed locations and the posterior state estimates (Lawson 2009).

State-space models were run using R2WinBUGS, the R interface for WinBUGS 1.4. Models were specified with three independent Markov Chain Monte Carlo (MCMC) chains, each with 10,000 sampling iterations and a "burn in" of 5,000 iterations. Chains were examined for autocorrelation and convergence to stationary parameter distribution (Ntzoufras 2009). We interpreted only parameters with unimodal distributed samples using the Potential Scale Reduction Factor, which tests convergence between MCMC chains. A total of 2,500 parameter values were sampled from these chains, with the mean of each parameter and its 95 % Bayesian credibility intervals estimated from the samples. We specified vague priors for all unknown parameters. A uniform distribution was assumed for η, a Dirichlet distribution was assumed for P_η, while a beta distribution was specified for p_t. Truncated normal distributions were specified using a WinBUGS code provided by Lunn (2008).

Testing corridor function

The likelihood of riparian strips functioning as drift fences, guiding edges or habitat (Fig. 1) was assessed using movement parameters fitted by the state-space models (see above). Habitat differences in the mean movement length (H) were directly assessed by comparing their mean and 95 % Bayesian credibility intervals. Since the arithmetic mean of angles is not a good measure of central tendency, movement directions (η) and turning rates (κ) were analyzed using circular statistics (e.g., Batschelet 1981).

We estimated the circular mean and circular variance of η from their estimated posterior distributions. Circular variance ranges between 0 and 1, with higher values indicating a more concentrated distribution of angles around the mean value (Jammalamadaka and SenGupta

2001). In order to determine if movement directions were associated with the riparian strip edge, we converted η values to angles relative to the mean riparian strip direction (ω), with values ranging between 0 and 90°, and representing movements completely perpendicular and parallel to the riparian strip, respectively (Table 1). Since ω values of 0 and 90° were extreme cases, we defined a priori three levels of angular response to riparian strip edge: (1) movement perpendicular to the riparian strip edge: if $0 \leq \omega < 15°$; (2) movement parallel to the riparian strip edge: if $75° < \omega \leq 90°$; (3) neutral response otherwise. In cases where ω values were parallel or perpendicular to the riparian strip edge a Rayleigh test of uniformity was used to assess if ω values had a unimodal distribution with a mean direction equal or perpendicular (see above) to the mean riparian strip direction. The mean riparian strip direction was estimated as the mean bearing angle for the set of 100 m segments in which each riparian strip was partitioned. Some birds exhibited movements in the direction opposed to the focal patches, an edge-following behavior that could have been influenced by the distance to focal patch (Fig. 1). In a posterior analysis, in which data set were pooled in a single model, we included the distance to focal patch as a covariate (see below). Turning rate was assessed by fitting von Mises concentration parameters (κ, a reciprocal measure of dispersion) to state estimates of turning angles. From a bootstrap procedure with 10,000 replications each we calculated the 95th percentile confidence intervals of κ values. Habitat differences in κ were evaluated using a Bartlett's Chi-squared test (Jammalamadaka and SenGupta 2001).

We used SSM-estimated behavioral states to make population-level inferences about movement behavior of thrushes (e.g., see Breed et al. 2009). Movement lengths and behavioral modes inferred from SSMs at each time step t (μ_t and $\eta_{(t)}$, respectively; see Table 1) were analyzed using mixed-effects models. Each combination of landscape (agricultural or forest plantation) and habitat type (matrix or corridor) was included as a dummy variable in order to test for corridor function (see Fig. 1). We used a three-state multinomial logit model including the following states: movement that were perpendicular and parallel to the riparian strip edge as well as no oriented movements (see above for details). We considered no oriented movements to be the reference level, and hence exponentiated coefficients represented the ratio of the probability of choosing a

particular behavioral mode (i.e., perpendicular or parallel) over the probability of displaying a no oriented movement. Movement length was assessed using a log linear model. We included the distance to the riparian strip and the distance to the focal patch as covariates because of the ability of thrushes to perceive both habitat types could be distance dependent. The thrush identity and landscape unit were included as random factors. We used the Akaike's information criterion (AIC) and Akaike weights (W) to evaluate the support for competing a priori models explaining behavioral states.

Results

Overall movement

A total of 14 individuals were tracked, seven in agricultural landscapes and another seven in forest plantation landscapes (Appendix 1, Supplementary Material). MSPE and the Euclidean distances between the observed fixes and state estimates from models indicated acceptable model performance for all fitted models with extreme locations accurately predicted (Appendix 2, Supplementary Material).

Visual observations revealed differences in the thrush behavior between agricultural landscapes and forest plantation landscapes. In agricultural landscapes, thrushes perched frequently on branches located along the riparian strip edge, and from these sites they tended to move into the matrix. Thrushes were also observed displaying short displacements on the pasture ground (< 25 m), apparently while they fed on invertebrates, or perching momentarily on scattered poles. In forest plantation landscapes observations were hampered by the dense vegetation and by the fact that thrushes tended to perch high in the canopy layer. However, we observed thrushes on the ground and in the understory of forest plantations feeding on blackberry (*Rubus ulmifolius*) scrubs.

Movement direction

Movement directions (η) of austral thrushes and their angular response to the riparian strip edge (ω) varied between habitats (matrix-riparian strips), landscapes (agricultural-forest plantation) and among individuals. Five thrushes tracked in agricultural landscapes exhibited basic movement directions that were parallel to the

riparian strip edge when thrushes moved in the matrix (i.e., $\omega < 15°$, $P < 0.001$; Table 2), whereas only one of them (AT7 individual) moved perpendicular to the edge (i.e., $\omega > 85°$, $P < 0.001$; Table 2). All assessed thrushes that moved within riparian strips surrounded by pasture exhibited movement directions parallel to the riparian strip's edge. One of these birds (AT4) moved in the opposite direction to the focal patch (Table 2). In forest plantation landscapes thrushes exhibited neither perpendicular moves nor parallel movements toward the riparian strip when they moved on the plantation matrix. Only one thrush (AT10) exhibited movements parallel to the riparian strip when moved within riparian strips surrounded by eucalyptus plantations, although in the opposite direction to the focal patch (Table 2). Multinomial logit models indicated that behavioral modes inferred from SSMs may be generalized at the population level (Table 3). The best supported model (ΔAIC < 2) had the interaction between landscape and habitat type as predictors (L × H; Table 3). In the matrix and riparian strips of agricultural landscapes movements parallel to the strip edge were respectively 7.32 and 7.40 times more likely than no oriented movements (Table 4). On the contrary, movements parallel and perpendicular to the strip edge were respectively 15.01 and 9.80 times less likely than no oriented movement when birds moved in the matrix and strips of forest plantation landscapes (Table 4). The distance to the riparian strip and the distance to the focal patch had no effect on behavioral modes (Table 4).

Movement speed

In agricultural landscapes thrushes moved 49.5 ± 13.2 and 45.8 ± 6.7 m on the matrix and the riparian strips respectively, while in forest plantation landscapes movements in the matrix and riparian strips averaged 29.2 ± 4.8 and 24.5 ± 3.7 m, respectively. The Bayesian credibility intervals did not overlap in just five out of the eight birds (Table 5). In agricultural landscape the mean movement length was longer in the riparian strip than in the matrix only for one individual (AT3), while another individual (AT6) exhibited the reverse pattern (Table 5). In forest plantation landscape only one individual (AT9) had a mean movement length longer in the matrix than in the riparian strip (Table 5). Log linear models assessing the movement length inferred from SSMs supported the results obtained from the individual SSMs (Table 3). Two

Table 2 Basic movement directions ($\eta_{j,i}$) and their respective angular responses to corridor edges (ω) of austral thrushes (AT) in agricultural (A) and eucalyptus forest (E) landscapes

Landscape	Individual	Matrix								
		$\eta_{1,1}$					$\eta_{1,2}$			
		Mean	Var	$P(\eta)$	ω		Mean	Var	$P(\eta)$	ω
A1	AT1	2.76	0.38	0.62	57.22		−2.48	0.26	0.38	2.74***
A1	AT2	−2.36	0.14	0.55	9.34***		2.27	0.20	0.45	85.05***
A1	AT3	−2.33	0.58	0.50	11.12***		2.56	0.59	0.50	68.82
A2	AT4	2.33	0.46	0.51	9.55***		−2.87	0.83	0.49	71.89
A2	AT6	2.26	0.52	0.48	5.88***		2.28	0.41	0.52	6.79***
A3	AT7	−2.46	0.81	0.52	81.68***		−2.58	0.62	0.48	88.55***
E1	AT8	−2.12	0.26	0.49	52.81		2.50	0.17	0.51	42.53
E1	AT10	−2.37	0.56	0.46	38.23		2.67	0.46	0.54	32.58
E2	AT11	2.48	0.63	0.46	51.86		−1.66	0.66	0.54	81.89
E2	AT12	2.48	0.98	0.54	51.69		−2.08	0.56	0.46	47.06
Landscape	Individual	Corridor								
		$\eta_{2,1}$					$\eta_{2,2}$			
		Mean	Var	$P(\eta)$	ω		Mean	Var	$P(\eta)$	ω
A1	AT2	−2.53	0.42	0.51	0.22***		2.49	0.30	0.49	72.63
A2	AT4	3.00	0.54	0.51	48.33		−1.08	0.43	0.49	5.60***
A2	AT6	2.42	0.61	0.49	14.94***		−2.21	0.74	0.51	70.56
E1	AT9	−2.09	0.68	0.51	54.64		−1.12	0.76	0.49	78.07***
E1	AT10	−3.07	0.80	0.46	1.78***		0.56	0.54	0.54	26.47
E2	AT11	−2.43	0.13	0.52	26.46		2.38	0.15	0.48	57.89
E2	AT12	−1.63	0.72	0.53	72.57		−0.41	0.15	0.68	37.74
E3	AT14	−2.39	0.79	0.45	41.45		−2.83	0.77	0.55	66.22

The circular mean and variance of $\eta_{j,i}$ are in radian units, with subscript j representing the habitat type (matrix or corridor) and subscript i indexing the behavioral mode for two-state switching models. $P(\eta)$ represents the probability of being in each behavioral mode. Values of ω are presented in degrees and range between 0 and 90° (i.e., from perpendicular to parallel movements). Model parameters where convergence in MCMC estimation was not reached were not included in this Table (see text)

*** $P < 0.001$

models were supported by the data (ΔAIC < 2), but these models explained a low fraction of the variance in movement length (i.e., R^2 < 0.7; Table 3). No model-averaged coefficient was significant at 5 % (Table 4).

Turning rate

The concentration parameter (κ) of the turning angles of austral thrushes ranged between 0.58 and 2.49 in the matrix and between 0.22 and 2.16 in the riparian strips (2.0 ± 0.1 vs. 1.35 ± 0.1, respectively, $n = 11$; Table 6). On the average, κ values were larger in the matrix than in the riparian strips for both landscape types, with this difference more pronounced in agricultural (2.6 ± 4.1 vs. 1.2 ± 0.3, $n = 6$, respectively; Table 4) than in forest plantation landscapes (1.6 ± 1.7 vs. 1.4 ± 3.6, respectively, $n = 5$; Table 4). However, the 95 % bootstrap confidence intervals of κ values showed large variation in the distribution of the estimated κ values, with five individuals showing upper confidence intervals greater than 10 (Table 4). This large variation resulted in only two individuals (AT3 and AT6) having κ values in the matrix significantly larger than κ values

Table 3 Candidate models explaining the behavioral mode and movement distance of austral thrushes inferred from state-space models (SSM; see Table 1)

Model[a]	AIC	ΔAIC	Weight	R²
SSM estimated behavioral mode				
L × H	211.5	0.00	0.69	0.35
L × H + DIST.COR + DIST.PATCH	213.5	2.07	0.25	0.35
L × H + DIST.PATCH	216.2	4.74	0.06	0.33
DIST.COR + DIST.PATCH	263.6	52.11	0.00	0.06
DIST.COR	265.3	53.82	0.00	0.05
SSM estimated movement distance				
L × H	332.7	0.00	0.47	0.06
L × H + DIST.COR	333.9	1.23	0.25	0.05
L × H + DIST.PATCH	334.7	1.96	0.18	0.06
L × H + DIST.COR + DIST.PATCH	335.9	3.17	0.10	0.05

DIST.COR and DIST.PATCH refer to the effect of distance to the riparian strip and distance to the focal patch, respectively

[a] L × H term indicates that a single coefficient was estimated for each combination of landscape (agricultural or forest plantation) and habitat type (matrix or corridor)

Table 4 Model-averaged coefficients, standard errors (SE) and P values from models explaining the behavioral mode (parallel or perpendicular to the riparian strip) and movement distance of austral thrushes inferred from state-space models (SSM; see Table 2 and Table 3)

Variable	Coefficient	SE	P
SSM estimated behavioral mode[a]			
Matrix in agricultural (parallel)	1.99	0.43	<0.001
Matrix in agricultural (perpendicular)	−0.07	0.44	0.884
Matrix in forest plantation (parallel)	−18.32	288.28	0.995
Matrix in forest plantation (perpendicular)	−2.28	0.73	0.002
Corridor in agricultural (parallel)	2.00	0.40	<0.001
Corridor in agricultural (perpendicular)	−17.86	257.11	0.994
Corridor in forest plantation (parallel)	−2.71	0.64	<0.001
Corridor in forest plantation (perpendicular)	13.80	249.94	0.996
Distance to the riparian strip (parallel)	−0.011	0.01	0.370
Distance to the riparian strip (perpendicular)	0.014	0.01	0.124
Distance to the focal patch (parallel)	−0.001	0.00	0.485
Distance to the focal patch (perpendicular)	−0.001	0.00	0.690
SSM estimated movement distance			
Matrix in agricultural	−0.11	0.36	0.762
Matrix in forest plantation	0.02	0.10	0.799
Corridor in agricultural	0.32	0.36	0.375
Corridor in forest plantation	−0.32	0.36	0.375
Distance to the riparian strip	0.002	0.002	0.353
Distance to the focal patch	0.00	0.00	0.702

[a] Coefficients of multinomial models indicate that the behavioral mode (parallel or perpendicular) is more probable that a non-oriented (random) movement, if positive, and otherwise if negative

Table 5 Mean movement lengths of austral thrushes (AT) in agricultural (A) and eucalyptus forest (E) landscapes

Landscape	Individual	Matrix			Corridor		
		Lower	Mean	Upper	Lower	Mean	Upper
A1	AT1	5.8	21.2	54.5	10.52	28.77	59.76
A1	AT2	13.3	29.0	49.1	25.69	53.23	72.14
A1	AT3	1.2	14.9	24.6	53.32	63.92	80.51
A2	AT6	91.3	142.6	181.2	2.66	50.15	122.29
A3	AT7	1.5	11.4	21.7	2.79	15.71	29.82
E1	AT9	32.6	42.5	54.9	9.54	27.49	41.41
E1	AT10	17.3	29.9	51.1	10.66	29.63	47.20
E2	AT12	2.2	15.1	28.5	1.56	16.45	25.83

The posterior mean and the 95 % Bayesian credible intervals (lower: 2.5th percentile, upper: 97.5th percentile) of movement lengths are shown. Model parameters where convergence in MCMC estimation was not reached were not included in this Table (see text)

Table 6 Von Mises concentration parameter (κ) of turning angles estimated from state–space models for austral thrushes (AT) in agricultural (A) and eucalyptus forest (E) landscapes

Landscape	Individual	Matrix				Corridor				P
		k				k				
		Lower	Mean	Upper	n	Lower	Mean	Upper	n	
A1	AT1	1.11	1.65	2.43	62	0.25	0.84	1.92	23	0.099
A1	AT2	0.65	1.15	2.00	45	0.90	1.46	2.62	23	0.556
A1	AT3	1.67	2.86	6.28	35	0.36	0.78	2.58	9	0.047
A2	AT4	0.17	0.58	1.58	18	0.06	0.22	0.81	40	0.445
A2	AT6	0.28	1.64	6.75	8	0.34	0.13	2.12	7	0.037
A3	AT7	2.49	3.81	14.29	13	1.75	3.36	12.40	24	0.851
E1	AT8	0.49	0.90	1.45	41	1.01	1.88	4.13	15	0.142
E1	AT9	0.26	0.75	2.20	12	0.34	1.37	26.42	6	0.729
E1	AT10	1.01	1.66	3.13	25	1.20	2.16	12.72	12	0.620
E3	AT13	0.73	1.47	2.97	22	0.25	1.64	16.01	10	0.836
E3	AT14	0.74	1.10	1.67	33	0.86	1.75	5.11	8	0.408

The mean κ and its respective 95 percent bootstrap confidence intervals (Lower, Upper) are shown with differences between Matrix and Corridor assessed by using Bartlett's Chi-squared test (P). Individuals with $n \leq 4$ were not included in this Table

in the riparian strips, both in agricultural landscapes (Table 4).

Discussion

We did not find support for our hypothesis that riparian forests are used as guiding edge corridors in forest plantation landscapes and as drift fences in agricultural landscapes (Fig. 1). This mismatch between the expected and the actual movement response of birds to riparian strips arises from a series of mechanisms linking individual-level attributes with the structure and composition of the landscape. In particular, the following mechanisms may be considered as the basis for understanding the dependence of corridor effectiveness on matrix composition:

1) Corridor use pattern results from the combination of different movement behaviors. In fact, animal pathways can be understood as the contribution of several distinct behaviors that switch over time as a result of changes in the perception of the landscape

and the level of importance that the animal gives to ecological processes such as energy requirements or predation risk (Morales et al. 2004; Nathan et al. 2008). Accordingly, in this study we detected important changes in the movement orientations of birds that occurred within and between habitat types (i.e., riparian strip and matrix). For agricultural landscapes these were associated with the orientation angle of the riparian strips. However, the modal switching behavior of birds in agricultural and forest plantation landscapes was not in agreement with the expectations. In agricultural landscapes we found that the directions displayed by most birds when they moved in the open pasture matrix were consistent with an edge-following behavior (as predicted for guiding edge corridors) instead of moving perpendicularly to the edge of the riparian strip (as predicted for drift-fence corridors). However, when birds entered into the riparian strips they tended to use them as movement conduits, as expected from the drift-fence effect.

2) The drift-fence effect is a passive rather than an active functional process. In this sense, our prediction that drift fence corridors would act as an attracting habitat, biasing the movement directions of birds toward the riparian strip edge, was not supported by the results (cf. Haddad and Baum 1999; Tewksbury et al. 2002). Instead, "passive drift-fence corridors" only functioned as ecological filters that intercept individuals moving on the matrix, but without affecting the movement directions before the birds intercept a riparian strip. Our results suggest that riparian strips functioned as passive drift-fences in agricultural landscapes, and to some extent in the forest plantation landscapes (see individual AT10 in Table 2), with riparian strips being used as conduits for movements once the birds entered a riparian strip.

3) Visual perception of corridors is hampered by complex habitat structure in the matrix. Most bird species use visual information acquired from current and previous experiences to make decisions such as food acquisition, habitat use or predator avoidance (Fernandez-Juricic et al. 2004). Such decisions, however, are scale-dependent because they are affected by the resolution level at which birds perceive the landscape when sampling feeding resources, shelter habitats or nesting sites (Kristan 2006). In this sense, although the frugivory activity of austral thrushes is closely associated with fruit abundance at the landscape scale, a dense micro-habitat structure could

decrease the bird's ability to locate fruit resources within forest fragments (Vergara et al. 2010). Similarly, riparian strips may be less conspicuous for austral thrushes that move in the eucalyptus plantation matrix, becoming especially likely as both species tended to move and perch on the canopy of the eucalyptus trees (which typically are taller than the trees located in the riparian strips). Thus, a decreased perception of the riparian strips could have resulted in the lack of an edge-following behavior in eucalyptus forest landscapes.

4) The use of corridors as habitat is influenced by the surrounding matrix. Depending on the level of feeding or nesting resources, the matrix could provide landscape supplementation for those species that have a broad habitat use pattern, such as austral thrushes. Open pastures offer invertebrates (e.g., insects or worms) to birds, food items that are alternative to fruits that are only found in the riparian strips and fragments. However, these bird species seemed to be exposed to a higher predation risk by raptors searching for prey in open areas (Vergara 2011). Corridors acting as movement conduits could negatively affect population persistence as predation risk increases within the corridor or in the matrix (Hudgens and Haddad 2003; Vergara 2011). Thus, riparian strips not only could provide fruits to thrushes, but also may represent a safe habitat suitable for perching and nesting. These observations are supported by our results that showed a larger turning rate in the riparian strips than in the matrix with two significant cases (i.e., AT3 and AT1). In forest plantation landscapes, however, the results showed less support for the habitat function of riparian strips. Probably, riparian strips surrounded by eucalyptus plantations were underutilized by birds due to their decreased ability to detect riparian strips (see above) or because differences in habitat characteristics between the riparian strips and the matrix are less conspicuous to birds (i.e., making the riparian strip boundary less noticeable). In fact, the understory of eucalyptus plantations is composed of a mix of shrubs, many of them bearing fruits (e.g., *Rubus ulmifolius*), which are also present along the edges of riparian strips.

Translocation experiments constitute an emergent approach to test for corridor function because they allow standardizing the willingness of birds to move in a direction within a certain type of habitat (e.g., Castellon and Sieving 2006; Gillies and St. Clair 2008;

Ibarra-Macias et al. 2011). Although tranlocated individuals might not exhibit the natural movement pattern of birds or be influenced by others behaviors, it is probably that our methodological approach was not affected by these problems. First, our experiments were designed to test for the short-term movement response of birds to riparian strips rather than if birds disperse between distant patches, hence it is highly improbable that homing affected the distance range over which individuals moved. Second, central-place foraging could not affect the movement pattern of thrushes because this study was carried out in autumn, when this species exhibits an extensive searching behavior (Vergara et al. 2010). Such a reduced territoriality, however, does not imply necessarily that individuals lack the cognitive ability to return to the patches that they have previously visited (e.g., Armsworth and Roughgarden 2005; Mueller and Fagan 2008). Third, the study matrices (i.e., forest plantation and pasture) are secondary habitats for thrushes (Vergara 2011), and therefore, the movement of translocated individuals may have hardly been affected by unfamiliar environmental conditions (e.g., Heidinger et al. 2009).

The real effectiveness of corridors in improving landscape connectivity has given rise to a long debate among ecologists and conservation practitioners (e.g., see McEuen 1993; Bennett 1999; Davies and Pullin 2007; Öckinger and Smith 2008). In practice, corridors will only be useful as landscape connectors if they contribute to increase the flow of individuals across the landscape, rescuing demographically and genetically local populations while facilitating the re-colonization of empty suitable patches (Schippers et al. 2009). Although such emergent proprieties of corridors are key processes for ensuring metapopulation persistence, proximate mechanisms explaining corridor use and effectiveness occur at the individual level. Determining the basic movement rules of animals in fragmented landscapes, therefore, constitutes a necessary condition for using corridors as habitat connectors for wildlife. In this sense, the results of this study reinforce this approach by showing that riparian strips may be useful conservation tools in agricultural landscapes, providing landscape connectivity for tree species that are dispersed by thrushes.

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