Tree loss impacts on ecological connectivity: Developing models for assessment

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ARTICLE INFO

ABSTRACT

Trees along linear features are important landscape features, and their loss threatens ecological connectivity. Until recently, trees outside of woodlands (TOWs) were largely unmapped however; the development of innovation mapping techniques provides opportunities to understand the distribution of such trees and to apply spatially explicit models to explore the importance of trees for connectivity. In this study, we demonstrate the utility of models when investigating tree loss and impacts on connectivity. Specifically, we investigated the consequences of tree loss due to the removal of roadside trees, a common management response for diseased or damaged trees, on wider landscape functional connectivity. We simulated the loss of roadside trees within six focal areas of the south east of the UK. We used a spatially explicit individual-based modelling platform, RangeShifter, to model the movement of 81 hypothetical actively dispersing woodland breeding species across these agriculturally fragmented landscapes. We investigated the extent to which removal of trees, from roadsides within the wider landscape, affected the total number of successful dispersers in any given year and the number of breeding woodlands that became isolated through time. On average roadside trees accounted for < 2% of land cover, but removing 60% of them (~1.2% of land cover) nevertheless decreased the number of successful dispersers by up to 17%. The impact was greatest when roadside trees represented a greater proportion of canopy cover. The study therefore demonstrates that models such as RangeShifter can provide valuable tools for assessing the consequences of losing trees outside of woodlands.

1. Introduction

The loss and fragmentation of habitats is a major threat to biodiversity (Haddad et al., 2015). Scattered trees within a fragmented landscape have a significant role to play in combating the effects of habitat loss and fragmentation. In a recent global meta-analysis, Prevedello et al. (2017) found landscapes with scattered trees supported greater levels of biodiversity than landscapes without scattered trees, reinforcing the idea that scattered trees are 'keystone' structures of landscapes (Fischer and Lindenmayer, 2007; Gibbons et al., 2008). In particular, hedgerows and scattered trees alongside roads and railway lines are often cited as examples of habitat corridors (Bailey, 2007; Bennett, 1990; McCollin et al., 2000; Roy and de Blois, 2008). Hedgerows and other linear tree features have been shown to aid the dispersal

of some forest plants (Roy and de Blois, 2008), pollen (Van Geert et al., 2010), mammals (De Lima and Gascon, 1999; Laurance and Laurance, 1999), birds (Fernandez-Juricic, 2000) and insects (Petit and Burel, 1998; Tischendorf et al., 1998). Trees present outside woodlands can also act as stepping stones, increasing connectivity and facilitating range expansion (Rossi et al., 2016). In a recent study, Fischer et al. (2010) found that scattered trees in an agricultural landscape had a disproportionately positive effect on species richness, thus emphasising their role as keystone structures in fragmented landscapes.

Many of these ecologically important landscape features are now under threat. Loss of scattered trees and connectivity is often associated with anthropogenic land use change, such as agricultural intensification and management. However, tree mortality rates and die-off events have increased greatly in some parts of the world as trees suffer from

elevated temperatures and water stress due to climate change (Bigler et al., 2006; Breshears et al., 2005; McDowell et al., 2010; Peñuelas et al., 2001). Furthermore, in recent years, the number of tree diseases and their rate of spread appear to have increased across the globe, due to several factors including climate change and global trade (Woodward and Boa, 2013). For example, in North America, chestnut blight *Cryphonectria parasitica* has caused near complete loss of chestnuts *Castanea dentata* (Jacobs, 2007). Dutch elm disease *Ophiostoma* spp. has caused a similar loss of mature elms *Ulmus* spp. in Europe and North America (Potter et al., 2011): some 26 million landscape trees were lost in the UK alone during the major outbreak in the 1970s. Across Europe, ash *Fraxinus* spp. trees are also dying due to the ascomycete *Hymenoscyphus fraxineus* widely known as ash dieback (Baral et al., 2014; Kjær et al., 2012) (previously called *Chalara fraxinea* and *H. pseudoalbidus*). The impact of woodland tree loss due to threats such as deforestation, disease and climate change on biodiversity has been documented (Barlow et al., 2016; Brook et al., 2003; Mitchell et al., 2014). However, trees outside of woods (TOWs) are often overlooked and rarely mapped (see Levin et al., 2009; Gullick et al., 2017 as mapping exceptions). Yet the recent development of innovative high resolution mapping for mapping individual TOWs (Bluesky National Tree Map, 2015) indicates that a large proportion of trees are present outside of existing mapped woodlands, thus the importance of TOWs for ecological connectivity may be undervalued. With the development of mapping techniques, opportunities to consider the value of TOWs for biodiversity and connectivity have arisen. In particular, the loss of TOWs, principally those close to infrastructure such as roads and railways, on wider landscape connectivity can be explored.

A suite of approaches already exists for modelling landscape ecological processes and new ones are emerging (Synes et al., 2016). Connectivity is one of the key attributes maintaining linkages between fragmented habitat patches within landscapes. Among the spatially explicit approaches for modelling connectivity are three distinct methods, least-cost path (LCP) (Adriaensen et al., 2003), circuit theory (e.g. Circuitscape, McRae et al., 2008) and emerging mechanistic or process models, such as the stochastic movement simulator (SMS) which is embedded in the spatially explicit modelling platform RangeShifter (Bocedi et al., 2014; Palmer et al., 2011). Within all three, landscapes are characterised by habitat and matrix elements, each of which has a permeability or cost value associated with moving through it (related to the resistance/preference). The three approaches differ in the way they model the potential pathways individuals may use to travel between patches. At one extreme, LCP calculates a single, deterministic, optimum route between any two patches, whereas in Circuitscape (McRae et al., 2013) all possible pathways are evaluated by analogy to electrical resistance. SMS explicitly incorporates the movement behaviours of individuals, simulating the trajectories of many individuals making probabilistic decisions regarding each step evaluated within a limited perceptual range. In a recent study, the degree to which each estimator (LCP, Circuitscape and SMS) correlated with genetic estimates of connectivity was compared for an amphibian and a bird species having contrasting movement abilities: SMS was the best performer and Circuitscape outperformed LCP (Coulon et al., 2015). The improvement in performance gained by using SMS comes unavoidably with an increase in the number of parameters required for the model. However, embedding detailed individual movements into spatially explicit population models can offer important advantages over alternative methods for estimating connectivity (Aben et al., 2016; Coulon et al., 2015). Spatial modelling approaches have been used to estimate ecological connectivity and to inform landscape management options in other contexts (Aben et al., 2016; Binzenhöfer et al., 2005; Conlisk et al., 2014; Synes et al., 2015). Yet, there is considerable untapped potential to develop and apply spatially explicit models, incorporating mechanistic dispersal, to address landscape connectivity questions related to the impact of climate change, tree disease and/or management actions that lead to the loss of TOWs.

In this study, we construct a spatially explicit individual-based model for actively dispersed virtual species that are assumed to use roadside trees as stepping stones and/or corridors between woodland breeding habitats in real UK landscapes. We use the recently developed innovative high resolution national tree map for mapping individual TOWs (Bluesky National Tree Map, 2015). In an intensively managed landscape such as the UK, TOWs are often an important ecological component within the highly fragmented and hostile agricultural matrix. As field sizes have expanded with the intensification of agriculture, trees along infrastructure features such as roads, railways and watercourses have occupied an increasing proportion of all TOWs. However, infrastructure brings people into contact with such trees and concerns over perceived danger presented by diseased or dying trees (i.e. their inherent tendency to limb failure or collapse) increases the likelihood of management actions targeting the removal of trees close to infrastructure in the event of a disease epidemic or climate-induced dieback (Gullick et al., 2017). We aim to consider the impact of this manner of tree loss on wider ecological landscape connectivity, as a first step towards understanding the most appropriate management and recovery response. Specifically, we model actively dispersing woodland breeding species, and investigate the extent to which the removal of roadside trees affects the total number of successful dispersers in any given year and the number of breeding patches that become isolated through time. We present results demonstrating the utility of individual-based spatial models, incorporating mechanistic dispersal, for addressing questions related to connectivity and tree loss, and discuss the potential of modelling to inform applied management.

2. Methods

2.1. Study landscapes

Our study landscapes consisted of six 10 km × 10 km squares in the south east of the UK (Table 1, Fig. 1). This region is a good example of an area with trees under threat; ash dieback is prevalent within the region and is expected to cause the catastrophic loss of ash trees that comprise a substantial proportion of all trees in the wider landscape. Furthermore, climate change and subsequent increasing heat and drought in the south and east of the UK are also likely to increase tree loss, particularly of young trees and mature trees outside of woodlands (Broadmeadow et al., 2009).

The squares were selected to provide a representative range of landscapes in the region. Baseline maps were created using canopy tree data extracted from the National Canopy Map (NCM) for England and Wales provided by BlueSky (Bluesky National Tree Map, 2015) under licence to the Woodland Trust. The NCM provides the location, height and canopy/crown extents where canopy exceeds 3 m in height. It is created from high resolution aerial photography, terrain and surface data, and from colour/infrared satellite imagery. Using ArcGIS, NCM tree cells were classified as woodland trees if they fell within the Forestry Commission's National Forest Inventory (Forestry Commission,

Table 1
Tree cover as a percentage of land cover within each of the 10 km × 10 km study squares, and in parentheses the percentage of the total tree cover for the three classes, matrix, roadside and woodland trees.

Square	SW corner co-ordinates (°Lat, °Lon)	Tree cover (%)			
		Total	Matrix	Roadside	Woodland
TM18	52.108, 1.065	13.3	6.4 (48.3)	2.2 (16.3)	4.7 (35.4)
TL96	52.205, 0.779	15.7	5.6 (35.8)	2.4 (15.5)	7.6 (48.7)
TL54	52.038, 0.185	14.2	5.6 (39.2)	2.0 (14.4)	6.6 (46.4)
TM17	52.288, 1.078	12.1	5.8 (47.6)	2.1 (17.7)	4.2 (34.7)
TL74	52.032, 0.477	10.3	5.0 (49.1)	1.7 (16.9)	3.5 (34.0)
TL90	51.667, 0.746	6.1	3.5 (58.2)	1.4 (22.4)	1.2 (19.4)
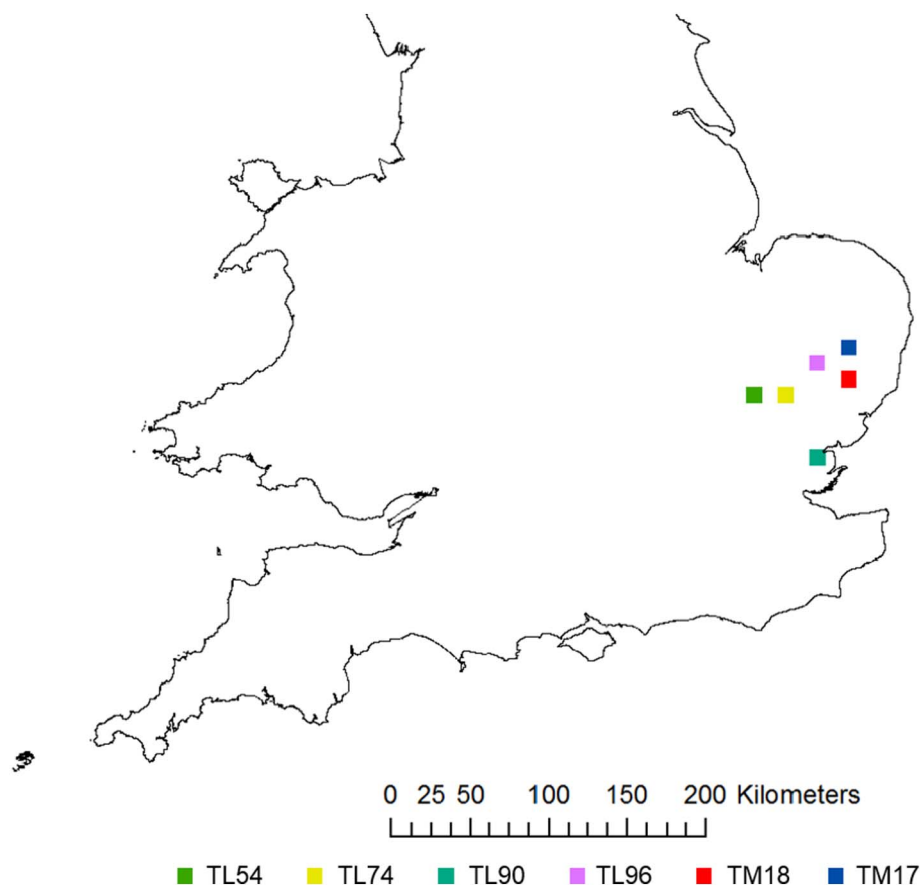
Fig. 1. Map of southern England showing square locations.

■ TL54 ■ TL74 ■ TL90 ■ TL96 ■ TM18 ■ TM17

2015) woodland polygons of > 0.5 ha extended by a buffer of 10 m width. Road data for the study area were downloaded from Edina (http://digimap.edina.ac.uk) OS open roads. Linear road features were buffered to 25 m either side and tree cells were classified as roadside trees if they fell within the road buffer. Matrix trees were those that did not fall within the boundaries of NFI woodlands or road buffers. The remainder of the landscape was dominated by agricultural land classified within our model as hostile matrix habitat. Woodland patches were defined as the breeding habitat for the 81 virtual species (described below), and other habitat types (roadside trees, matrix trees, matrix habitat) formed the inter-patch matrix (Fig. 2) each with a habitat-dependent movement cost associated (Table 2). Thus, we restricted the models to species that need a woodland patch for reproduction. For these species, the trees outside of woodland improve the permeability of the matrix. We have not focused on species for which single trees outside of woodland provide suitable breeding habitat. 10 m raster maps were then created from the ArcGIS shapefile layers with cells identified as woodland trees, roadside trees, matrix trees and inter-patch matrix (Fig. 2a).The percent of the tree cover for each square and the composition of the tree cover (matrix, road side, or woodland trees) is given in Table 1.

2.2. Tree removal scenarios

We simulated the removal of 20%, 40% and 60% of roadside trees in each square due to anticipated felling of diseased and damaged trees along roads. For each of the six squares and for each of the 20%, 40% and 60% removal scenarios, we generated ten landscape replicates in which roadside trees were removed at random from the baseline landscape (for an example of this see Fig. 3). Thus for each of the six squares, breeding patches remained the same in the baseline landscape and in each of the 30 generated removal landscape replicates, but the

inter-patch matrix differed.

2.3. Model

We modelled the effects of the tree removal scenarios on connectivity using RangeShifter, an individual-based spatially explicit modelling platform (Bocedi et al., 2014), which combines demographic and dispersal sub-models, notably accounting explicitly for the three phases of dispersal (emigration, transfer, settlement). Within Range-Shifter, the distribution of individuals' dispersal distances is an emergent property of behavioural rules at each phase and interaction with the landscape (e.g. the dispersal of an individual between two woodland patches depends upon the quality of the matrix). For the purpose of this study, the movement of individuals was modelled using SMS, which is embedded within Rangeshifter. SMS simulates the movement of individuals between breeding sites across a cost surface, subject to two key movement parameters, namely perceptual range (*PR*, the distance within which an individual evaluates surrounding habitat costs) and directional persistence (*DP*, an individual's predisposition to follow a correlated path). In addition to matrix cells having a substantially higher movement cost than cells with trees, they also had a much higher mortality risk in terms of the habitat-dependent risk of mortality per step taken.

2.4. Simulations

For each of the landscapes, we simulated the dynamics of virtual species. The use of virtual species in spatial ecological modelling is increasing used (Feng and Papeş, 2017; Fukuda and De Baets, 2016) and presents advantages in terms of facilitating the development, testing and showcasing of methods (e.g. Leroy et al., 2016). Furthermore it can provide initial insights on potential impacts of
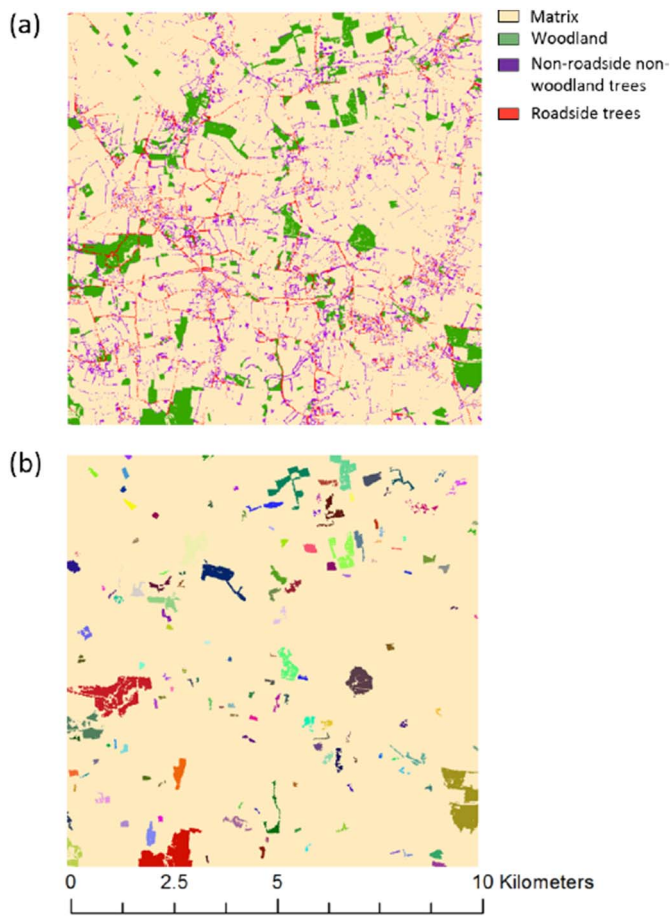
Fig. 2. Example of one of the six landscape squares (TL96) showing (a) the classification into four habitat types and (b) the 144 discrete breeding patches in the square (unique colours).

Table 2
Parameters used in RangeShifter, varied parameters shown in red.

Demographic parameter	
Reproduction	Asexual/female only
Stage structure	Non-overlapping generations
Intrinsic growth rate ($Rmax$)	10
Competition coefficient (b_c)	1
Carrying capacity (inds/ha) (K)	25, 50, 75
Dispersal characteristics	
Emigration probability	Density-dependent
Max. emigration probability (D_0)	0.7
Slope at inflection point (α)	10
Inflection point (β)	0.5
Movement model	SMS
Perceptual range (cells)	3,6,12
Perceptual range method (PR)	Harmonic mean
Directional persistence (DP)	5.0,7.0,9.0
Memory size (cells)	2
Maximum number of steps (cells)	2000
Cost value/mortality risk (HM) of:	
Matrix	500/0.02, 750/0.035, 1000/0.05
Woodland	1/0.0001
Matrix trees	1/0.0001
Roadside trees	1/0.0001
Settle-if	Find a suitable patch (not the natal one)

environmental changes and management activities even when data are lacking for sets of real species (e.g. Saura et al., 2011; Synes et al., 2015). We considered actively dispersing species that might use road-side trees as stepping stones and/or corridors for movement between woodlands. We assumed that such species would have sensory abilities
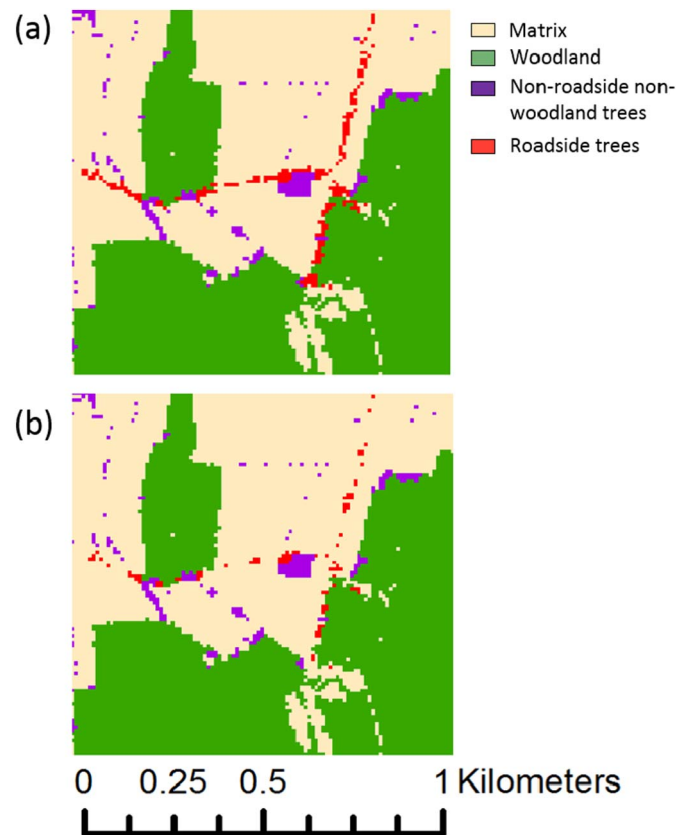

Fig. 3. (a) Example of a 1 km × 1 km area within one of the six landscape squares (TL96) (b) Example of 60% roadside tree removal for the area shown in (a).

to navigate towards trees in the landscape, and would display a strong preference for doing so rather than moving across open fields. A list of species within the study area and their associated demographic and dispersal parameters was not available; thus the set of model species is not based on particular species, but has been designed to represent the characteristics of a broad range of potential invertebrate taxa, varying in their population densities and dispersal abilities.

The virtual species were modelled as asexual with non-overlapping generations. The choice to model asexual populations does not imply only asexual reproduction, but rather represents invertebrate species that mate prior to emigrating from their natal patch; hence new co-lonies are founded by fertilised females and the dispersal of males does not need to be modelled. The 81 species were chosen using a fully factorial design by applying three levels of each of the following parameters: carrying capacity (K = 25, 50, 75 inds/ha), perceptual range (PR = 3, 6, 12 cells), directional persistence (DP = 5.0, 7.0, 9.0) and the mortality risk incurred by crossing unsuitable matrix habitat (HM = 0.02, 0.035, 0.05). Other parameters within RangeShifter were held constant for all simulations (Table 2).

For each of the 81 species, 10 demographic replicate scenarios were run on the baseline landscapes to generate baseline measures of con-nectivity. Then, for each species, 10 demographic replicates were run on each of the 30 removal scenario landscapes for each of the six squares (10 replicate landscapes for each of the 20%, 40% and 60% roadside tree removal scenarios). For each species, landscape and re-plicate combination, populations were initialised at half carrying ca-pacity in every breeding patch. The models ran for 30 years, but the first 10 years were taken as a burn-in period and discarded, as trial simulations had demonstrated that this allowed for the population dynamics to stabilise before results were taken.

2.5. Data analysis

For each generation, RangeShifter provides a connectivity matrix presenting counts of the number of successful dispersers from each breeding patch to every other breeding patch in the study area. The connectivity matrices were used to calculate the total number of successful dispersers (individuals that did not die during dispersal) in any given year and the number of breeding patches that become isolated (patches receiving no immigrants in the 20 years after the burn-in period).

2.6. Baseline landscapes

General linear models were fitted in R using package lme4 (Bates et al., 2015; R Team, 2017) to apportion the variance explained by each of the four varied factors (perceptual range, directional persistence, carrying capacity, matrix per step mortality risk). For all squares, demographic replicate and year, together with their interactions with the four varied factors, accounted for < 0.01% of the variance in the number of successful dispersers (Appendix A, Table A1) and in the number of isolated patches (Appendix A, Table A2). Therefore, counts of successful dispersers and the number of isolated patches were averaged across all demographic replicates and years.

2.7. Removal scenarios

For all tree removal scenarios (20%, 40%, 60%) on all squares, demographic replicate and year, together with their interactions with the four varied factors, accounted for < 0.01% of the variance in the number of successful dispersers (Appendix A, Tables A3,A4,A5). Therefore, as with the baseline, the number of successful dispersers was averaged across all demographic replicates and years for each landscape replicate within a given square and removal scenario. The mean number of successful dispersers was then scaled as a proportion of the baseline mean for the corresponding simulation (i.e. combination of K, HM, PR and DP).

Similarly, the number of isolated patches was averaged across all demographic replicates and years, and the effect of tree removal was represented by the increase in the mean number of isolated patches relative to the corresponding baseline simulation.

To account for all species simulations being run on the same 10 landscapes replicates (LR) for a given removal scenario in a particular square, the data were fitted separately for each square to linear mixed models in which landscape replicate was included as a random effect. The least squared means for the four varied factors (K, HM, PR, DP) were extracted from these models using R package lsmeans (Lenth, 2016) to illustrate the main effects of each model parameter.

3. Results

3.1. Successful dispersers

For each square, the mean proportion of successful dispersers declined as the percent of trees removed increased (Table 3). In general, the reduction in successful dispersers due to tree removal was < 10%, but for some individual parameter and landscape replicate combinations, the reduction in successful dispersers could be up to 17%. Removing roadside trees also changed the dispersal trajectories of individuals and increased the frequency of disperser visits to cells containing non-roadside matrix trees (Fig. 4).

The proportion of variance in successful dispersers explained by landscape replicate was between 3% and 30%, indicating that the actual spatial pattern of tree removal is likely to be important for connectivity. As the percent of trees removed increased, the proportion of variance explained by landscape replicate (LR) decreased (TL90 was the exception). Thus, in general as more trees were removed the spatial

pattern of tree removal becomes less important. Conversely, as more trees were removed the variance explained by carrying capacity (K) and directional persistence (DP) increased and the proportion of variance explained ranged from 5% to 50% and < 1% to 18% respectively. The interaction of carrying capacity and per-step mortality risk accounted for between 0.7% and 12% of the variance, but otherwise interactions were relatively unimportant.

Increasing carrying capacity (K) and matrix per step mortality risk (HM) (Fig. 5a and b, appendix B table B1) decreased the mean proportion of successful dispersers. Conversely, increasing SMS directional persistence (DP) increased the mean proportion of successful dispersers (Fig. 5c, appendix B table B1).

3.2. Isolated patches

At only 20% roadside tree removal, the increase in patch isolation over baseline levels was very limited, but larger increases in isolation were observed at higher levels of removal (Table 4, Fig. 6). Overall, the mean change was limited because some spatial configurations allow for a more substantial decrease and some an increase in patch isolation. For example, in the worst-case scenario the maximum increase in the number of isolated patches was 3.9 above the baseline (Table 4). However, in some cases tree removal also decreased the number of isolated patches compared to the baseline, minimum values ranging between − 1.2 and − 2.1 (Table 4). Increasing the per-step mortality risk led to larger increases in the number of isolated patches, whereas increasing directional persistence resulted in smaller increases (Appendix B Table B2, Fig. 6). Main effects and their first-order interactions generally accounted for a small proportion of the variance in the isolation metric, although the influence of mortality risk and directional persistence increased considerably as the proportion of trees removed increased.

4. Discussion

Here, we have demonstrated a novel approach for modelling how the removal of TOWs can affect the connectivity between woodlands in a fragmented landscape. A number of approaches have been used to assess and model landscape connectivity, ranging from simple pattern based metrics (e.g. nearest neighbour), to more complex techniques to model potential connectivity (e.g. graph theory) and the use of individual-based models to capture the process of dispersal (Calabrese and Fagan, 2004). We demonstrate that using a spatially explicit individual-based model provides advantages over other approaches, as it allows for greater detail in the dispersal process so that inter-patch dispersal rates become an outcome of context and behaviour-dependent dispersal decisions rather than deterministic connectivity metrics or a fixed distribution (O'Brien et al., 2006; Saura et al., 2011). Using RangeShifter, there were clear indications that the removal of roadside trees would lead to loss of connectivity in our case study landscapes. While roadside trees accounted for < 2% of land cover, removing 60% of these roadside trees (~1.2% of land cover) nevertheless decreased the number of successful dispersers by up to 17%. For some species, this could represent substantial degradation to ecological and/or genetic function. The impact of removing roadside trees on dispersal success was greatest where these trees represented a greater proportion of total canopy cover in the landscape. The effect of roadside tree removal on the mean proportional reduction in the total number of successful dispersers per year was roughly linear, i.e. for each successive 20% of trees removed; there was a consistent reduction relative to the baseline.

The relative proportion of successful dispersers decreased slightly with increasing carrying capacity and per-step mortality risk but increased slightly with increasing directional persistence and perceptual range, although in all cases there was less than a 10% change compared with the baseline landscape. At higher levels of tree removal, the modelled species suffering greater risk when crossing open terrain were

Table 3

Mean, minimum and maximum proportion of successful dispersers relative to the baseline landscape for each tree removal scenario on each square and the proportion of variance explained by the main model parameters LR (landscape replicate). PR (perceptual range). DP (directional persistence). K (carrying capacity). HM (matrix per step mortality risk). Variance values $s > 0.2$ are highlighted in bold.

| Square | % of trees removed | Mean | Min | Max | Proportion of variance explained by | | | | |
					LR	PR	DP	K	HM
TM18	20	0.979	0.964	0.991	**0.210**	0.023	0.063	0.090	0.128
TM18	40	0.959	0.934	0.979	**0.202**	0.013	0.090	**0.321**	0.088
TM18	60	0.941	0.913	0.967	0.030	0.015	0.151	**0.427**	0.064
TL96	20	0.979	0.953	0.994	0.166	0.048	0.107	**0.274**	0.038
TL96	40	0.959	0.926	0.984	0.081	0.084	0.147	0.344	0.096
TL96	60	0.941	0.896	0.973	0.086	0.077	0.157	0.302	0.148
TL54	20	0.979	0.965	0.992	0.124	0.025	0.123	0.185	0.197
TL54	40	0.959	0.933	0.981	0.077	0.042	0.162	**0.254**	**0.230**
TL54	60	0.938	0.900	0.967	0.052	0.037	0.182	**0.282**	**0.253**
TM17	20	0.979	0.954	0.999	0.163	0.051	0.111	**0.212**	0.068
TM17	40	0.959	0.925	0.989	0.045	0.038	0.158	**0.381**	0.064
TM17	60	0.940	0.901	0.977	0.040	0.028	0.139	**0.496**	0.019
TL74	20	0.982	0.959	1.003	0.141	0.024	0.083	**0.277**	0.017
TL74	40	0.967	0.936	0.996	0.048	0.026	0.110	**0.408**	0.052
TL74	60	0.952	0.909	0.984	0.063	0.023	0.084	**0.496**	0.032
TL90	20	0.974	0.940	1.018	0.178	0.015	0.001	0.045	0.068
TL90	40	0.944	0.897	0.983	0.102	0.033	0.011	**0.336**	0.062
TL90	60	0.916	0.832	0.962	**0.302**	0.029	0.009	**0.280**	0.025

likely to experience the greatest reduction in connectivity, whereas species with better sensory abilities and those that tended to move more directly through the landscape, regardless of tree availability, were to some extent able to compensate during dispersal. In a recent study of connectivity in European forests, using a network based approach with theoretical species, results similarly indicated that more mobile species would be better able to cope with changing spatial forest patterns and increasing forest cover increased connectivity overall (Saura et al., 2011).

The effect of roadside tree removal on patch isolation was more complex than its effect on overall disperser success. In most cases, roadside tree removal resulted in increased patch isolation; both

empirical and theoretical studies have similarly found that maintaining habitat between breeding patches reduces the risk of patch isolation and is also important for facilitating range expansion (Aben et al., 2016; Conlisk et al., 2014; Rossi et al., 2016; Roy and de Blois, 2008; Saura et al., 2014). However, in some simulations individual patches became better connected when roadside trees were removed. An explanation for this result is that some roadside trees made certain pairs of patches well connected, and thus their removal encouraged dispersers away from those patches and into patches that would have otherwise remained poorly connected. Effectively, in the baseline, some of the non-woodland trees acted to direct dispersers in particular directions and away from routes linking patches that are less attractive due to an absence of
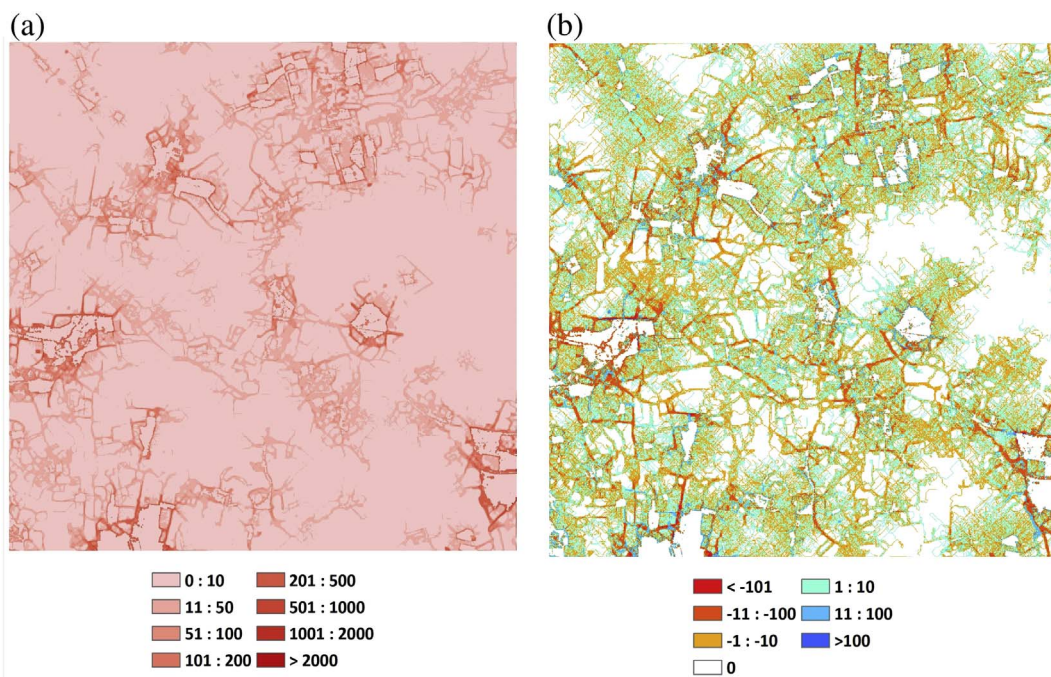

Fig. 4. Examples of (a) the number of times each cell of the baseline landscape of square TL96 was traversed by a dispersing individual during the course of 20 years and (b) the change in visit frequency for a single landscape replicate following removal of 60% of the roadside trees (red – fewer visits; blue – more visits). RangeShifter parameter values were as shown in Table 2, varied parameters being set to their intermediate values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
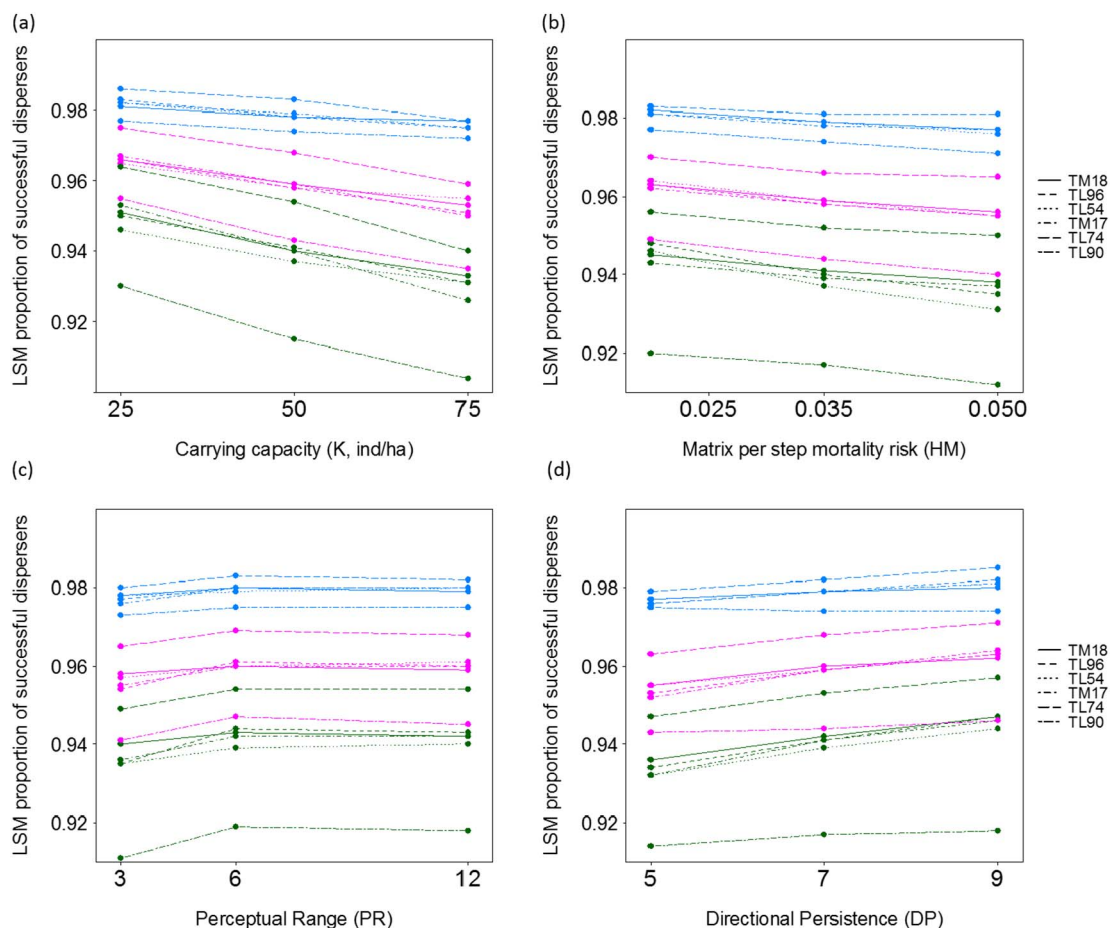
Fig. 5. Least squares mean proportion of successful dispersers illustrating the effect of carrying capacity (a), matrix per step mortality risk (b), SMS perceptual range (c), and SMS directional persistence (d) in the 20% (blue), 40%(pink) and 60%(green) removal scenarios for each square. For each factor of interest, results were averaged over the levels of the remaining factors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Mean, minimum and maximum increase in the number isolated patches relative to the baseline landscape and the proportion of variance explained by the main model parameters LR (Landscape Replicate), PR (perceptual range), DP (directional persistence), K (carrying capacity), HM (matrix per step mortality risk). Variance values > 0.2 are highlighted in bold.

					Proportion of variance explained by				
Square	% of trees removed	Mean	Min	Max	LR	PR	DP	K	HM
TM18	20	0.148	− 1.9	2.6	0.019	0.000	0.017	0.023	0.020
TM18	40	0.383	− 1.3	3.4	0.016	0.001	0.072	0.031	0.092
TM18	60	0.501	− 1.2	2.8	0.034	0.003	0.085	0.016	0.126
TL96	20	0.223	− 1.9	3.2	0.026	0.024	0.029	0.006	0.066
TL96	40	0.450	− 1.4	3.4	0.034	0.007	0.161	0.011	0.152
TL96	60	0.531	− 1.4	3.9	0.027	0.018	0.165	0.011	0.198
TL54	20	− 0.036	− 1.9	1.2	0.013	0.013	0.042	0.012	0.001
TL54	40	− 0.037	− 1.4	1.7	0.020	0.009	0.046	0.008	0.007
TL54	60	0.011	− 1.6	1.9	0.055	0.009	0.018	0.009	0.081
TM17	20	0.228	− 2.1	2.7	0.015	0.007	0.062	0.015	0.042
TM17	40	0.366	− 1.3	2.9	0.014	0.003	0.120	0.001	0.096
TM17	60	0.596	− 1.2	3.1	0.027	0.003	0.147	0.002	0.132
TL74	20	0.023	− 2.1	1.9	0.009	0.000	0.001	0.005	0.009
TL74	40	0.075	− 1.9	2.4	0.008	0.000	0.001	0.022	0.006
TL74	60	0.034	− 1.7	2.6	0.012	0.000	0.015	0.010	0.011
TL90	20	0.160	− 1.6	1.9	0.012	0.032	0.003	0.001	0.055
TL90	40	0.404	− 1.3	2.3	0.009	0.021	0.029	0.009	0.167
TL90	60	0.610	− 1.2	3.1	0.017	0.007	0.050	0.013	**0.256**

non-woodland trees on route. A similar dichotomous result arose in a modelling study of the European Lynx (*Lynx lynx*) (Kramer-Schadt et al., 2011). The introduction of stepping stones had a positive effect on lynx populations but in some cases could also distract dispersers from more suitable breeding habitat patches. Such contrasting potential outcomes indicate that conservation planning needs to consider trade-

offs that may arise when considering the functional connectivity of landscapes (Kramer-Schadt et al., 2011).

The squares used in the study all had similar proportions of trees. Furthermore, tree cover only accounted for < 16% of the landscapes, this being typical of many UK landscapes, and the proportion of road-side trees accounted for on average 17.2% of canopy cover. Our results
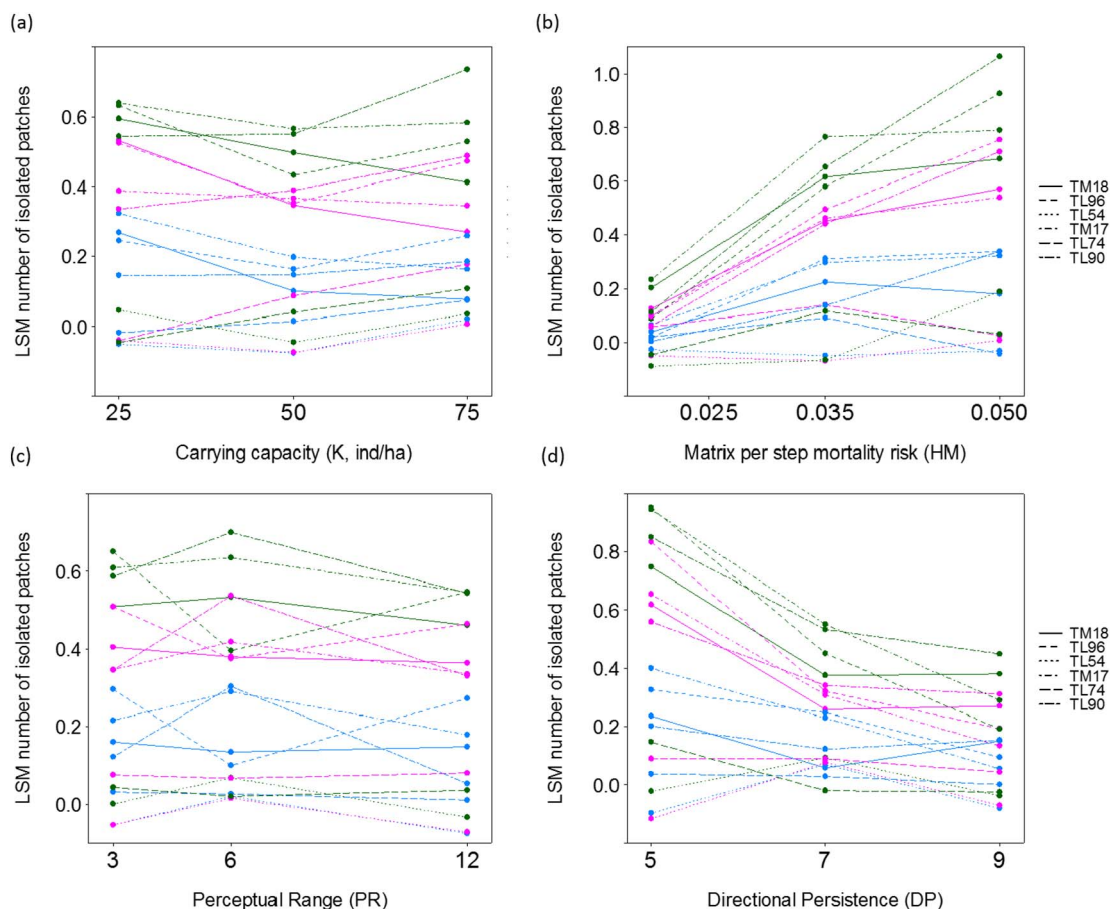
Fig. 6. Least squares mean change in the number of isolated patches illustrating the effect of carrying capacity (a), matrix per step mortality risk (b), SMS perceptual range (c), and SMS directional persistence (d) in the 20% (blue), 40%(pink) and 60%(green) removal scenarios for each square. For each factor of interest, results were averaged over the levels of the remaining factors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highlight that the loss of a small proportion of trees can have a substantial impact on connectivity, but on our case study landscapes the non-roadside matrix trees may have somewhat buffered the loss of roadside trees. In the worst case, for 60% tree removal in square TL90, the number of successful dispersers was reduced to 83% of its mean in the baseline landscape. TL90 had the lowest tree cover of all the squares, and a smaller proportion of woodland trees, whereas roadside trees accounted for a greater proportion of trees than in other squares. In the current study, we chose to investigate the targeted removal of trees close to infrastructure, and did not model the loss of matrix trees or woodland trees that may occur due to increasing natural mortality caused by disease outbreaks and/or climate change. Furthermore, while we model the loss of up to 60% of roadside trees, the true extent future road- and rail-side trees loss is uncertain and it could be greater. Thus, the combined loss of roadside, matrix and woodland trees due to the combined effect of felling and natural mortality may lead to greater losses in connectivity.

In this study, we made simplifying assumptions about the spatial patterns of tree removal; roadside trees were randomly removed. However, it may be that trees will be felled in spatially aggregated patches for a number of reasons. For example, individuals of the same species may tend to be clustered and thus, depending on disease epidemiology, clusters may need be felled if all become diseased. Furthermore, when a dying tree is identified along a roadside, it is economically more efficient to remove all potentially dangerous roadside trees in close proximity at the same time. In our study, between 3 and 30% of the variance in the proportion of successful dispersers was explained by landscape replicate, and therefore the location of tree removal was clearly important. An interesting extension of this study

would be to investigate explicitly the spatial pattern of tree removal. In particular, when tree loss is driven by tree disease, combining models of disease spread (Gilligan and Van Den Bosch, 2008; Meentemeyer et al., 2011; Potter et al., 2011) with models describing human decision making in terms of tree felling (Gullick et al., 2017) could predict realistic patterns of tree loss when estimating connectivity. Moreover, although our selected squares reflected a range of canopy coverage typical of an area of the South East of the UK, the scope of this initial limited study was such that inferences for individual UK counties or for the wider UK landscape cannot be drawn. Future work should randomly sample a greater number of locations from across counties of interest or indeed, across the UK, to draw county/country level conclusions. Nevertheless, results here demonstrate the utility of modelling approaches for addressing pressing landscape ecological questions.

We considered only the impact of tree loss on connectivity, but spatially explicit population models could also be used to investigate the impact of tree loss and the loss of linear woody features on the genetic health of populations. Indeed, Athayde et al. (2015) found that scattered trees held between 64 and 85% of the total functional and phylogenetic diversity in agricultural landscapes, and functional and phylogenetic diversity levels were higher in agricultural landscapes with scattered trees than expected for random assemblages of species. The use of models can also be extended to investigate mitigation options for tree disease. For example, Gibbons et al. (2008) used a model to explore management options to mitigate the decline of scattered trees in an agricultural landscape, identifying key variables that can be manipulated to reduce the impact. In terms of connectivity, modelling efforts investigating the costs/benefits of alternative management strategies, such as maintaining selected ecologically important trees to

maintain ecological connectivity, would be a worthy future step. There is clearly much scope for models to address key ecological and management questions related to tree loss, particularly if models can be parameterised to reflect local conditions.

In general, while the model here was parameterised to represent a range of dispersers, if none of the actual species present in the study area possesses any of the factor combinations leading to poor dispersal, then it is possible that there would be no decline in connectivity. Alternatively, if such combinations of factors are common in real species, then the decline may be much more severe than predicted. Ultimately, better dispersers may be less affected by tree loss, while highly sensitive species, suffering higher mortality risks when crossing hostile habitat, may fare poorly in landscapes without scattered trees (Prevedello et al., 2017). Virtual species explorations such as those presented here provide valuable general insights; however, for most studies, ours included, there remain insufficient data to parameterise models for multiple species of interest (Saura et al., 2011). Yet this modelling framework could yield more robust management recommendations, for maintaining connectivity, when combined with high quality field-based estimation of parameters and/or a trait space approach (Aben et al., 2016; Santini et al., 2016). Furthermore, by identifying factors that make species vulnerable to tree loss, this type of virtual study could be used as an early indicator of risk for species found to possess those traits. Increasing and maintaining landscape connectivity is widely recognised as an essential component of biodiversity conservation, preventing population declines and facilitating adaptation to climate change. TOWs are vital landscape components that maintain connectivity and their loss, not only in areas close to infrastructure but also in the wider landscape, threatens ecosystems. There is clearly a pressing need to combine models of realistic tree loss with real species data quantifying traits, to ensure that future conservation actions are based upon robust evidence to deliver real biodiversity benefits.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2017.10.010.

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