



Getting lost in the matrix? On how the characteristics and arrangement of linear landscape elements influence ecological connectivity

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Abstract

Context Linear landscape elements (LLEs) such as ditches and hedgerows can increase the ecological connectivity of habitat embedded within agricultural areas by acting as corridors for animal movement. However, we lack knowledge on how the spatial arrangement of LLEs influence dispersal, impeding our ability to offer robust advice on how best to add new LLEs to improve connectivity.

Objectives To examine how the width and spatial orientations of LLEs composing an intersecting network might influence connectivity across landscapes.

Methods We used an individual-based dispersal model to simulate the stochastic movement of small organisms through stylised LLEs of different characteristics. Landscapes were composed of two habitat patches separated by a grid-like network of LLEs composed of two types: (1) *connecting-edges*

(touching patches on either end) and (2) *transecting-edges* (running perpendicular to *connecting-edges*). By altering numbers and widths of each LLE type we sought to understand the effect of these variables on inter-patch dispersal rates.

Results Increasing the number or width of *connecting-edges* improved connectivity but, conversely, increasing numbers or widths of *transecting-edges* reduced it. The greater freedom of movement offered by increasing numbers of *transecting-edges* may have inhibited connectivity, as individuals with limited perceptual-range were more likely to become trapped in complex networks and thus fail to navigate to suitable habitat patches.

Conclusions Orientation of LLEs with respect to landscape resources greatly affects their impact on connectivity. The addition of LLEs to landscapes may decrease their connectivity for small, flightless species if they do not directly channel dispersers toward landscape resources.

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Introduction

As socio-economic development often involves extensive modification of landscape structures to meet human needs, conservation efforts must often contend with the negative impacts of habitat destruction and

fragmentation (Baldock 1990; Scanes 2018). One of the ways in which habitat loss negatively affects biodiversity and increases the extinction probability of remaining species is by reducing the overall carrying capacity of a landscape, as smaller populations are generally more vulnerable to the potentially negative impacts of demographic and environmental stochasticity (Lande 1993; Fahrig 1997; Newman and Pilson 1997; Ovaskainen and Meerson 2010). In a similar fashion, the fragmented distribution of remaining habitat may further endanger the viability of surviving populations by reducing them to even smaller sub-populations associated with the remnant habitat patches (Fahrig 2003). Informed by the theoretical framework of meta-population dynamics, it has been suggested that effective conservation of a population distributed across patchy habitat may be pursued by improving the connectivity of their landscape (Taylor et al. 1993), thereby mitigating local extinction risks by permitting greater dispersal and hence demographic and genetic exchange between habitat fragments (Brown and Kodric-Brown 1977; Hansson 1991; Fahrig and Merriam 1994; Hanski and Ovaskainen 2000). Increasing connectivity might be achieved by the maintenance, improvement or creation of landscape elements that more readily permit long movements through the matrix, perhaps by providing less dangerous and/or energetically taxing routes of travel relative to the wider landscape, and thereby act as corridors through which individuals are more likely to successfully traverse hostile matrix (Tischendorf and Wissel 1997).

Linear landscape elements (LLEs), such as hedgerows or ditches, are a common feature of developed agricultural landscapes and are often created primarily to serve socio-economic purposes, such as demarcating the boundaries of adjacent fields or controlling the hydrology of low-lying areas. As these LLEs can contain diverse vegetation profiles, often a signature of the landscape's historical habitat (Forman and Gordon 1981; Saunders et al. 1991), they may provide a more sheltered and hospitable environment for dispersing species than the exposed and highly disturbed arable, pastoral or urban elements of the wider matrix and thus be relatively permeable to the movement of small animals along their lengths (Merckx et al. 2010; Graham et al. 2018). LLEs such as fence-rows, treelines and ditches have been documented to promote the connectivity of agricultural landscapes

for a variety of small mammal and insect taxa (Fahrig and Merriam 1985; Henderson et al. 1985; Mech and Hallett 2001; Van Geert et al. 2010; Schulp et al. 2014). However, LLEs can fall short of providing adequate resources in which populations can maintain sustainable growth to the degree achieved in patches; for example, the diversity of arthropod taxa within LLEs, such as uncultivated field boundaries, declines with increasing distance from nearby source populations in remnant habitat patches (Ökinger and Smith 2007; Jauker et al. 2009; Krewenka et al. 2011; Ekroos et al. 2013; Villemey et al. 2015). This may be due to the comparatively small carrying capacity and/or a greater vulnerability to edge effects of LLEs relative to habitat patches (Simberloff et al. 1992). Thus, though species can use LLEs as relatively permeable corridors for movement, they may not always be able to utilise LLEs as locations in which to permanently reside and reproduce (Pryke and Samways 2001).

The configuration of LLE networks can vary substantially in density and continuity both between and within agricultural landscapes; the location of drainage ditches will reflect both the topography and hydrology of the terrain, whilst patterns of land-ownership determine where hedgerows are planted or maintained to act as barriers to livestock movement. Similarly, urban LLEs such as road or railway verges will reflect patterns of urban development that have rarely been planned with ecology in mind. LLEs will often intersect, for example, where they demarcate the corners of fields or roadway intersections (Joyce et al. 1999), and thereby collectively form a semi-continuous network composed of nodes and edges, varying in density and shape across the landscape.

The creation of additional novel LLEs in a network might be expected to increase connectivity by providing a greater abundance of corridors for dispersal and offering greater freedom of movement through a greater number of LLE nodes to avoid predators, forage and disperse to novel patches (Forman & Gordon 1981). However, it might not always be so straightforward. For instance, in one of the only studies to date which experimentally tested the impact of LLE intersections on dispersal patterns, Eriksson et al. (2013) found that 50% of released bush-crickets (*Metrioptera roeseli*) would change their initial direction of travel through a linear grassy verge at least once upon encountering a node. This highlights a potential downside of the greater freedom of movement

offered by a denser LLE network. An individual moving along a LLE in the direction of suitable habitat may be less likely to reach that habitat efficiently if it encounters nodes formed with transecting LLEs. This raises the possibility that too many LLEs in a network might potentially decrease landscape-wide connectivity by overwhelming individuals with redundant options for movement.

Increasing the width of LLEs may also have a similarly counterintuitive impact on their suitability as corridors for animal movement. Though wider ecological corridors can be easier for individuals to move through (Baur and Baur 1992; Tischendorf et al. 1998) and hence broader LLEs might be expected to contribute positively to connectivity, there is also evidence that individuals can make larger lateral movements within wider corridors that extend their time taken to traverse its length, which in turn reduces their final likelihood of moving from one end of the feature to the other (Andreassen et al. 1996). This suggests that wider LLEs can be less effective in some regards as corridors to connect ecologically significant locations. We may observe here another example of how a greater freedom of movement (in this case *within* single LLEs) might negatively impact the connectivity of LLE networks if it induces individuals to move less efficiently through LLEs of larger dimensions.

Therefore, there is a need to gain improved understanding of how the number, characteristics and spatial arrangement of LLEs within a landscape impacts on connectivity between ecologically important sites.

Here, we developed in-silico experiments to investigate how varying the LLE network configuration between habitat patches in a synthetic, hypothetical landscape might affect connectivity. An individual-based model of species movement was used to predict dispersal rates and thus connectivity across a series of landscapes. The experiments sought to determine how the configuration of a network of intersecting LLE corridors might affect connectivity by experimentally altering:

- (1) the number and width of LLEs *connecting patches to each other* and
- (2) the number and width of LLEs *transecting* the connecting LLEs to form a distribution of nodes.

This distinction was designed to reflect the grid-like structure of real LLE lattices where hedgerows,

ditches or verges often intersect roughly at right angles, and where it is a frequent pattern to observe large, straight formations intersected throughout their lengths by numerous LLEs running in roughly perpendicular directions.

Methodology

Our modelling approach was to simulate the dispersal of many individuals into landscapes comprised of intersecting high-quality LLE corridors permitting movement between two habitat patches. By varying the spatial arrangements of LLEs between landscapes we sought insight into how LLE characteristics enhance and/or inhibit the per-individual probability of successful dispersal from natal to novel habitat patches as a metric of landscape connectivity. To simulate individual movements through LLE networks, we used the Stochastic Movement Simulator (SMS; Palmer et al. 2011) provided within the ecological software RangeShifter v. 2.0 (Bocedi et al. 2021; see also Bocedi et al. 2014). The SMS accounts for the role of individual perception to predict emergent patterns of connectivity. Naïve individuals respond to landscape structure within a limited perceptual range, producing stochastic movement behaviours that can deviate substantially from those predicted by least-cost path or circuit theory-based models, which ignore the potential for dispersers to become lost or disoriented when traversing large complex landscapes. In at least one study, SMS was demonstrated to provide better estimates of inter-patch connectivity than these alternative approaches (Coulon et al. 2015).

TartanGraphs

In order to investigate how the connectivity of an LLE network might be affected by its configuration, a series of stylised cell-based landscapes were created as inputs for RangeShifter. These landscapes consisted of identical, rectangular habitat patches arranged into pairs separated by an impermeable matrix and straight LLEs providing corridors for movement. Corridors were parametrised with zero carrying capacity, preventing individuals from reproducing outside of patches and excluding LLEs as potential habitat. Corridor networks were composed

of two LLE types; *connecting-edges*, terminating at either end at each patch, and *transecting-edges*, forming nodes with the *connecting-edges* on perpendicular axes. Based on the pattern of intersecting lines created by this stylised landscape structure, we dubbed these landscapes *TartanGraphs* (Fig. 1.).

The scale of *TartanGraphs* was inspired by the landscape structure of parts of the Fens, a coastal plain of eastern England containing fragmented wetland remnants separated by matrix of intensive agriculture and dense webbing of drainage ditch LLEs. Several remnant wetland patches are in relative proximity, such as the ~5.0 km distance between Wicken Fen and Chippenham Fen nature reserves, and this informed positioning of *TartanGraph* patches at ~5.5 km apart which, at a cellular resolution of 32 m, placed patches 177 raster-cells apart. This inter-patch distance also provided ample space to experimentally increase the numbers and widths of *transecting-edges* in order to answer our study aims.

To accommodate comparable experimental widening or addition of *connecting-edges*, habitat patches were made much wider than long, measuring 0.5 km (17 cells) by 6.0 km (188 cells). The least-costly path of inter-patch dispersal made available to individuals by virtue of *connecting-edges* was therefore identical on all graphs, requiring individuals to make at least 178 “steps” (single cell-to-cell movement) to disperse from natal to novel patches.

Cells between LLEs were set to “no data” values, rendering the matrix inaccessible to simulated individuals and bestowing impenetrable, reflective boundaries to LLEs. Upon encountering a matrix cell in their line of travel, the angle of trajectory adjustment individuals undertake to continue moving is governed by the Directional Persistence parameter, which assigns a likelihood to each new available trajectory that declines with greater difference in angle from the initial direction of movement. Hence, when individuals encounter corridor boundaries, they are

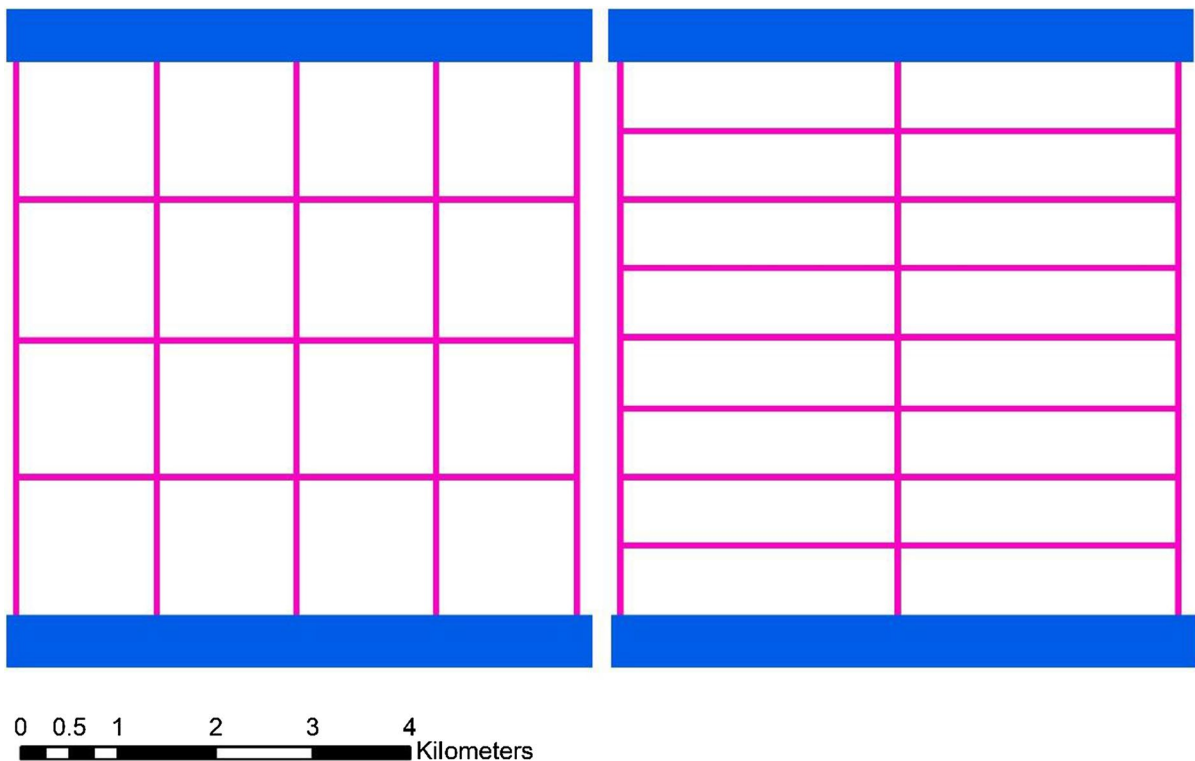


Fig. 1 Example of two *TartanGraphs*. Habitat-patch cells displayed in blue and LLE corridor cells in violet. Matrix cells in white. Both measure 188 cells in width and 221 cells in length. Habitat patches are both 17 cells long and *connecting-edges*

are 177 cells long. All LLEs are two cells wide. Left: *TartanGraph* consisting of five *connecting-edges* and three *transecting-edges*. Right: *TartanGraph* consisting of three *connecting-edges* and seven *transecting-edges*

more likely to make the smallest trajectory adjustment available to continue dispersal than to make larger directional changes, and the higher Directional Persistence is the stronger will be the preference for smaller adjustments.

To investigate the effect of LLE density and width on connectivity, three Experimental Sets of *TartanGraphs* (Table 1) were created and employed in-silico to assess whether connectivity, measured as probability of inter-patch dispersal, responded significantly to different treatments of *edge* numbers and widths.

The 25 *TartanGraphs* of the first Experimental Set exhibited networks consisting of every combination of five treatments of *connecting* and *transecting-edge* number and were used to analyse the impact of LLE quantity and orientation on connectivity. The number of *edges* contained within *TartanGraphs* was experimentally increased by inserting novel *edges* into the intervals between LLEs or between LLEs and the patch boundary (e.g. 16 new LLEs were added to the 17 *connecting-edge* landscapes to create *TartanGraphs* with 33 *connecting-edges*).

A second and third Experimental Set of *TartanGraphs* were created to investigate the impact of altering widths of *connecting* and *transecting-edges*, respectively. The second Experimental Set contained 48 *TartanGraphs* exhibiting every combination of four treatments of *connecting* and *transecting-edge* number and three treatments of *connecting-edge width*. Results from this Experimental Set were used to assess the influence of increasing the width of *connecting-edges* on connectivity. The third Experimental Set of 36 *TartanGraphs* contained every combination of four treatments of *connecting-edge* number, three treatments of *transecting-edge* number and

three treatments of *transecting edge width*, employed to assess the effect of increasing *transecting-edge width* on inter-patch dispersal.

Simulations in RangeShifter

We used the SMS equipped in the RangeShifter platform to simulate thousands of individuals moving on *TartanGraphs* according to different sets of movement rules. To achieve this, we specified a simple demography that yielded stable populations and induced hundreds of dispersals per-year. Namely, populations of a sexually reproducing species with a juvenile and adult stage were parameterised so that only adults could disperse and emigration from patches was density-dependent; this was inspired by the movement behaviours of insect species where adults are highly mobile in contrast to larvae. Each simulated year allowed adults one breeding season, and the species was parameterised to have high fecundity and mortality rates. With this demography, habitat patches sustained a mean population size of 862.2 adults at equilibrium and generated a mean of ~410 emigrants (SD: ±32.4) per year. For a full account of demographic and movement parameterisation see supplementary material 1.0.

In the SMS, individuals can only undergo dispersal once in their lifespan and they begin dispersal by appearing in a random cell within their natal patch and initiating movement in a random direction, though movement costs are not applied until they pass the patch boundary. Once outside, individuals are prevented from resettling in their natal patch and continue movement until they either locate and settle in another suitable patch or expire from movement

Table 1 Summary of the Experimental Sets of *TartanGraphs* used in experiments

Experimental Set	No. Tartan-Graphs	Connecting-edge numbers	Transecting-edge numbers	Connecting-edge widths	Transecting-edge widths
1	25	Five treatments: 3, 5, 9, 17, 33 edges	Five treatments: 0, 3, 7, 15, 31 edges	Controlled: Two cells	Controlled: Two cells
2	48	Four treatments: 3, 5, 9, 17 edges	Four treatments: 0, 3, 7, 15 edges	Three treatments: 2, 4, 6 cells	Controlled: Two cells
3	36	Four treatments: 3, 5, 9, 17 edges	Three treatments: 3, 7, 15 edges	Controlled: Two cells	Three treatments: 2, 4, 6 cells

First row: experimental set used to analyse effect of LLE quantity and orientation. Second row: experimental set used to analyse effect of increasing *connecting-edge* width. Third row: experimental set used to analyse effect of increasing *transecting-edge* width

costs. Each year begins with the generation of dispersing patch-emigrants and ends with settlement or mid-dispersal mortality of all individuals before moving on to the next year. Individuals do not interact with each other during dispersal and there is no limit to the number of dispersers that can occupy a cell simultaneously. Dispersal mortality was based on a per-step mortality risk, incurred every time individuals moved into an LLE cell. Though individuals could move an unlimited number of steps, this per-step mortality served to limit the distance individuals could feasibly travel through corridors before expiring. Per-step mortality probability of LLE corridors was parameterised at 0.01 and, in these conditions, the mean number of steps made by all individuals in-silico was ~100 before mortality. SMS assumes that patch populations are fully mixed.

Individuals were parameterised with a low perceptual range of their landscape (1 cell radius), designed to simulate conditions approximating the reality of water-filled drainage networks or lattices of linear grassy verges, wherein small organisms might struggle to perceive their environment beyond what is immediately surrounding their location. To examine how movement behaviour might impact dispersal rates, different treatments of *Directional Persistence* (DP) were applied to all *TartanGraphs* in separate simulations. DP is a dimensionless parameter that determines the autocorrelation of movement patterns. As DP is increased, individuals are less likely to change direction during dispersal and they move in straighter trajectories. The parameter determines the likelihood of changing direction as the inverse of its value to the power of 0, 1, 2, 3 or 4; where power scales with the angle of five possible trajectory changes on a cellular landscape (0°, 45°...180°). Three values of DP (5.0, 7.5 and 10.0) were simulated to test the hypothesis that increasing this parameter would produce a positive impact on the connectivity of *TartanGraph* systems irrespective of LLE characteristics, which we expected based on the belief that highly correlated individuals would be less likely to change direction at the nodes of LLE intersections and thus more likely to encounter novel habitat by maintaining trajectory along *connecting-edges*. In-silico individuals were not only able to change direction at nodes but could readily make lateral movements or turn full-about within the narrowest LLEs and move backwards on corridor sections already traversed.

Reproduction and dispersal over a period of 210 years was simulated nine times on each *TartanGraph*; three replicate simulations for each *TartanGraph* and DP treatment. Habitat patches were initialised with a population of adult-stage individuals numbering half of patch carrying-capacities. To access detailed information on behaviour of individuals in-silico, we set RangeShifter to produce text files detailing specific information on all individuals for each time-step (year in this case) of simulations; including their sex, age, origin, current location and number of steps made in dispersal mode. Observations from the first decade of simulations were excluded from results before analysis, as this covered the initialisation period of populations reproducing to attain equilibrium.

Data analysis

From individual-based data, we quantified the total number of individuals leaving habitat patches over a period of 200 years by consulting the number of steps recorded for individuals. As RangeShifter does not record within-patch movements and individuals can only disperse once throughout their lives, the *Total-Dispersers* observed in each *TartanGraph's* LLE system over 200 years was quantified by counting the number of observations where individuals originating from one of its two habitat patches were recorded making one or more steps. To evaluate how the number of LLEs might affect patch-emigration rates, we fitted *connecting* and *transecting-edge numbers* (as five-level factors) to separate analysis of variance tests (implemented in R version 4.0; R Core Team 2020) to see if any significant effect of LLE density upon *Total-Dispersers* across all *TartanGraphs* and DP treatments ($n = 327$) could be detected.

We then quantified inter-patch dispersal rates across *TartanGraphs* as a metric of landscape connectivity. The *PatchID* variable included in results recorded the unique ID of the habitat patch individuals inhabited at each simulation time-step. For each *TartanGraph* and simulation, we calculated the number of individuals that dispersed from either patch of the landscape into the other (*Inter-patch Dispersers*) by counting the subset of *Total-Dispersers* whose *PatchID* was greater than 0, indicating that they were inside another patch at year's conclusion. A *PatchID* value of 0 indicates that a disperser was not located

within any habitat patch at the end of that simulated year and must therefore have expired from movement costs inside an LLE. By dividing quantity of *Inter-patch Dispersers* by *Total-Dispersers*, we calculated a per-individual *Traversal-Probability* for each *TartanGraph* within different simulations, quantifying the likelihood of an individual reaching the other side of their *TartanGraph* after having left natal patches. By comparing *Traversal-Probabilities* across different *TartanGraphs* under experimental treatments we sought to distinguish changes in dispersal rates that correlated with alterations in LLE networks or changes to movement autocorrelation.

Results

Rate of Patch-egress

All *TartanGraphs* implemented in the experiments produced similar quantities of over a hundred-thousand individuals leaving habitat patches and initiating movement through LLEs (see SM 2.0). A mean of 163,822 *Total-Dispersers* were recorded across all simulations with an average standard deviation of 1,027 between replicate simulations. Analysis of variance tests detected weak effects on *Total Dispersers* of *transecting-edge* numbers ($p=0.01$) and of *connecting-edges* ($p=0.03$) (SM 3.1 & 3.2), presumably arising through density-dependant emigration. Increasing

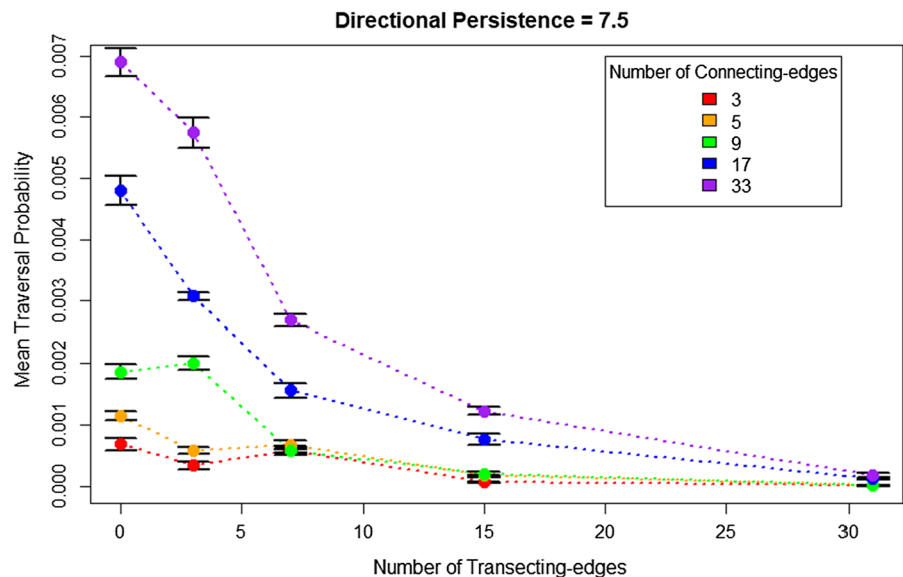
transecting-edge numbers from zero to 31 induced a mean reduction of 0.2% in patch-emigration. The largest difference in mean *Total-Dispersers* between two *connecting-edge* treatments amounted to ~510 individuals (nine versus 33 *connecting-edges*).

Corridor network density

Density and orientation of LLEs overlaying the matrix of *TartanGraph* systems exerted a substantial impact on their ecological connectivity. Most strikingly, while the two different edge types (*connecting* and *transecting*) represented in the *TartanGraphs* both had significant effects, the direction of their effects were opposite. This pattern was clearly seen across the first experimental set of 25 *TartanGraphs*. Number of *connecting-edges* was positively correlated with *Traversal-Probability* whilst the number of *transecting-edges* was negatively correlated (Fig. 2).

The *TartanGraph* whose structure was least conducive to inter-patch dispersal was composed of 3 *connecting-edges* and 31 *transecting-edges*, wherein highly correlated dispersers had a less than 0.01% probability of undergoing inter-patch dispersal ($1.0e-4$) and individuals set with lower movement correlation had no prospect of advancing to novel habitat. Conversely, the *TartanGraph* most conducive to inter-patch exchange had 33 *connecting-edges* and no *transecting-edges*, providing individuals with a 1.3% chance of encountering novel habitat ($1.3e-2$).

Fig. 2 The per-individual Traversal-Probabilities of 25 TartanGraphs. Each point represents a single TartanGraph with a unique combination of numbers of connecting (indicated by the key) and transecting edges (x-axis). Error bars indicate standard deviation of Probability across three replicate simulations under DP 7.5 treatment. Generally negative trend in Traversal-Probability with increasing transecting-edge number is clearly contrasted with a positive effect of greater connecting-edge quantities



Individuals were substantially more likely to undertake inter-patch dispersal when they were parameterised to disperse with more correlated movements. The mean *Traversal-Probability* of individuals in all *TartanGraphs* was as small as $\sim 3.0e-4$ under DP 5.0 treatments and increased by a factor of ten to $\sim 3.0e-3$ under DP 10.0 treatments, indicating the utility of greater directional persistence to facilitate inter-patch dispersal (see SM 3.3 and 3.4).

Trends in *Traversal-Probability* were reflected closely by connectivity measured as number of *Inter-patch Dispersers*. The mean number of *Inter-patch Dispersers* recorded across all simulations was 247 and the largest inter-patch exchange of individuals in any simulation numbered 2,166 across the *Tartan-Graph* with 33 *connecting-edges* and no intersecting LLEs. All simulations in which no inter-patch exchange occurred were conducted on *TartanGraphs* bearing 31 transecting-edges, concurring with the lowest mean *Dispersal Probabilities* observed on these same landscapes. The similar response of *Traversal-Probability* and *Inter-patch Dispersers* to experimental treatments also indicates the relative stability of *Total-Disperser* quantities across simulations and suggests that patch-emigration rates were largely independent from experimental treatments.

Though the contrasting general effects of the two edge types are evident from results, small deviations from the general trends occurred, particularly at smaller numbers of edges. *TartanGraphs* with nine *connecting-edges* experienced slightly lower inter-patch dispersal than those with less of the same LLE type in some instances (Fig. 2. Green points). Conversely, *TartanGraphs* with small numbers of *connecting-edges* showed single instances of greater *Traversal-Probability* when *transecting-edges* were added, though the negative effect of *transecting-edges* re-established themselves in subsequent, larger additions.

Width of edges

In the second Set of 48 *TartanGraphs*, we observed the same positive and negative correlations of *Traversal-Probability* with the number of *connecting* and *transecting-edges*, respectively, as well as a less substantial correlation of *connecting-edge* width with connectivity. Mean *Traversal-Probability* of

TartanGraphs with the widest *connecting-edges* (six cells) was slightly higher than that recorded from *TartanGraphs* with narrower inter-patch corridors, recording mean *Probabilities* of $1.7e-3$ and $\sim 1.3e-3$, respectively. The response of inter-patch dispersal rates to LLE width treatments changed noticeably depending on movement correlation of individuals, where mean *Traversal-Probability* exhibited almost no significant change with increasing corridor width under DP 5.0/7.5 but was improved by wider *connecting-edges* only for individuals parameterised to move in straighter, more correlated patterns (Fig. 3.).

Response of connectivity to wider *connecting-edges* was also different depending on *transecting-edge* density. In *TartanGraphs* with no or three perpendicular LLEs, connectivity showed improvement with the addition of *connecting-edges* but did not exhibit any consistent difference between LLE width treatments when controlling for *connecting-edge* quantity (Fig. 4: left). It actually appears from this data that connectivity improvement induced by adding *connecting-edges*, in the absence of intersecting LLEs, was more gradual when the edges added were of the widest breadth. However, at higher concentrations of *transecting-edges* there was a more consistent difference in connectivity between *TartanGraphs* with wide and narrow *connecting-edges*, whereby wider corridors better facilitated inter-patch exchange than narrower corridors of the same quantity (Fig. 4: right).

The third experimental set of 36 *TartanGraphs* demonstrated a less ambiguous impact of corridor width on connectivity, whereby wider *transecting-edges* consistently resulted in lower likelihood of inter-patch dispersal regardless of other experimental conditions (Fig. 5).

Mean *Traversal-Probability* of all *TartanGraphs* across all DP treatments declined from $1.0e-3$ to $3.1e-4$ as *transecting-edges* were increased from two to six cells diameter. This readily apparent difference between LLE width treatments could be observed when controlling for all treatments of *connecting-edge* number and movement correlation, demonstrating that increasing the width of perpendicularly oriented LLE corridors inhibited the likelihood of inter-patch dispersal, reflecting the negative effect of increasing the quantity of these same LLEs.

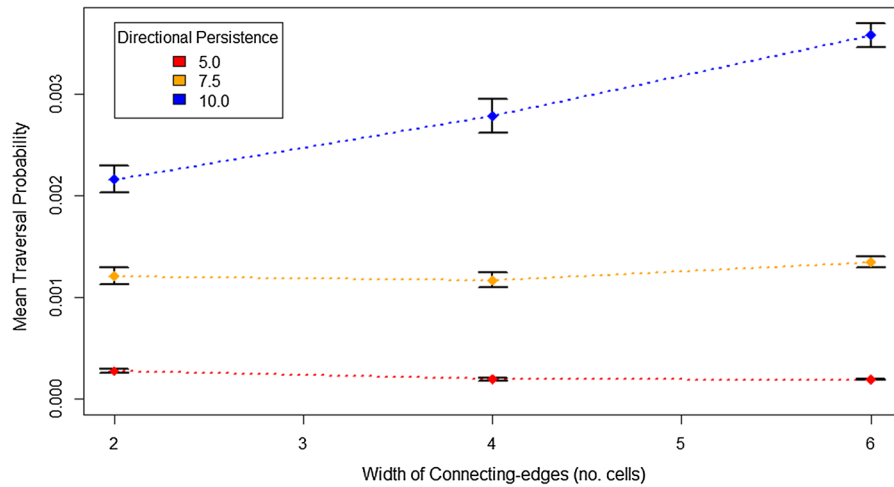


Fig. 3 The mean *Traversal-Probability* recorded from 48 *TartanGraphs* in response to *connecting-edge* width (x-axis) and movement correlation (DP parameter; coloured). Each point shows mean *Probability* of sixteen *TartanGraphs* with varying numbers of both edge types. Bars indicate standard error. Results show positive trend in likelihood of inter-patch disper-

sal and corridor width only for highly correlated movers (blue). Individuals parameterised to change direction more frequently fail to show same benefit from widening of *connecting-edges* and show very limited inclines or declines in connectivity in response to wider corridors (red, orange)

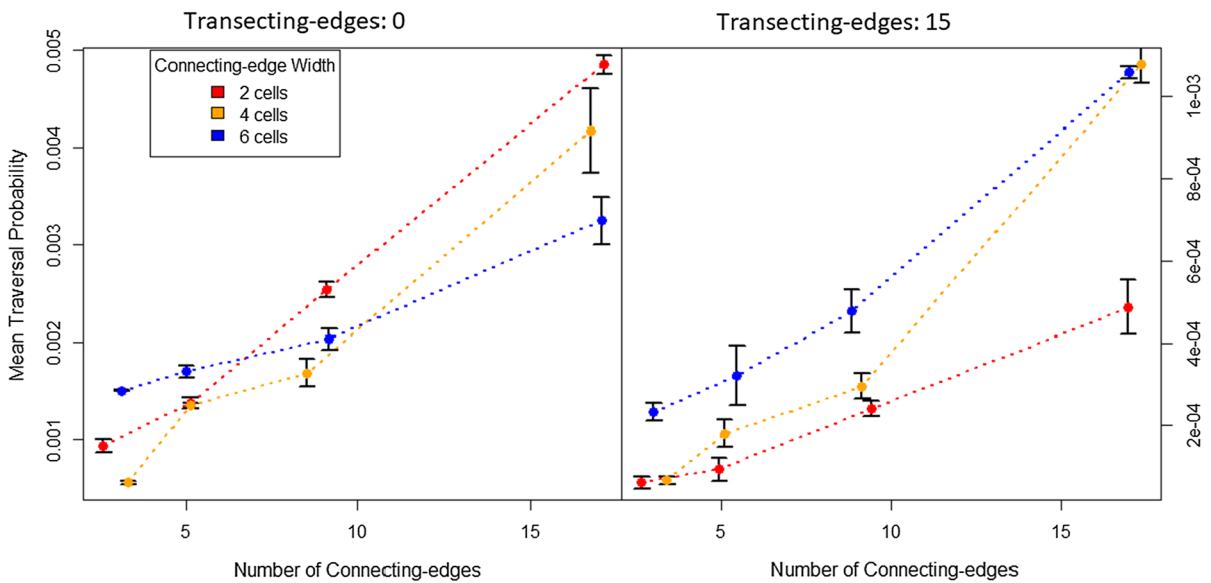


Fig. 4 Both panels: Mean *Traversal-Probability* across twelve *TartanGraphs* under DP 7.5. X-axis indicates number of *connecting-edges* in each landscape and their cellular widths by colour. Error bars show standard deviation between replicate three simulations and points are offset along the x-axis to improve clarity. Left: all *TartanGraphs* with zero *transecting-*

edges. Inter-patch dispersal rates show considerable overlap between corridor width treatments and no treatment appears constantly better for connectivity than the others in the absence of intersecting LLEs. Right: all *TartanGraphs* with 15 *transecting-edges*. Dispersal rates are consistently higher when *TartanGraphs* bear wider *connecting-edges*

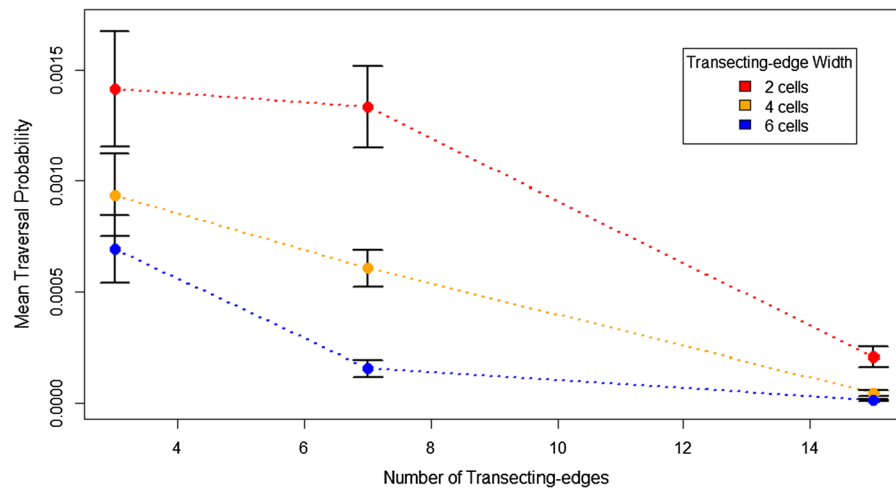


Fig. 5 Mean *Traversal-Probability* of 36 *TartanGraphs* under DP 7.5. Each point indicates the mean *Traversal-Probability* of four *TartanGraphs* sharing the same number of *transecting-edges* (X-axis) and cellular width of *transecting-edges* (coloured). Bars indicate standard error within *TartanGraph*

Discussion

Our findings suggest that the greater freedom of movement offered by linear features acting as dispersal corridors can negatively impact a landscape’s connectivity by increasing the likelihood of dispersing individuals becoming lost during transfer and thereby demographically isolating embedded habitat patches. Though previous in-silico studies have examined the effect of creating novel LLEs to connect habitat patches, these focused on addition of single patch-to-patch corridors (Lefkovich and Fahrig 1985; Anderson and Danielson 1997). We simulated two-patch systems connected by networks of intersecting LLEs to examine the effect of adding multiple inter-habitat corridors and the impact of LLE nodes on movement. Our results appear to demonstrate that LLEs can act as “traps” for dispersing individuals, depressing inter-patch connectivity by channelling dispersers away from habitat patches. The potential for linear features to adversely impact connectivity by acting as sinks has been theorised by landscape ecologists (Saunders and Hobbs 1991; Simberloff et al. 1992) and empirical research of invertebrate assemblages in LLEs suggests they can be demographic sinks for source populations in nearby habitat patches (Öckinger & Smith, 2007; Krewenka et al. 2011). By simulating

groupings. A consistently negative correlation between *Probability* and both explanatory variables is apparent, whereby a greater quantity or diameter of *transecting-edges* reduced an individual’s chance of inter-patch dispersal

individual dispersal through a permeable yet uninhabitable network, we have recreated this LLE-trap dynamic in-silico and demonstrated that increasing the number of linear elements may, depending on spatial orientation, have counter-productive effects on fragmented habitat connectivity.

An explanation for this may be found in empirical results reported by Eriksson et al. (2013). They demonstrated that a node formed by intersecting LLEs caused an approximately 50/50 division of dispersing crickets into individuals that maintained direction and moved past the node and those who changed direction and moved into the transecting LLE. By assuming a limited perception of environment and set probabilities of changing direction on the part of dispersers, the SMS replicated this tendency of individuals in nature to exploit the freedom of movement offered by nodes, whether to the benefit or detriment of their survival. As *transecting-edges* would permit individuals to make lateral movements across the landscape but provide no additional routes by which they could approach either patch, movements through them would have been unproductive toward finding habitat whilst nonetheless extracting a movement-cost, and a greater portion of disperser cohorts may have initiated movement into *transecting-edges* when more nodes were present. This effect may also

account for the significant correlation between LLE numbers and patch-egress rates, as emigration was parameterised to be density-dependant and changes in inter-patch dispersal rates induced by LLE density treatments may have been sufficient to significantly affect *Total-Dispersers* by increasing/alleviating density-dependant pressures on in-patch individuals to initiate dispersal.

Our hypothesis that increasing the movement correlation of individuals would improve dispersal rates was supported by results. Prior in-silico experiments have demonstrated that greater autocorrelation in movement increases the dispersal-potential of populations across homogenous areas (such as our *TartanGraphs* LLEs), because individuals can attain greater distances under constraints on movement, such as timeframe or movement-costs (Cain 1991; Tischendorf and Wissel 1997). Thus, highly correlated individuals may have made more efficient use of LLEs during movement, closing the distance to novel habitat patches in a smaller number of steps than less correlated movers. It is also possible that highly correlated movers were less likely to make use of intersections to move between LLEs, and a lower propensity to use nodes to change direction might have contributed to their greater dispersal rates independent of their greater efficiency of movement through LLEs.

Based on the results of these simulations it appears LLEs exerted a highly focussed and unidirectional impact on connectivity whereby they significantly increased landscape permeability along their axes but restricted perpendicular movements. These results add to a body of empirical evidence demonstrating how LLEs may exert dual effects of facilitating or inhibiting movement across landscapes depending on orientation (Fabritius et al. 2015; Klaus et al. 2015).

The effect of widening either edge type appears to produce similar though sometimes weaker effects on dispersal as increasing LLE numbers. The *TartanGraphs* that possessed wider *connecting-edges* generally experienced greater connectivity than those with the same number of narrower LLEs. Other in-silico studies have also found that wider corridors are more conducive to facilitating connectivity along their lengths (Baur and Baur 1992; Tischendorf et al. 1998; Delattre et al. 2010; Christies and Knowles 2015) as wider corridors offer less resistance to movement by lowering the chance of dispersers encountering

corridor's boundaries or edge elements (Tischendorf and Wissel 1997). However, we found that increasing the width of *connecting-edges* had a weakly positive impact on connectivity only when individuals were parameterised with the highest degree of correlated movement (Fig. 3). For less correlated dispersers, positive effects of increased corridor width may have been offset by the greater freedom of lateral movement permitted by a broad *connecting-edge*, allowing individuals to make meandering movements along LLEs and hence use *connecting-edges* inefficiently. Empirical studies on the movement of animals through corridors of different widths reveal potential real-world parallels to our simulation results. Andreassen et al. (1996) found that released voles had a higher chance of traversing 1 m wide corridors than 3 m wide ones to disperse toward habitat patches and suggests that cross-sectional movements inside the wider corridors may explain lower traversal rates therein. Similarly, Kowalski et al. (2019) found that voles moved faster through narrower grassy corridors than in other treatments, and Pryke and Samways (2001) observed vagile butterfly species moving faster through narrow grassland corridors than wider ones. Findings such as these suggest that boundaries situated at proximity may serve to channel dispersers through faster than if they were wider apart (Tischendorf and Wissel 1997).

Such a boundary-channelling dynamic may account for why dispersal rates of our individuals were sometimes higher on *TartanGraphs* with narrower *connecting-edges*, as the combined assumptions of reflecting LLE boundaries and moderate-to-high movement correlation would have significantly limited individual's opportunities to change direction when adjacent to matrix cells and compelled individuals to move in straighter trajectories regardless of parametrisation. The assumption of impenetrable matrix may thus have generated a more powerful channelling effect than if matrix were merely accessible but hostile. The assumptions of our model may therefore be less relevant to many terrestrial species exploiting LLE corridors, as agriculture elements are likely more penetrable to walking and flying species than what is presented in this study. Future investigations may expand upon results presented here to verify whether connectivity effects of LLE orientation can be observed in species less confined by the dimensions of ecological corridors. Though the

reflecting boundaries assumption is more extreme than what is generally implemented for in-silico corridor studies, our results may be quite applicable to understanding the role of LLEs in aquatic organism dispersal (eg. fish, snails or brachypterous beetles) using drainage ditches to traverse agricultural areas. Though less studied than hedgerows, ditches are a feature of many developed landscapes and are known to provide corridors for aquatic species (Hurtez-Boussès et al. 2010; Favre-Bac et al. 2016). The boundaries of *TartanGraph* LLEs may differ little in effect from how the steep sides of ditches and dependency on water for respiration confines the movement of such aquatic dispersers.

Our findings highlight the importance of incorporating behavioural variables into models of dispersal in order to detect sometimes unintuitive consequences of landscape structure on connectivity. Dispersal rates through *TartanGraphs* derived from least-cost theory would have been identical for all network configurations, as inter-patch distance and movement resistance of LLEs were controlled for in landscape design. Only by incorporating limited perceptual range on the part of individuals did RangeShifter identify the trapping effect exerted by some LLEs, as naïve individuals used nodes to enter corridors regardless of whether they led closer or further from novel habitat. In-silico studies using an individual-based approach have previously found evidence that the addition of features designed to promote connectivity can have the opposite effect, such as in the case of “steppingstones”, where it was suggested via individual-based modelling that small patches of novel habitat designed to encourage movement between larger remnant patches could disrupt dispersal rates by encouraging individuals to settle in them (Hein et al. 2004; Kramer-Schadt et al. 2011). Like our *transecting-edges*, steppingstones might be expected to improve connectivity by easing overall landscape resistance to movement. However, precluded as they are from an ecologist’s view of the landscape, individuals in nature react to landscape structure within a limited range of perception and may use permeable features in ways that cause wild populations to make only partial use of available landscape resources.

Our model was parameterised to simulate the demography and movement behaviour of a hypothetical insect species based on limited knowledge available on how such organisms perceive landscape

features, thus our model makes conservative assumptions about species capabilities that might not be generalisable to all taxa. In the same way stylised *TartanGraph* landscapes were designed to control for confounding geographic effects on connectivity, we specified stable populations to minimise the noise emitted by demographic stochasticity and allow us to evaluate the consequences of experimentally altered variables. These assumptions may be less relevant to conservation efforts on species in demographic decline as a result of habitat fragmentation, and ecologists may have to decide on a case-by-case basis how the dual effects of LLEs corridors indicated here might either ease or exacerbate population extinction risks, by acting as conduits for metapopulation connectivity or traps for dispersing individuals, respectively. We initially intended to measure connectivity as the number of years one or more inter-patch dispersal events took place, but instead opted for a per-individual probability of dispersal after leaving habitat patches, reasoning that measuring connectivity as dispersal event number could have been sensitive to population parameters as it does not control for the number of individuals attempting dispersal in the first place.

We assumed limited perception and high dispersal mortality on the part of individuals, which may have generated lower dispersal rates than would be expected for more robust or perceptive species that could have more opportunity to encounter or detect novel habitat, respectively. We have included supplementary material showing the effect of increasing these variables on dispersal probabilities in fifteen *TartanGraphs* and demonstrated therein that increasing perceptual range and lowering step-mortality improved dispersal probabilities, but also that the dual effects of corridors and their orientations were still apparent at all levels (see SM 4.0). Thus, we believe that the trends identified in our paper may apply to taxa with a range of dispersal and perceptual abilities.

Parameters used to determine species movement behaviours remained static throughout simulations and we assumed no adaptation in movement behaviour on the part of individuals. It is possible that species located in real agricultural landscapes may adapt to the challenges of navigating LLE corridors by such changes as increasing movement correlation to avoid the risk of misdirection by nodes, and future studies might investigate how selective processes

and inter-individual variability alter the behaviour of species to mitigate the negative effects of LLEs identified in this study. However, we believe that the results of this investigation are nonetheless relevant to understanding how species may be impacted by LLE configuration in contemporary landscapes as the length of time some populations have had to adapt to exploiting these unnaturally-shaped elements may be relatively short on an evolutionary timescale. Our model also assumed no explicit predation upon individuals, and in real landscapes high predator density in shortest inter-patch corridors may alter the connectivity benefits of these LLEs relative to longer and more indirect routes between habitat patches (Dickie et al. 2019). A fruitful avenue of future study into the role of corridor intersection on dispersal might be to determine whether increasing freedom of movement, such as by adding *transecting-edges*, can become a greater asset than liability to connectivity if the negative effects of trapping and overwhelming individuals with choice for movement is offset by reducing their chances of encountering predators.

The insights presented in this study are particularly valuable given the increasing interest in the use of conservation corridors to facilitate connectivity and movements of wildlife between parts of the landscape (Hilty et al. 2020). Improving connectivity is an intrinsic part of the international community's response to the biodiversity and climate change crises (Saura et al. 2018). In countries with large-scale intensive agriculture, like the UK, where the landscape is criss-crossed by field boundaries made up of hedgerows or ditches, this research is particularly useful. For example, current guidance on the design of corridors as part of England's plans for the development of national Nature Recovery Network did not consider the possible impacts of how conservation corridors could act as a hindrance to dispersal if effectively providing cul-de-sacs for dispersing individuals (Crick et al. 2020).

Conclusion

According to our results, the number, width and orientation of the LLEs that compose an intersecting network can have significant and sometimes counter-intuitive impacts on connectivity. By taking an individual-based approach, we found that connectivity

might be negatively impacted by the greater freedom of movement offered by LLE corridors and their intersections, as dispersers were vulnerable to being drawn into traps where they would expire from movement costs. Increasing the width of LLEs exerted a similar effect on dispersal as increasing LLE numbers, though the beneficial effect of increasing *connecting-edge* width was weaker than increasing their number. Wide LLEs allow greater movement of directionally persistent dispersers, but narrower LLEs may in some instances better promote the movement of individuals that move in a less correlated manner through channelling effects. The results of this study provide further evidence of the utility of individual-based methods to investigate how the creation of novel elements may improve landscape permeability but can also harm connectivity over larger spatial scales by orienting individuals away from optimal habitats and landscape resources.

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Data availability The data reported this study are publicly available in a compressed folder at <https://github.com/r01ca17/Anderson-TartanGraph-Connectivity-Matrices>.

Code availability The R-script code used to analyse raw data and produce the four graphs in the manuscript are available at the same GitHub account as above.

Declarations

Conflict of interest None.

Ethical approval N/A.

Consent to participate N/A.

Consent to publication N/A.

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References

- Anderson GS, Danielson BJ (1997) The effects of landscape composition and physiognomy on metapopulation size: the role of corridors. *Landscape Ecol* 12:261–271
- Andreasson HP, Halle S, Ims RA (1996) Optimal width of movement corridors for root voles: not too narrow and not too wide. *J Appl Ecol* 33:63–70
- Baldock D (1990) Agriculture and habitat loss in Europe. CAB Direct. <https://www.cabdirect.org/cabdirect/abstract/19901884403>. Accessed 21 May 2021.
- Baur A, Baur B (1992) Effect of corridor width on animal dispersal: a simulation study. *Global Ecol Biogeogr* 2:52–56
- Bocedi G, Palmer SCF, Pe'er G, Heikkinen RK, Matsinos YG, Watts K, Travis JMJ, (2014) RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Meth Ecol Evol* 5:388–396
- Bocedi G, Palmer SCF, Malchow A-K, Zurell D, Watts K, Travis JMJ (2021) RangeShifter 2.0: an extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. *Ecography* 44(10):1453–1462
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445–449
- Cain ML (1991) When do treatment differences in movement behaviours produce observable differences in long-term dispersal placements? *Ecology* 72:2137–2142
- Christie MR, Knowles LL (2015) Habitat corridors facilitate genetic resilience irrespective of species dispersal abilities or population sizes. *Evol Appl* 8:454–463
- Coulon A, Aben J, Palmer SCF, Stevens VM, Callens T, Strubbe D, Lens L, Matthysen E, Baguette M, Travis JMJ (2015) A stochastic movement simulator improves estimates of landscape connectivity. *Ecology* 96(8):2203–2213
- Crick HQP, Crosher IE, Mainstone CP, Taylor SD, Wharton A, Langford P, Larwood J, Lusardi J, Appleton D, Brotherton PNM, Duffield SJ, Macgregor NA (2020) Nature Networks Evidence Handbook. Natural England Research Report NERR081. Natural England. York.
- Delattre T, Pichancourt JB, Burel F, Kindlmann P (2010) Grassy field margins as potential corridors for butterflies in agricultural landscapes: A simulation study. *Ecol Model* 221:370–377
- Dickie M, McNay SR, Sutherland GD, Cody M, Avgar T (2019) Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *J Anim Ecol* 89:623–634
- Ekroos J, Rundolf M, Smith HG (2013) Trait-dependent responses of flower-visiting insects to distance to semi-natural grasslands and landscape heterogeneity. *Landscape Ecol* 28(7):1283–1292
- Eriksson A, Low M, Berggren A (2013) Influence of linear versus network corridors on the movement and dispersal of the bush-cricket *Metrioptera roeseli* (Orthoptera: Tettigoniidae) in an experimental landscape. *Euro J Etymol* 110(1):81–86
- Fabritius H, Rönkä, K, Ovaskainen, O (2015) The dual role of rivers in facilitating or hindering movements of the false heath fritillary butterfly. *Mov Ecol* 3 (4)
- Fahrig L (1997) Relative effects of habitat loss and fragmentation on population extinction. *J Wildlife Manage* 61(3):603–610
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol S* 34:487–515
- Fahrig L, Merriam G (1985) Habitat patch connectivity and population survival. *Ecology* 66(6):1762–1768
- Fahrig L, Merriam G (1994) Conservation of fragmented populations. *Conserv Biol* 8(1):50–59
- Favre-Bac L, Mony C, Ernoult A, Burel F, Arnaud J-F (2016) Ditch network sustains functional connectivity and influences patterns of gene flow in an intensive agricultural landscape. *Hereditary* 116:200–212
- Forman RTT, Gordon M (1981) Patches and Structural Components for a Landscape Ecology. *Bioscience* 31(10):733–740
- Graham L, Gaulton R, Gerard F, Staley JT (2018) The influence of hedgerow structural condition on wildlife habitat provision in farmed landscapes. *Biol Conserv* 220:122–131
- Hanski I, Ovaskainen O (2000) The metapopulation capacity of a fragmented landscape. *Nature* 404:755–758
- Hansson L (1991) Dispersal and connectivity in metapopulations. *Biol J Linn Soc* 42:89–103
- Hein S, Pfenning B, Hovestadt T, Poethke HJ (2004) Patch density, movement pattern, and realized dispersal distances in a patch-matrix landscape—a simulation study. *Ecol Model* 174:411–420
- Henderson MT, Merriam G, Wegner J (1985) Patchy environments and species survival: Chipmunks in an agricultural mosaic. *Biol Conserv* 31(2):95–105
- Hilty J, Worboys GL, Keeley A, Woodley S, Lausche B, Locke H, Carr M, Pulsford I, Pittock J, White JW, Theobald DM, Levine J, Reuling M, Watson JEM, Ament R, Tabor GM (2020) Guidelines for conserving connectivity through ecological networks and corridors. Best Practice Protected Area Guidelines 30 Gland, Switzerland: IUCN
- Hurtrez-Boussès S, Hurtrez J-E, Turpin H, Durand C, Durand P, De Meeüs T, Meunier C, Renaud F (2010) Hydrographic network structure and population genetic differentiation in a vector of fasciolosis. *Galba Truncatula Infect Genet Evol* 10(2):178–183
- Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape

- structure and distance from main habitat. *Landscape Ecol* 24:547–555
- Joyce KA, Holland JM, Doncaster CP (1999) Influences of hedgerow intersections and gaps on the movement of carabid beetles. *B Entomol Res* 89:523–531
- Klaus F, Bass JJ, Müller B, Marholt L (2015) Hedgerows have a barrier effect and channel pollinator movement in the agricultural landscape. *Landscape Ecol* 8(1):22–31
- Kramer-Schadt S, Kaiser TS, Frank K, Wiegand T (2011) Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape Ecol* 26:501–513
- Krewenka KM, Holzschuh A, Tschirntke T, Dormann CF (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biol Conserv* 144:1816–1825
- Kowalski GJ, Grimm V, Herde A, Guenther A, Eccard JA (2019) Does animal personality affect movement in habitat corridors? Experiments with common voles (*Microtus arvalis*) using different corridor widths. *Animals* 9(291)
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* 142(6):911–927
- Lefkovich LP, Fahrig L (1985) Spatial characteristics of habitat patches and population survival. *Ecol Model* 30:297–308
- Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. *Trends Ecol Evol* 11(3):131–135
- Mech SG, Hallett JG (2001) Evaluating the effectiveness of corridors: a genetic approach. *Conserv Biol* 15(2):467–474
- Merckx T, Feber RE, McLaughlan C, Bourn NAD, Parsons MS, Townsend MC, Riordan P, McDonald DW (2010) Shelter benefits less mobile moth species: The field-scale effect of hedgerow trees. *Agr Ecosyst Environ* 138:147–151
- Newman D, Pilson D (1997) Increased probability of extinction due to decreased effective population size: experimental populations of *Clarika pulchella*. *Evolution* 51(2):354–362
- Ökinger E, Smith HG (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *J Appl Ecol* 44:50–59
- Ovaskainen O, Meerson B (2010) Stochastic models of population extinction. *Trend Ecol Evol* 25(11):643–652
- Palmer SCF, Coulon A, Travis JMJ (2011) Introducing a ‘Stochastic Movement Simulator’ for estimating habitat connectivity. *Meth Ecol Evol* 2:258–268
- Pryke SR, Samways MJ (2001) Width of grassland linkages for the conservation of butterflies in South African afforested areas. *Biol Conserv* 101:85–96
- R Core Team (2020) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Saunders DA, Hobbs RJ (1991) The role of corridors in conservation: what do we know and where to we go? In: *Nature Conservation 2: The Role of Corridors*. Surrey Beatty & Sons, Chipping Norton. pp 421–427
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conserv Biol* 5(1):18–32
- Saura S, Bertzy B, Bastin L, Battistella L, Mandrici A, Dubois G (2018) Protected area connectivity: Shortfalls in global targets and country-level priorities. *Biol Conserv* 219:53–67
- Scanes CG (2018) Chapter 19 - Human Activity and Habitat Loss: Destruction, Fragmentation and Degradation. In: *Animals and Human Society*. Academic Press, London. pp 451–482
- Schulp CJE, Lautenbach S, Verburg PH (2014) Quantifying and mapping ecosystem services: Demand and supply of pollination in the European Union. *Ecol Indic* 36:131–141
- Simberloff D, Farr JA, Cox J, Mehlman DW (1992) Movement Corridors: Conservation Bargains or Poor Investments? *Conserv Biol* 6(4):493–504
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity Is a Vital Element of Landscape Structure. *Oikos* 68(3):571–573
- Tischendorf L, Irmiler U, Hingst R (1998) A simulation experiment on the potential of hedgerows as movement corridors for forest carabids. *Ecol Model* 106:107–118
- Tischendorf L, Wissel C (1997) Corridors as conduits for small animals: attainable distances depending on movement pattern, boundary reaction and corridor width. *Oikos* 79:603–611
- Van Geert A, Van Rossum F, Treist L (2010) Do linear landscape elements in farmland act as biological corridors for pollen dispersal? *J Ecology* 98(1):178–187
- Villemey A, Van Halder I, Ouin A, Barbaro L, Chenot J, Tessier P, Calatayud F, Martin H, Roche P, Archaux F (2015) Mosaic of grasslands and woodlands is more effective than habitat connectivity to conserve butterflies in French farmland. *Biol Conserv* 191:206–215

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