Landscape Ecol
DOI 10.1007/s10980-014-0111-2

RESEARCH ARTICLE

Do corridors promote connectivity for bird-dispersed trees? The case of *Persea lingue* in Chilean fragmented landscapes

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Received: 13 May 2014 / Accepted: 19 October 2014

Abstract Disentangling the contribution of corridors to landscape connectivity is crucial for adopting efficient measures in conservation, but their actual role in heterogeneous landscapes is not yet fully understood. We assessed the hypothesis that corridors, consisting of hedgerows and riparian vegetation strips, are important landscape elements promoting functional connectivity for the lingue (*Persea lingue*), a tree endemic to southern Chile and Argentina whose seeds are mainly dispersed by the habitat generalist austral thrush (*Turdus falcklandii*). For this purpose, we used empirical estimates of seed production, fruit consumption and bird movement patterns, in combination with a seed dispersal model and a graph-theoretical approach for network connectivity analysis. We found that for this plant-animal interaction, the hypothesis mentioned above is not supported. Functional connectivity decreased as the structural connectivity provided by corridors increased, and stepping stones were much more effective connectivity providers than corridors. Our findings are not generalizable to other situations because thrushes contribute to the dispersal of seeds along narrow and sinuous corridors, which provide unsuitable conditions for the establishment of lingues. We conclude that (a) the effectiveness of corridors for promoting connectivity and successful dispersal is landscape- and species-specific; and that (b) effective conservation of Chilean forest biodiversity involves a tradeoff between enhancing the availability of stepping stones and providing corridors of sufficient width and appropriate shape to meet the needs and dispersal modalities of different species.

Keywords Seed dispersal model · Corridors · Stepping stones · Ecological networks · Frugivores

Introduction

Narrow and continuous landscape elements like riparian strips and hedgerows can act as movement corridors for biodiversity in fragmented landscapes, structurally and functionally connecting patches of habitat (Anderson and Danielson 1997; Ockinger and Smith 2008). Depending on their intrinsic movement

Electronic supplementary material The online version of this article (doi:10.1007/s10980-014-0111-2) contains supplementary material, which is available to authorized users.

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capabilities and the environmental conditions prevailing in the matrix, animals may use corridors as movement conduits, drift fences, or guiding edges (Tewksbury et al. 2002; Baum et al. 2004; Levey et al. 2005; Vergara 2011; Vergara et al. 2013). In all these cases, animals perceive the corridor as a distinctive landscape element, following it to reach a distant patch (Beier and Noss 1998; Tewksbury et al. 2002; Haddad et al. 2003).

Landscape experiments with a few replicates involving a few corridors and patches have provided a valuable mechanistic description of how animals use and move through corridors (e.g., Beier and Noss 1998; Baum et al. 2004; Levey et al. 2005; Damschen et al. 2006; Davies and Pullin 2007; Gilbert-Norton et al. 2010). The larger-scale contribution of corridor networks to the persistence of metapopulations, however, is not fully understood yet (e.g., see Hudgens and Haddad 2003; Schippers et al. 2009; Tang et al. 2014). From a landscape planning perspective, supporting decision making in biodiversity conservation programs requires disentangling the contribution of corridors to functional connectivity, i.e., the influence of landscape structure on the ability of species to move through the landscape (Taylor et al. 1993).

Individual corridors usually represent, or are assumed to represent, the most favorable paths (in terms of dispersal costs) between habitat patches, and hence they contribute to the maintenance of overall landscape connectivity by facilitating the landscape-scale movement of genes and individuals (Fig. 1; Tewksbury et al. 2002). For this reason, landscape planning strategies focused in the conservation and restoration of corridor networks are based on the premise that the presence of corridors is the best and most efficient way to uphold connectivity and, thus, to ensure population persistence (Forman and Godron 1986; Awade et al. 2012; Segurado et al. 2013). However, these beneficial corridor effects could become less evident, or could even be reversed, depending upon how species-specific movement attributes, and other landscape elements, interact with corridors over time (e.g., Baum et al. 2004; Chetkiewicz et al. 2006; Evans et al. 2013). As shown in Fig. 1, the relative contribution of a corridor to the connectivity of animal-dispersed plants may be influenced by its structural attributes (e.g., shape and position), as well as the presence of other landscape connectors, such as stepping stones.

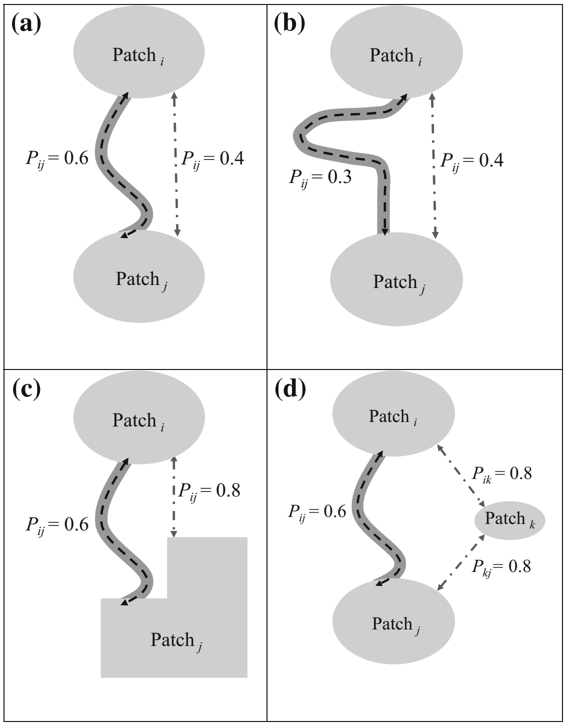

Fig. 1 The effectiveness of a corridor for an animal-dispersed plant depends on its shape and position relative to the patch, as well as the presence of other landscape connectors, such as stepping stones. Corridor effectiveness is here given by the probability value (p_{ij}) representing the likelihood of seed dispersal between patch i and patch j following that corridor. **a** A corridor provides the best linkage between two patches (i and j) when compared to the direct movement through the matrix. **b** A tortuous-shaped corridor represents a longer route for dispersed seeds than the path followed by animals when moving through the matrix. **c** A corridor represents a long route for dispersed seeds when it connects distant sections of two irregular-shaped patches. **d** A stepping stone (patch k) minimizes the effective length of the route taken by animals that disperse seeds between patches i and j ($p_{ij}^* = 0.64$), hence decreasing the risk of seed deposition outside patches

First, the dispersal ability of plants whose seeds are dispersed by frugivorous animals can be intrinsically low if seeds are deposited shortly after their ingestion (e.g., Cain et al. 2000; Levey et al. 2008). Therefore, seed dispersal events between patches would be unlikely to occur when dispersing animals use corridors connecting distant sections of two habitat patches as well as corridors with tortuous shapes (Fig. 1; Baum et al. 2004). In these cases, long corridors may induce seed dispersers to move large distances along them, increasing the likelihood that seeds are deposited along the corridor before reaching other patches that are suitable for plant establishment (Fig. 1). Indeed, in some cases the corridor may not meet the conditions for successful seedling germination and survival, due for instance to increased edge effects (e.g., microclimatic variations, higher light exposure, increased grazing rates or soil compaction) that reduce the habitat quality in the corridor compared to that in larger forest patches (Laurance 2004). Second, functional redundancy between corridors and other landscape elements acting as connectors (e.g., stepping stones, i.e., patches that contribute to facilitate movement among other patches), may reduce the relative importance of corridors for overall landscape connectivity (Fig. 1; Baum et al. 2004). Therefore, the role of corridors in maintaining functional connectivity may be difficult to establish in structurally heterogeneous landscapes with varying types of connecting elements, as well as with corridors of different quality, shape and length.

In this study, we assessed functional landscape connectivity for the fleshy-fruited lingue (*Persea lingue* Lauraceae), a tree endemic to southern Chile and Argentina (Donoso 1993). Old-growth forests harboring populations of lingues have declined more than 40 % in the last decades (Echeverría et al. 2012). Lingue seeds are mostly dispersed by the austral thrush (*Turdus falcklandii*) (Vergara et al. 2010; Vásquez 2011). In temperate forest landscapes the abundance of thrushes is not largely affected by forest loss and fragmentation (e.g., Vergara and Armesto 2009), but their ecological service as dispersers of lingue seeds is scale-dependent and less efficient, in terms of the number of seeds dispersed, as forest patches become more isolated (Vergara et al. 2010). Austral thrushes use hedgerows and strips of riparian vegetation (hereafter corridors) as connectors by displaying an edge following behavior while moving between forest patches surrounded by open matrix (Vergara 2011; Vergara et al. 2013). Despite thrushes' intensive use of corridors for moving between patches, the presence of corridors does not necessarily ensure that thrushes are more efficient in dispersing seeds of lingues between forest patches, or in increasing its functional connectivity.

In order to establish the basis for effective landscape planning focused on the conservation of lingues, we hypothesized that corridors are important landscape elements promoting functional connectivity for lingues. Two predictions may be derived from this hypothesis: (i) the functional connectivity of lingues should increase as the structural connectivity provided by corridors increases, such that the loss of all corridors should cause a decline in connectivity; (ii) corridors should be more important in providing connectivity than other landscape elements such as stepping stones. These predictions were tested by using a novel methodological framework based in the following steps: (1) We determined the structural connectivity provided by corridors in different landscapes and spatial scales, in order to evaluate if higher structural connectivity through corridors translated or not into increased functional connectivity for lingues, as assessed by the next four steps of the analysis. (2) We quantified fruit production in each patch to estimate the seeds available to be dispersed by thrushes. (3) We determined seed dispersal probabilities between patches connected by corridors and between patches surrounded by the open matrix. For this analysis, seed dispersal kernels were fitted to data simulated from a mechanistic seed dispersal model. (4) Based on the dispersal probabilities from previous step, we performed a network analysis intended to determine overall functional connectivity in the landscape and the contribution to functional connectivity provided by individual connectors (i.e., corridors and stepping stones). (5) Finally, we used a statistical model to test the actual relationship between the functional and structural connectivity of corridors and to compare the contribution to functional connectivity of corridors and stepping stones.

Methods

Study species description

Lingues are shade-tolerant trees endemic to the temperate forests of South America. Lingues can reach up to 30°m high and 80°cm of diameter and their fruiting peak period occurs during the mid to late austral autumn (Donoso 1993). Lingue fruits are drupes with black epidermis and fleshy endocarp, each containing only a single seed, which averages 10.2 mm wide and 13.0 mm long (Vergara et al. 2010).

In temperate forests of South America austral thrushes are the most abundant seed disperser/frugivorous species during the fruiting peak of lingues

(Amico and Aizen 2005; Vergara et al. 2010). Austral thrushes tend to be generalist in their habitat preferences, so that the open matrix is not a hostile element acting as a barrier for their movements (Vergara 2011). During summer and autumn thrushes change their foraging behavior by switching from omnivory to frugivory (Orellana et al. 2011). During this season thrushes actively track ripening lingue fruits within and between forest fragments (Vergara et al. 2010; Orellana et al. 2011). Foraging thrushes tend to aggregate in large forest patches because these patches exhibit higher levels of fruit production (Vergara et al. 2010). Thrushes also feed on lingues located along the forest edges as these trees have an abundant fruit production (e.g., Gho 2010; Vergara et al. 2010). Lingue fruits are swallowed by thrushes, which deposit the seeds by regurgitation (Vergara et al. 2010).

Study area and the structural connectivity provided by corridors (Step 1)

We selected a 480 km^2 area (30 km × 15 km) located west of Rupanco Lake (40°52′S, 72°52′W) in the Central Valley region of southern Chile (Fig. 2). The study area is less than 200 m above the sea level and its average annual rainfall is about 1,800 mm. The Central Valley has systematically been opened for livestock pastures, thus causing the extensive loss and fragmentation of these forests (Armesto et al. 1994). Currently, three distinctive elements dominate in these agricultural landscapes: (1) a matrix of open vegetation (mostly pastures); (2) remnant forest patches (typically <150 ha), dominated by the deciduous *Nothofagus* species accompanied by evergreen tree species such as the lingue (Fig. 2; Donoso 1993); (3) hedgerows and strips of riparian vegetation along watersheds, both of which are used as corridors by forest birds like austral thrushes (Vergara 2011). Hedgerows are living fences composed by exotic *Eucalyptus* spp. and native *Nothofagus* spp. trees. Riparian strips, which are used to separate crops and keep livestock within fields, are on average narrower than 20 m and are composed by swamp tolerant trees and shrubs (e.g. *Drimys winteri* and Myrtaceae species). It is highly likely that hedgerows and riparian strips provide unsuitable conditions for lingue seed establishment and recruitment (Vásquez 2011). First, shade-tolerant seedlings of lingues can be sensitive to microclimatic edge-effects across narrow riparian strips and hedgerows as those here considered. Second, riparian strips provide unsuitable soil conditions for lingue recruitment as they are exposed to seasonal flooding (Donoso 1993). Therefore, narrow riparian patches and hedgerows were considered to act exclusively as corridors for lingues, rather than as a suitable, permanent habitat for the establishment of lingue populations (Vergara et al. 2013).

Photointerpretation was carried out using high resolution satellite images available from Google Earth based on spectral brightness, color, shape, size, texture and shadow. These criteria were applied to discriminate among forest patches, corridors and the matrix. Available GIS vegetation databases and field data ($n = 120$ points) were used to validate our resulting classification. We subdivided the total study area (480 km^2) into landscape units of similar size (see below) in order to have a replicated dataset. We considered three spatial extents: 1 km × 1 km, 2 km × 2 km and 4 km × 4 km. A total of 480, 120 and 30 landscapes were obtained for each spatial extent, respectively, each being considered as a spatial replicate for subsequent analysis (see Data Analysis section). These spatial extents are ecologically relevant for the dispersal of lingue seeds as they are comparable with the movement distances (range: ca. 200 to 3,600 m) exhibited by radio-tagged thrushes in fragmented forest landscapes (Vergara et al. 2013). In addition, these spatial extents are consistent with the spatial response of Chilean bird species to forest fragmentation and loss (Vergara and Armesto 2009).

Corridor length was measured by drawing a line through the center of each corridor linking two patches. Within each landscape, we also distinguished between patches connected by corridors and stepping stones, considering as potential stepping stones all patches that were not structurally connected to each other through corridors. Landscapes differed in their mean patch size and isolation as well as structural connectivity metrics (Table 1, Table S1), thus providing enough variability in landscape structure and configuration to test our research predictions (see above).

For each landscape we quantified the following structural metrics: number of patches (n), number of corridors, number of patches connected by corridors, total forest area connected by corridors and the maximum number of potential corridors (m) linking

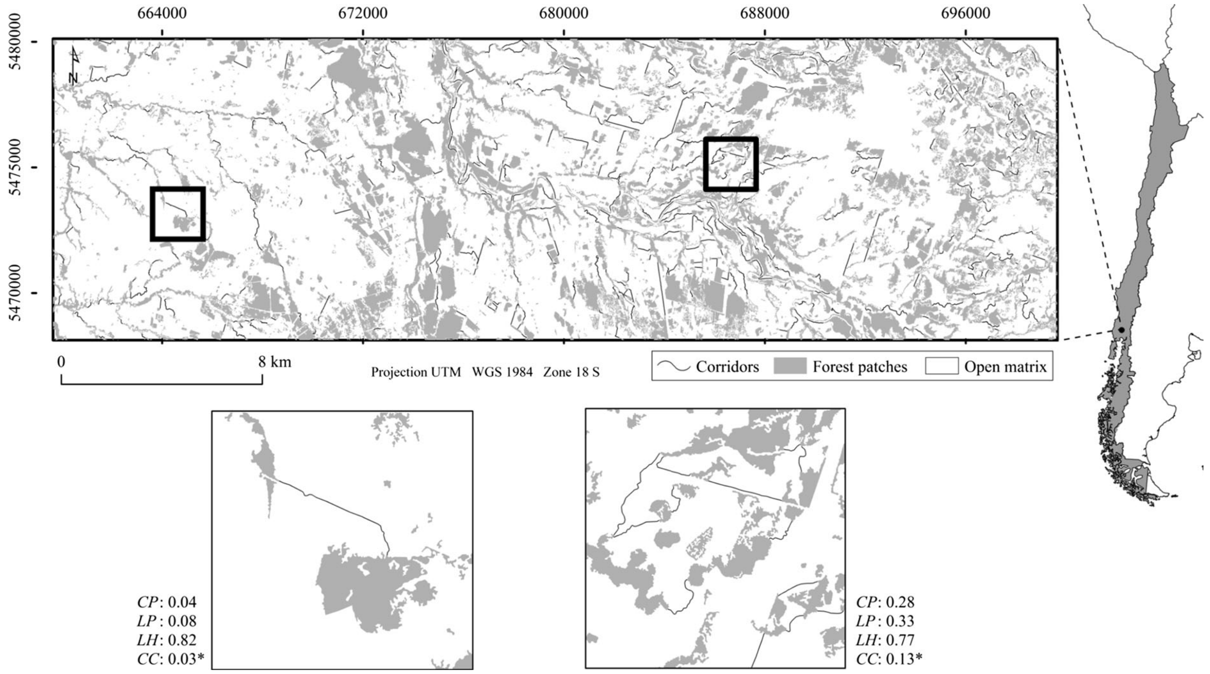

Fig. 2 Map of the study area in southern Chile, comprising a matrix of open vegetation, patches of native forest and corridors (hedgerows and riparian strips). Two 2 × 2 km landscapes are shown in the lower panels, a landscape harboring a dense corridor network (*right*) and another harboring a sparse corridor network (*left*). For each landscape, values of structural connectivity provided by corridors are given (Table 1). *CC values were multiplied by 10

patches ($m = n[n - 1]/2$). On the basis of these metrics, and for each landscape, we calculated four indices of structural connectivity (Table 1 and Table S1).We did not use other more complex indices of structural connectivity because our goal was to identify simple estimators that can be used in landscape planning (Forman 1995).

Fruit production (Step 2)

Individual patches were characterized according to their fruit production levels in order to include a quantitative component of seed dispersal in our network analyses (see below for Step 4). Fruit production can be considered as a realistic estimate of seed availability for thrushes (Vergara et al. 2010). We used empirical data of tree density and crop size of individual trees from 30 forest patches within the study region. In each sampled patch, we selected two different trees for estimation of fruit production (for methodological details see Vergara et al. 2010). Fruit production (fruits/patch) was calculated as the product between the crop size of lingue individuals (fruits/tree) and the expected number of lingues present in the patch (trees/patch). We used a regression model predicting the density of lingues (trees/ha) in each patch as a positive linear function of the patch size ($R^2 = 0.79$). Crop size of a tree was regressed as a power-law function of its diameter at the breast height (dbh). Since lingue fruits contain only one seed, the number of fruits per tree is an estimate of the number of seeds available. Crop size values were log transformed to reduce large variation among patches ($CV = 131$ %).

Interpatch seed dispersal probabilities (Step 3)

Seed dispersal kernels were used to estimate the probability of seed dispersal between each pair of forest patches in the landscape. Seed dispersal kernels provide a reliable distribution of dispersal distances from patches acting as seed sources (Levin et al. 2003). Two different types of seed dispersal kernels, each representing a potential modality of seed dispersal between two habitat patches, were specified: (1) A kernel for seeds dispersed by thrushes using

Table 1 Landscape-scale properties used in this study to represent the structural connectivity provided by corridors (see text)

Index name	Symbol	Definition
Corridors per patch	*CP*	Ratio between the number of corridors and the number of forest patches in the landscape. Higher *CP* values indicate there are more corridor connections between patches
Corridor-linked patches	*LP*	Ratio between the number of patches linked by corridors and the total number of forest patches present in the landscape. Higher *LP* values indicate that more patches are structurally connected by corridors in the landscape
Corridor-linked habitat	*LH*	Ratio between amount of forest area linked by corridors and amount of total forest area of all patches in the landscape. Higher *LH* values indicate that there are more corridors per unit of habitat in the landscape
Corridor connectance	*CC*	Ratio between the number of corridors linking patches and the total number of potential corridors that could exist in the landscape. Higher *CC* values indicate a larger density of corridors in the landscape

corridors to move between patches ("corridor" kernel); (2) A kernel for seeds dispersed by thrushes moving throughout the open matrix without using corridors ("matrix" kernel). Corridor and matrix kernels were fitted to stochastic simulations of a spatially explicit seed dispersal model. Mechanistic models have proved to be useful in predicting the locations of dispersed seeds because they are based on the observed movement, physiology and foraging behavior of individual animals (e.g., Levin et al. 2003). Specifically, our mechanistic model included three individual-based components:

(1) The number of seeds removed by individual thrushes feeding on lingue trees located in a forest patch (Table 2). Our 60 min focal sampling observations (including 58 individuals observed on 50 independent trees) indicate that each thrush remains on average 12.5 min in a lingue tree swallowing fruits at a rate of 0.47

Table 2 Main parameters of a spatially explicit mechanistic model used for predicting seed dispersal distances by individual thrushes when moving between two patches

Parameter name	Definition	Value*
Seed consumption rate	Rate of seeds (seeds min^{-1}) being swallowed by an individual thrush during a feeding event on a lingue tree located in a source patch of native forest	0.47 ± 0.15
Perching time	The time (min) that a thrush remains on a perch when a regurgitation event is predicted to occur	1–2
Foraging time	Residence time (min) over which a thrush is expected to remain in a lingue tree swallowing fruits	12.5 ± 2.2
Angular response to the corridor	Movement direction relative to the direction of the corridor edge scaled between 0° (movements parallel to the corridor edge) and 90° (movements perpendicular to the corridor edge). State-space models were used for estimating behavioral modes of individual thrushes moving along the corridor and through the matrix	0–15°
Corridor direction	The bearing of a corridor relative to the line perpendicular to the source patch. Corridor direction was set according to values observed in the landscapes	−20–20°
Velocity along corridors	Mean movement velocity (m/min) for thrushes dispersing along a corridor	45.8 ± 6.7
Velocity on the matrix	Mean movement velocity (m/min) for thrushes dispersing on the open matrix	49.5 ± 13.2
Gut passage time	The time (min) period taken by seeds of lingue in being regurgitated. Gut passage times recorded in feeding trials were assumed to be Poisson distributed	25.4 ± 1.59

Parameter values were drawn from Vergara et al. (2010); Gho (2010); Vergara et al. (2013); Vergara (unpublished data). A model simulation is shown in Fig. S2

* Mean ± SE

fruits/min (Table 2; see methodological details in Vergara et al. 2010).

(2) The between-patch movement pattern of thrushes after feeding on lingue fruits. We used state-space models (SSMs) fitted to radio-telemetry data of thrushes for predicting thrush's spatial location. SSMs provided a mechanistic framework for predicting thrush's spatial location from fixed parameters of movement (e.g., speed and angles; Table 2) and process error in movement. The general structure of such SSMs and their estimated parameters are fully described in Vergara et al. (2013), as well as in Table 2, and can be summarized as follows. First, based on empirical observations of thrush movement, the model assumes two modes of movements: in presence of a corridor individuals move according to a biased-correlated random walk by exhibiting an "edge-following behavior", whereas in the absence of a corridor, they move according to a correlated random walk, i.e. with movement direction being correlated with the direction taken during the previous time step (Fig S2). Second, movement velocity is assumed to be dependent on the habitat type (i.e., matrix or corridor; Table 2). Third, process errors arising from stochasticity in movement patterns were included in the transition equation of SSMs (Vergara et al. 2013).

(3) The time period over which thrushes regurgitate lingue seeds. We used gut passage times recorded from feeding trials where austral thrushes ($n = 8$) were fed with fleshy fruits of native trees, including lingues (Vergara, unpublished data). Distribution of gut passage times was fitted to a Poisson distribution ($\lambda = 25.4$ min, $SE = 1.59$, $\text{Likelihood} = -69.12$) because it provided better goodness of fit than other distributions (e.g., binomial distribution; Vergara unpublished data).

This seed dispersal model was used to estimate the distances over which seeds are dispersed between patches by thrushes that use corridors (i.e., as drift fence or guiding edge) and by thrushes moving over the open matrix. Thrush movement was simulated at 1 min intervals using SSMs and fitted parameters (Fig. S2). A simulation started with an individual thrush feeding on a fruiting lingue tree located in the boundary of a source patch. Simulations lasted 80 min, in order to ensure that most of the seeds are deposited (Fig. S2). Seed dispersal events were assumed to occur with probability $D(\mathrm{t})$, the probability that at least one seed was regurgitated by the thrush at the time interval t, i.e., $Pr(S \geq 1)$, with S representing the number of seeds ingested (Table 2). Since a seed dispersal event is a stochastic phenomenon (e.g., Levin et al. 2003), $D(\mathrm{t})$ was drawn from a binomial distribution, with $S \sim B(N,P)$ and $Pr(S \geq 1) = 1 - Pr(S = 0)$. Parameters N and P were set as the total number of seeds consumed at the beginning of the simulation and the Poisson probability of a seed being regurgitated at the time interval t, respectively.

For each simulated movement path we calculated the mean distance of all seed dispersal events. The model was programmed in *R*, version 2.15.1 (R Development Core Team 2014). After running 30,000 simulated paths we fitted one-dimensional dispersal kernels, including Exponential, Weibull and Gamma models. We determined that the Weibull kernel was the most parsimonious model (Table S3). Using the Weibull kernel, we estimated the seed dispersal probability (p_{ij}) between each pair of forest patches i and j as a function of the interpatch distance. The parameters of the corridor and matrix kernels were different, with the corridor kernel predicting a larger mode for the seed dispersal distances than the matrix kernel (78.0 m versus 46.2 m, respectively, Fig. 3 and Table S3). The matrix kernel was less right-skewed than the corridor kernel ($\text{Skewness} = 0.41$ versus 0.83, respectively), with these differences resulting in a larger fraction of the seeds being dispersed longer distances by thrushes when moving in presence of a corridor (Fig. 3).

Network analysis (Step 4)

We carried out a network analysis intended to estimate the contribution of corridors to functional connectivity, and compare it with the contribution of stepping stones. Connectivity was estimated using Conefor 2.6 (Saura and Torné 2009, available at www.conefor.org). Networks were established by developing undirected spatial graphs, where the probability of movement from patch i to patch j is the same as from patch j to patch i, with nodes corresponding to forest patches

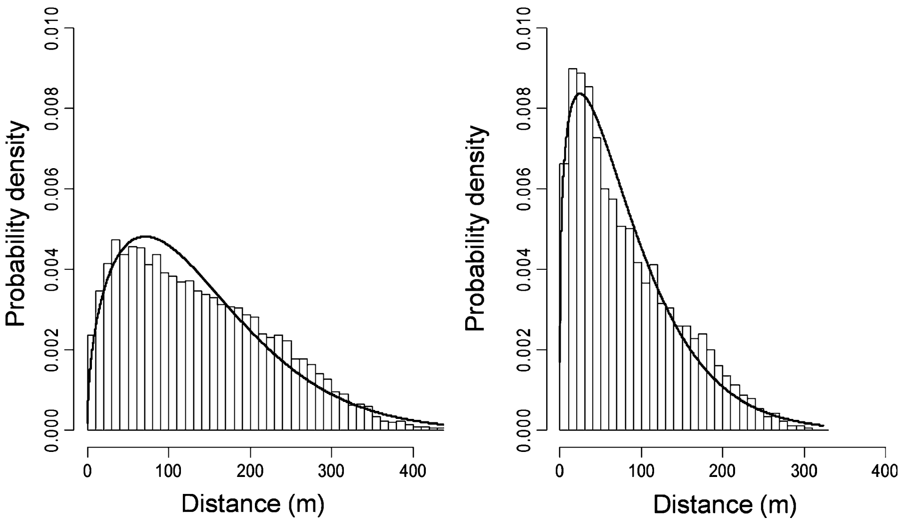

Fig. 3 Frequency distribution of dispersal distances of lingue seeds obtained from a mechanistic model simulating the movement of individual thrushes along a corridor (*left*) and through the matrix (*right*). Lines correspond to a fitted Weibull distribution

and links representing the potential of seed dispersal between forest patches. Nodes were weighted by the log-transformed fruit production of the patch (see above for Step 2) and links were weighted by the probability of seed dispersal (p_{ij}) given by the Weibull kernel (Step 3). In order to test our two working predictions (see above), we estimated the following connectivity metrics:

(1) Equivalent Connected Area (*ECA*). For each study landscape, ECA was calculated as the square root of the Probability of Connectivity (*PC*) index. ECA expresses the equivalent amount of habitat resources available (reachable) in the landscape (here given in units of crop size; Saura and Rubio 2010).

(2) The relative change (%) in ECA (*dECA*) when the existing corridors are completely removed from the landscape, estimated as: $[(ECA_C - ECA_0)/ECA_C] \times 100$, where ECA_C and ECA_0 are the corresponding *ECA* values for the landscape with and without corridors, respectively. Positive values of *dECA* indicate a positive contribution of corridors to overall functional connectivity while negative values indicate that functional connectivity (*ECA*) increases after removing all corridors in the landscape.

(3) The connector fraction (*dPCconnector*) of individual corridors and stepping stones. *dPCconnector* represents the relative importance of specific landscape elements in facilitating seed dispersal through the landscape (Saura and Rubio 2010). A positive mean *dPCconnector* for corridors and stepping stones suggests that, on average, they contribute to the connectivity by acting as effective dispersal linkages between patches, upholding connectivity further beyond than what provided by the other elements existing in the landscape (Rubio and Saura 2012). We used the "link change" option of Conefor 2.6 for estimating *dPCconnector* of corridors.

(4) The difference in the mean connector fraction ($\Delta dPCconnector$) between corridors and stepping stones, estimated as: $E(dPCconnector_C) - E(dPCconnector_S)$, where $E(dPCconnector_C)$ and $E(dPCconnector_S)$ are the mean connector fraction of the individual corridors and stepping stones present in the landscape, respectively (see above). Positive $\Delta dPCconnector$ values indicate that corridors are more important connectors than stepping stones.

Statistical modelling (Step 5)

We used Bayesian conditional autoregressive (CAR) models for testing our research predictions. CAR models are suitable for analyzing lattice dataset, as our landscapes, by accounting for spatial errors associated with local neighborhood dependencies. Dependent variables in CAR models were connectivity metrics measured at the landscape level, including *ECA*, *dECA*, *dPCconnector* and Δ*dPCconnector* (as explained above). We also included a random effect associated to each landscape.

Four structural connectivity indices, each representing the topological complexity of corridor networks in the landscape, were specified as predictor variables in *CAR* models. The structural connectivity provided by corridors was estimated using the following structural indices: (1) Corridors per patch (*CP*); (2) Corridor-linked patches (*LP*), (3) Corridor-linked habitat (*LH*); and (4) Corridor connectance (*CC*) (for details, see Table 1). According to our two predictions, we expected that landscapes harboring more complex and dense corridor networks (i.e., with larger values of *CP, LP, LH* and *CC*) would have larger values of *ECA*, *dECA* and Δ*dPCconnector*. The relative importance, and contribution, of structural connectivity indices to the functional connectivity of Lingue seeds was examined using CAR models.

Covariates pairs with Pearson's $r > 0.5$ were not included in the same model to avoid co-linearity. In addition, we also included the total forest area (*TF*), which was retained as a predictor in all candidate CAR models to control for the dependency of landscape connectivity upon habitat cover (Rubio and Saura 2012). The Deviance Information Criterion (DIC) was used to select the best models, with lower DIC values indicating a better trade-off between model fit and parsimony. For each candidate model we also computed the ΔDIC (i.e., the difference in DIC between each model and model with lowest DIC) and DIC weights (*w*) in order to assess relative model strength. We only reported models in which $\Delta\text{DIC} < 2$ were interpreted as being substantially supported by the data. *CAR* models were run from R using R2WinBUGS. Convergence was assessed by visual examination of trace plots and using the Gelman-Rubin statistics. Parameter estimates were derived using Markov Chain Monte Carlo (MCMC) algorithm. The posterior coefficient distribution was obtained by running three different chains of 35,000 iterations each after a burn-in of 10,000 iterations, thus ensuring the consistency of parameter estimation. We only interpreted model coefficients whose 95 % Bayesian credible intervals did not overlap zero, because they were considered to be statistically significant.

Results

Prediction (I): functional versus structural connectivity

The best supported CAR models (i.e., models with $\Delta\text{DIC} < 2$) fitted to functional connectivity metrics (*ECA*) indicated that the more connected by corridors a landscape is, the lower its functional connectivity (Tables 3 and 4). Specifically, corridor connectance (*CC*) was the only structural connectivity index affecting negatively and significantly *ECA* at the three spatial extents (Table 4 and Fig. 4). In addition, total forest area (*TF*) had a positive effect on *ECA* and this effect was consistent at the three spatial extents (Tables 3 and 4).

The removal of all corridors did not decrease overall landscape functional connectivity since the mean value of *dECA* was not significantly different from zero (mean ± SE: -0.47 ± 0.17, $p = 0.998$, -1.16 ± 0.39, $p = 0.998$, -2.17 ± 0.82, $p = 0.996$, for the 1 km × 1 km, 2 km × 2 km and 4 km × 4 km spatial extents, respectively). Contrary to our expectations, the best supported models fitted to *dECA* data (i.e., models with $\Delta\text{DIC} < 2$ in Table 3) showed that functional connectivity (*ECA*) increases after removing all corridors from the landscape (Table 4). Only two structural connectivity indices, *CP* and *LH*, contributed to decrease the functional connectivity when corridors were removed, but their effects were scale-specific (see model coefficients in Table 4).

Prediction (II): corridors versus stepping stones

When corridors and stepping stones were compared, the mean connector fraction (*dPCconnector*) of individual corridors estimated from CAR models was, contrary to expectations, significantly lower than the mean *dPCconnector* of stepping stones, with this difference being consistent across the three spatial extents that were analyzed (Fig. 5). In addition, the mean *dPCconnector* of corridors was negative at the three spatial extents, indicating that corridors do not act as effective dispersal linkages between patches (Fig. 5).

Contrary to expectations, the relative importance of corridors as ecological connectors, in relation to stepping stones did not increase as the landscape became structurally more connected by corridors, as

Table 3 Best supported candidate CAR models (only models with DIC < 2 are shown) explaining the effects of corridor structural connectivity indices (*CP*, *LP*, *LH* and *CC*, see Table 1) and the total forest area (*TF*) on functional connectivity over three increasing spatial extents (see the complete set of candidate models in Table S4)

Model	Spatial extent											
	1 km × 1 km				2 km × 2 km				4 km ×4 km			
	Variables	DIC	ΔDIC	*w*	Variables	DIC	ΔDIC	*w*	Variables	DIC	ΔDIC	*w*
ECA	*CC* + *LH* + *TF*	1,742.0	0.00	0.72	*CC* + *TF*	1,196.4	0.00	0.54	*CC* + *TF*	404.9	0.00	0.53
	CC + *TF*	1,743.9	1.85	0.28	*CC* + *LH* + *TF*	1,196.7	0.29	0.46	*CC* + *LH* + *TF*	406.1	1.23	0.29
dECA	*CP* + *TF*	1,261.3	0.00	0.37	*CC* + *LH* + *TF*	626.5	0.00	0.34	*CP* + *TF*	67.5	0.00	1
	CP + *LH* + *TF*	1,262.3	1.01	0.22	*LP* + *LH* + *TF*	626.8	0.33	0.29	–	–	–	–
	–	–	–	–	*CP* + *LH* + *TF*	626.9	0.42	0.27	–	–	–	–
Δ*dPCconnector*	*CC* + *TF*	1,088.1	0.00	0.22	*LP* + *TF*	471.1	0.00	0.36	*CC* + *LH* + *TF*	37.8	0.00	0.57
	CC + *LH* + *TF*	1,088.5	0.38	0.19	*CP* + *TF*	471.7	0.62	0.26	*CC* + *TF*	38.5	0.74	0.39
	LP + *TF*	1,088.5	0.42	0.18	*CC* + *TF*	472.1	1.02	0.22	–	–	–	–
	LP + *LH* + *TF*	1,088.9	0.82	0.15	–	–	–	–	–	–	–	–
	CP + *LH* + *TF*	1,089.2	1.08	0.13	–	–	–	–	–	–	–	–
	CP + *TF*	1,089.2	1.13	0.13	–	–	–	–	–	–	–	–

Dependent variables were: (1) the Equivalent Connected Area (*ECA*), (2) the relative percent change (%) in *ECA* (*dECA*) when the existing corridors are removed and (3) the difference in the mean connector fraction between individual corridors and stepping stones (*dPCconnector*)

Table 4 Means, standard deviations (SD) and the 95 % Bayesian credibility intervals of parameters (i.e., the 2.5 % and 97.5 % quantile of the marginal posterior distributions) in the best supported CAR models shown in Table 3

Model	Variables	Spatial extent											
		1 km × 1 km				2 km × 2 km				4 km × 4 km			
		Mean	SD	2.5 %	97.5 %	Mean	SD	2.5 %	97.5 %	Mean	SD	2.5 %	97.5 %
ECA models	*CC*	−0.41	0.02	−0.44	−0.37	−0.35	0.04	−0.43	−0.28	−0.26	0.13	−0.52	−0.01
	TF	0.01	0.00	0.01	0.02	0.05	0.01	0.03	0.06	0.02	0.01	0.01	0.03
dECA models	*CP*	–	–	–	–	–	–	–	–	−35.8	14.1	−64.2	−7.2
	LH	–	–	–	–	−5.03	1.88	−8.71	−1.41	–	–	–	–
	TF	−0.58	0.28	−1.13	−0.03	–	–	–	–	–	–	–	–
Δ*dPCconnector* models	*CC*	–	–	–	–	–	–	–	–	−193.6	65.2	−320.6	−61.0
	TF	−0.09	0.02	−0.13	−0.05	−0.02	0.00	−0.03	−0.01	−0.02	0.01	−0.03	−0.01

Only coefficients with 95 % credibility intervals excluding zero are shown because these are considered as significant

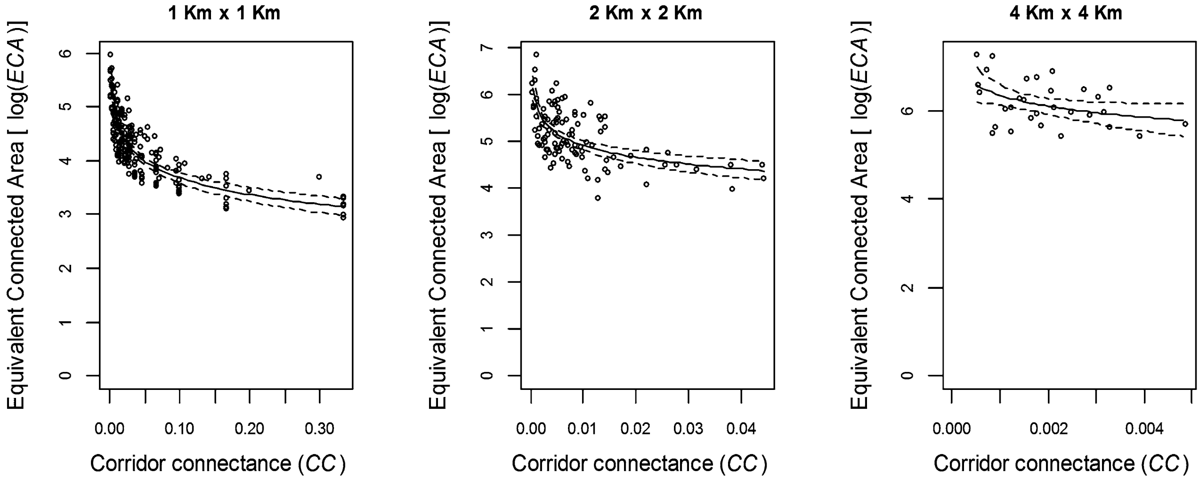

Fig. 4 Observed values (*open circles*) and fitted values (*solid line*) of univariate regression models (with their 95 % confidence bands) explaining the negative effect of corridor connectance (*CC*) on the Equivalent Connected Area (*ECA*) index for different landscapes at three increasing spatial extents

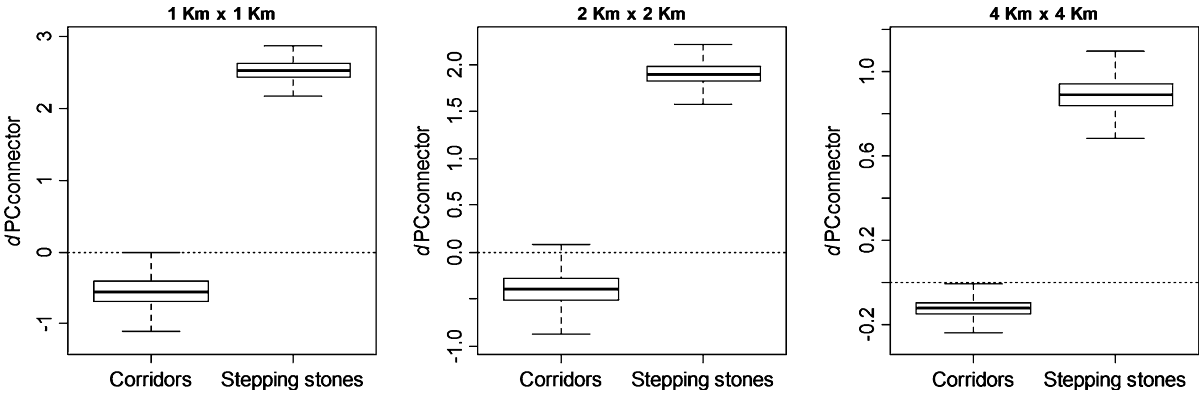

Fig. 5 Box plots comparing the expected (mean) connector fraction (*dPCconnector*) of individual corridors and stepping stones. Boxes encompass the 25 and 75 % quartiles of the posterior distributions of the coefficient parameter from a CAR model (see text)

shown by the best supported CAR models fitted to the difference in the mean connector fraction between individual corridors and stepping stones (see Δ*dPCconnector* models in Tables 3 and 4). Indeed, at the 4 km × 4 km spatial extent, we found a significant negative effect of corridor connectance (*CC*) on Δ*dPCconnector*, indicating that the relative importance of stepping stones as connectors increases as landscapes became more structurally connected by corridors (Table 4). In addition, Δ*dPCconnector* turned more negative as the total forest area (*TF*) increased in the landscapes and this effect was consistent at the three spatial extents that were analyzed (Table 4).

Discussion

There is considerable empirical evidence suggesting that riparian strips and hedgerows act as wildlife corridors by facilitating the movement of animals and plants in fragmented landscapes (e.g., Davies and Pullin 2007; Tremblay and St Clair 2009; Wehling and Diekmann 2009; Tang et al. 2014). Recent studies, however, suggest that the utility of corridors for promoting seed dispersal by birds is a complex question without a simple answer (e.g., Levey et al. 2005; Evans et al. 2013). Such a complexity arises from diverse sources, including limitations in the scale and replications of studies, as well as differences among disperser species in terms of their life history, movement attributes, response to the matrix and habitat preferences (Hudgens and Haddad 2003; Gilbert-Norton et al. 2010; Vergara 2011). In particular, determining if corridors improve landscape connectivity for the plant species that depend on animals to disperse their seeds has become an important concern for conservationist and ecologists (e.g., Levey et al. 2005, 2008). Although there are studies supporting the contribution of corridors to connectivity of animal dispersed plants (e.g., Tewksbury et al. 2002), frugivores may also respond to the heterogeneity in the shape, length, quality and spatial arrangement of corridors by exhibiting movement patterns that are not necessarily the most effective for conservation of plant metapopulations.

Our results clearly did not support the importance of corridors in promoting functional connectivity for a particular plant-animal interaction in southern Chile. Corridors may reduce the seed dispersal effectiveness of thrushes to the extent that they induce thrushes to move along corridors while reducing the likelihood of moving more efficiently to other target patches that are suitable for the establishment of lingue seeds. The distance and time required to move seeds between patches were greater when thrushes used corridors, thus overcoming the benefits of the longer-distance dispersal through corridors here reported (Fig. 3). Factors increasing the distance that thrushes move through corridors include the nonlinearity of corridors, the irregularity in the shape of patches and the broad habitat use by dispersers (Fig. 1). It is probable that the edge-following behavior exhibited by individual thrushes induces them to deposit lingue seeds along corridors or in adjacent sites over the matrix, which are unsuitable habitat for lingue establishment.

As shown in our results, corridors not only may be functionally redundant in the landscape, or less efficient as connectivity providers when compared with stepping stones, but also may contribute to reduce functional connectivity for lingues (e.g., see Schippers et al. 2009). These findings, however, cannot be generalized to other plant-animal interactions involving forest-dependent seed-dispersing animals even in the same region, such as some small mammal species of the temperate forests of Chilean and Argentina (e.g., Smith-Ramirez et al. 2010), as well as in other forest regions of the world (Hudgens and Haddad 2003). We have studied a particular mutualistic association between a tree species with specific habitat requirements (including shelter for recruitment and not flooded soils) and a habitat-generalist seed disperser whose movement is influenced by the amount of edge in the landscape. In fact, habitat specificity is a key species trait influencing the role of corridors as connectors or habitat (Vergara 2011; Dennis et al. 2013). Thrushes track lingue fruits during the austral autumn but, unlike many forest specialist dispersers, they do not perceive the open matrix as an unsuitable area or a barrier (Vergara et al. 2010). The broad habitat preferences exhibited by thrushes could reduce their effectiveness as seed dispersers (compared to other forest specialist birds or mammals) because they are not constrained to move only between (and rapidly to) core forest areas that are those suitable for lingues. Habitat generalist frugivores can have an important role as suppliers of seed dispersal service in fragmented landscapes, where they are more abundant (Moore and Swihart 2007), but their effectiveness as seed dispersers is likely to be dependent on the spatial attributes of connecting elements in the landscape, as shown in this study.

Our integrated methodological approach and analyses addressed the complex nature of forest patch networks linked by corridors. On one hand, dispersal kernels developed from seed dispersal models constitute a robust approach to assess dispersal distances by incorporating stochastic variation in ecological processes (e.g., animal behavior or physiology; e.g., Levin et al. 2003), a component that may be neglected in observational studies. On the other hand, we have developed a graph-theoretic model whose nodes and links were specified on basis of observed parameters. To date few studies have applied graph theory in describing the network pattern of animal-dispersed plant species (but see Minor et al. 2009; Mueller et al. 2014).

Contrary to expectations, we not only found that corridors were less efficient landscape connectors than stepping stones, but also that the relative contribution to functional connectivity of stepping stones increased as the landscape became more connected by corridors. Our findings suggest that the retention of networks of stepping-stone patches is an efficient strategy to promote effective seed dispersal of lingues by thrushes. Although our results indicate that corridors do not promote functional connectivity for lingues, they have a positive impact on the overall biodiversity of the fragmented landscapes in southern Chile. Forest specialist birds and mammals dwelling in the same landscapes may find the open matrix largely hostile for their movement between patches. This is the case of the endemics tapaculos (family Rhinocryptidae) and mouse opossum (*Dromiciops gliroides*), for which the riparian corridors not only act as movement conduits, but also as a primary habitat (Sieving et al. 2000; Smith-Ramirez et al. 2010). Therefore, effective landscape planning focused on the conservation of the full set of endemic plants and animals of temperate Chilean forests should involve a compromise between the requirements and dispersal behavior of different focal species, maintaining or increasing the number of both stepping stones and corridors, but not completely relying on the latter. We conclude that landscape planners should focus on a mixed strategy that involves the restoration of corridor networks for improving their use as connectors and suitable habitat by wildlife as well as the conservation of stepping stones for promoting the dispersal of seeds and forest animals that move more efficiently using stepping stones in between core habitat areas. We acknowledge the widely demonstrated utility and high conservation value of corridors, as summarized for example in the meta-analysis by Gilbert-Norton et al. (2010). Our findings are not in conflict with these previous results on this topic but rather highlight that, in agreement with Gilbert-Norton et al. (2010), although corridors may be used by many species, they are unlikely to be used by all species, and whether corridors are the best option for conservation management, compared for example to other measures for promoting species movement such as creating stepping stones or a more permeable landscape matrix, may depend on the particular characteristics of the species and landscapes under consideration.

Acknowledgments Fondecyt Grants (11080085 and 1131133) and GEFOUR Grant (AGL2012-31099) provided the funds for this study.

References

Amico GC, Aizen MA (2005) Dispersión de semillas por aves en un bosque templado de Sudamérica austral: ¿quién dispersa a quién? Ecología Austral 15:89–100

Anderson GS, Danielson BJ (1997) The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. Landscape Ecol 12:261–271

Armesto JJ, Villagrán C, Donoso C (1994) Desde la era glacial a la industrial: la historia del bosque templado chileno. Ambient y Desarro 10:66–72

Awade M, Boscolo D, Metzger JP (2012) Using binary and probabilistic habitat availability indices derived from graph theory to model bird occurrence in fragmented forests. Landscape Ecol 27:185–198

Baum KA, Haynes KJ, Dillemuth FP, Cronin JT (2004) The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85:2671–2676

Beier P, Noss RF (1998) Do habitat corridors provide connectivity? Conserv Biol 12:1241–1252

Cain ML, Milligan BG, Strand AE (2000) Long-distance seed dispersal in plant populations. Am J Bot 87:1217–1227

Chetkiewicz CLB, St Clair CC, Boyce MS (2006) Corridors for conservation: integrating pattern and process. Annu Rev Ecol Evol Syst 37:317–342

Damschen EI, Haddad NM, Orrock JL, Tewksbury JJ, Levey DJ (2006) Corridors increase plant species richness at large scales. Science 313:1284–1286

Davies ZG, Pullin AS (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. Landscape Ecol 22:333–351

Dennis RLH, Dapporto L, Dover JW, Shreeve TG (2013) Corridors and barriers in biodiversity conservation: a novel resource-based habitat perspective for butterflies. Biodivers Conserv 22:2709–2734

Donoso C (1993) Bosques templados de Chile y Argentina. Variación, estructura y dinámica. Editorial Universitaria, Santiago

Echeverría C, Newton A, Nahuelhual L, Coomes D, Rey-Benayas JM (2012) How landscapes change: integration of spatial patterns and human processes in temperate landscapes of southern Chile. Appl Geogr 32:822–831

Evans DM, Levey DJ, Tewskbury JJ (2013) Landscape corridors promote long-distance seed-dispersal by birds during winter but not during summer at an experimentally fragmented restoration site. Ecol Restor 31:23–30

Forman RTT (1995) Some general principles of landscape and regional ecology. Landscape Ecol 10:133–142

Forman RTT, Godron M (1986) Landscape Ecology. Wiley, New York

Gho D (2010) Consumo de frutos de *Persea lingue* (Lauraceae) en el valle central del sur de Chile. Undergraduate Thesis, Universidad Austral de Chile, Valdivia

Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. Conserv Biol 24:660–668

Haddad NM, Bowne DR, Cunningham A, Danielson BJ, Levey DJ, Sargent S, Spira T (2003) Corridor use by diverse taxa. Ecology 84:609–615

Hudgens BR, Haddad NM (2003) Predicting which species will benefit from corridors in fragmented landscapes from population growth models. Am Nat 161:808–820

Laurance SGW (2004) Responses of understory rain forest birds to road edges in central Amazonia. Ecol Appl 14:1344–1357

Levey DJ, Bolker BM, Tewksbury JJ, Sargent S, Haddad NM (2005) Effects of landscape corridors on seed dispersal by birds. Science 309:146–148

Levey DJ, Tewksbury JJ, Bolker BM (2008) Modelling long-distance seed dispersal in heterogeneous landscapes. J Ecol 96:599–608

Levin SA, Muller-Landau HC, Nathan R, Chave J (2003) The ecology and evolution of seed dispersal: a theoretical perspective. Annu Rev Ecol Evol S 34:575–604

Minor ES, Tessel SM, Engelhardt KAM, Lookingbill TR (2009) The role of landscape connectivity in assembling exotic plant communities: a network analysis. Ecology 90:1802–1809

Moore JE, Swihart RK (2007) Importance of fragmentation-tolerant species as seed dispersers in disturbed landscapes. Oecologia 151:663–674

Mueller T, Lenz J, Caprano T, Fiedler W, Böhning-Gaese K (2014) Large frugivorous birds facilitate functional connectivity of fragmented landscapes. J Appl Ecol. doi:10.1111/1365-2664.12247

Ockinger E, Smith HG (2008) Do corridors promote dispersal in grassland butterflies and other insects? Landscape Ecol 23:27–40

Orellana JI, Smith-Ramírez C, Rau J, Sade S, Gantz A (2011) Sincronía en la abundancia estacional de *Turdusfalcklandii* (Muscicapidae: Turdidae). X CongresoChileno de Ornitología, Santiago

R Development Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rubio L, Saura S (2012) Assessing the importance of individual habitat patches as irreplaceable connectivity providers: and analysis of simulated and real landscape data. Ecol Complex 11:28–37

Saura S, Rubio L (2010) A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. Ecography 33:523–537

Saura S, Torné J (2009) ConeforSensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environ Modell Softw 24:135–139

Schippers P, Grashof-Bokdam CJ, Verboom J, Baveco JM, Jochem R, Meeuwsen HAM, Van Adrichem MHC (2009) Sacrificing patches for linear habitat elements enhances metapopulation performance of woodland birds in fragmented landscapes. Landscape Ecol 24:1123–1133

Segurado P, Branco P, Ferreira MT (2013) Prioritizing restoration of structural connectivity in rivers: a graph based approach. Landscape Ecol 28:1231–1238

Sieving KE, Willson MF, De Santo TL (2000) Defining corridor functions for endemic birds in fragmented south-temperate rainforest. Conserv Biol 14:1120–1132

Smith-Ramirez C, Celis-Diez JL, von Jenstchyk E, Jiménez JE, Armesto JJ (2010) Habitat use of remnant forest habitats by the threatened arboreal marsupial *Dromiciops gliroides* (Microbiotheria) in a rural landscape of southern Chile. Wildl Res 37:249–254

Tang Q, Liang G, Lu X, Ding S (2014) Effects of corridor networks on plant species composition and diversity in an intensive agriculture landscape. Chin Geogr Sci 24:93–103

Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68:571–573

Tewksbury JJ, Levey DJ, Haddad NM, Sargent S, Orrock JL, Weldon A, Danielson BJ, Brinkerhoff J, Damschen EI, Townsend P (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. P Natl Acad Sci USA 99:12923–12926

Tremblay M, St Clair C (2009) Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. J Appl Ecol 46:1314–1322

Vásquez I (2011) Patrones espaciales de reclutamiento y dispersión de semillas del árbol *Persea lingue* Ness en el bosque del valle del sur de Chile. Undergraduate Thesis, Universidad de Chile, Chile

Vergara PM (2011) Matrix-dependent corridor effectiveness and the abundance of forest birds in fragmented landscapes. Landscape Ecol 26:1085–1096

Vergara PM, Armesto JJ (2009) Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecol 24:25–38

Vergara PM, Smith C, Delpiano CA, Orellana I, Gho D, Vásquez I (2010) Frugivory on *Persea lingue* in temperate Chilean forest: interactions between fruit availability and habitat fragmentation across multiple spatial scales. Oecologia 164:981–991

Vergara PM, Pérez-Hernández CG, Hahn IJ, Jiménez JE (2013) Matrix composition and corridor function for Austral Thrushes in a fragmented temperate forest. Landscape Ecol 28:121–133

Wehling S, Diekmann M (2009) Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. Biol Conserv 142:2522–2530