Evaluation of buffer-radius modelling approaches used in forest conservation and planning

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Summary

Spatial modelling approaches are increasingly being used to direct forest management and conservation planning at the landscape scale. A popular approach is the use of buffer-radius methods, which create buffers around distinct forest habitat patches to assess habitat connectivity within anthropogenic landscapes. However, the effectiveness and sensitivity of such methods have rarely been evaluated. In this study, Euclidean and least-cost buffer-radius approaches were used to predict functional ecological networks within the wooded landscape of the Isle of Wight (UK). To parameterize the models, a combination of empirical evidence and expert knowledge was used relating to the dispersal ability of a model species, the wood cricket (*Nemobius sylvestris* Bosc.). Three scenarios were developed to assess the influence of increasing the amount of spatial and species-specific input data on the model outcomes. This revealed that the level of habitat fragmentation for the model species is likely to be underestimated when few empirical data are available. Furthermore, the least-cost buffer approach outperformed simple Euclidean buffer in predicting presence and absence for the model species. Sensitivity analyses on model performance revealed high sensitivity of the models to variation in buffer distance (i.e. maximum dispersal distance) and permeability of common landscape features such as roads, watercourses, grassland and semi-natural habitat. This indicates that when data are lacking with which to parameterize buffer-radius models, the model outcomes need to be interpreted with caution. This study also showed that if sufficient empirical data are available, least-cost buffer approaches have the potential to be a valuable tool to assist forest managers in making informed decisions. However, least-cost approaches should always be used as an indicative rather than prescriptive management tool to support forest landscape conservation and planning.

Introduction

In many parts of the world, forested landscapes have undergone substantial changes as a result of anthropogenic activities such as agriculture and urban development (Forman, 1995; Dale *et al.*, 2000; Jongman and Pungetti, 2004; Lindenmayer and Fischer, 2006; Newton *et al.*, 2009a). This has resulted in an overall loss of forest cover and increased fragmentation of forest habitats within the landscape (e.g. Saunders *et al.*, 1991; Reed *et al.*, 1996; Newton, 2007). Forest habitat loss and fragmentation are widely recognized as principal causes of declines in biodiversity at many different geographical locations (Andrén, 1994; Fahrig, 2003; Driscoll and Weir, 2005; Niemelä *et al.*, 2007).

Many landscapes are now dominated by agricultural land with remnants of natural and semi-natural habitat embedded within them. In addition to the direct effects of area loss and isolation (MacArthur and Wilson, 1967), the degree of connectivity between such habitat fragments has a major influence on species persistence within these landscapes (Hanski and Gilpin, 1997; Bennett, 2003; Crooks and Sanjayan, 2006). Habitat connectivity, in terms of the ability of a species to move between distinct habitat patches in a landscape, is highly species specific (Lindenmayer and Fischer, 2006; Taylor *et al.*, 2006), and the degree of isolation between fragments is primarily influenced by the physical ability of individual species to disperse (Turchin, 1998). Furthermore, it is increasingly recognized that the characteristics of the matrix (i.e. non-natural habitat-like

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arable land) surrounding habitat fragments may have a strong influence on the degree of habitat connectivity and the responses of species to isolation (Lindenmayer and Franklin, 2002; Lindenmayer and Fischer, 2006; Taylor *et al.*, 2006). The resistance or permeability of the matrix may increase ecological isolation by reducing the probability of species movement between habitat patches, thereby influencing the species' sensitivity to fragmentation.

Creation of habitat networks provides a potential approach to combat the deleterious effects of habitat loss and fragmentation and has been implemented worldwide across a range of scales (Peterken, 2000, 2002; Bennett, 2003; Jongman and Pungetti, 2004; Bailey, 2007; Jones-Walters, 2007; Quine and Watts, 2009). For example, in the UK, financial support has been provided by the government to develop a program aimed at rejoining ancient woodland sites (Quine and Watts, 2009) towards creating forest habitat networks. The approach of creating habitat networks is based on the principle that increasing connectivity between habitat fragments within a landscape will facilitate movements and dispersal of organisms (Lindenmayer and Fischer, 2006; Boitani *et al.*, 2007). This is thought to benefit the persistence and survival of species, for example by facilitating genetic exchange and supporting the dynamics of metapopulations (Hanski and Gilpin, 1997; Crooks and Sanjayan, 2006; Driezen *et al.*, 2007). Across Europe, the importance of the creation of habitat networks to maintain and enhance biodiversity is now generally recognized in cross-sectoral policy initiatives (Jones-Walters, 2007), although validation of this approach is still limited (Bailey, 2007; Boitani *et al.*, 2007).

In order to aid the planning and development of forest habitat networks, a number of modelling approaches and tools have been developed. These tools are used to evaluate the degree of habitat connectivity, not only from a landscape/structural (i.e. human) perspective (e.g. Quine and Watts, 2009) but increasingly from a more functional (i.e. species-centred) point of view, accounting for matrix permeability (Crooks and Sanjayan, 2006; Driezen *et al.*, 2007). Such spatial modelling approaches are increasingly been used to inform the development of forest management and conservation plans at the landscape scale (Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Humphrey *et al.*, 2005; Fagan and Calabrese, 2006; Bailey, 2007; Watts *et al.*, 2007; Gillespie *et al.*, 2009; Humphrey *et al.*, 2009). Other approaches that account for species-specific habitat connectivity include the landscape ecological model LARCH (Landscape ecological Analysis and Rules for the Configuration of Habitat), which utilizes individual-based movement models (van Rooij *et al.*, 2003; Opdam *et al.*, 2006) and Conefor Sensinode (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007), which adopts a graph theory approach to connectivity.

A popular group of spatial models used to examine functional habitat connectivity within fragmented landscapes are buffer-radius models (Fagan and Calabrese, 2006). These combine spatial data describing landscape structure with species-specific data on dispersal (Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Fagan and Calabrese, 2006). A number of alternative buffer-radius approaches have been developed (Calabrese and Fagan, 2004) that incorporate Euclidean distances and functional distances, utilizing least-cost distance approaches (Adriaensen et al., 2003) to account for matrix permeability. Within the UK, the Forest Research Agency of the Forestry Commission has been developing and utilizing least-cost buffer-radius modelling approaches under the banner of Biological and Environmental Evaluation Tools for Landscape Ecology (BEETLE) (Watts *et al.*, 2005). This approach has been used to identify potential networks (Catchpole, 2006, 2007) and to assist forest and landscape managers to maintain and develop sustainable forest landscapes (Watts *et al.*, 2007, 2008).

Buffer-radius modelling approaches have been found to be sensitive to the buffer distance (Moilanen and Nieminen, 2002) and, in particular, to the permeability parameters used in least-cost approaches (Moilanen and Nieminen, 2002). This indicates that if specific species are targeted for habitat network analysis, the dispersal and permeability parameters need to be accurate in order to make sound predictions. However, these estimates are generally unavailable and/or difficult to obtain because of the amount of resources and time required to collect the species-specific information needed (Fagan and Calabrese, 2006). As a result, these parameters are often based on expert opinion alone (Beier *et al.*, 2009). Furthermore, the output of buffer-radius approaches is rarely tested for their accuracy in predicting functional habitat networks within real landscapes (Driezen *et al.*, 2007), and sensitivity analyses of these approaches have rarely been undertaken (Gillespie *et al.*, 2009; Humphrey *et al.*, 2009). However, testing the robustness of connectivity models is essential to evaluate the value and accuracy of the model outcomes (Beier *et al.*, 2008, 2009). As a consequence, the validity of simple buffer-radius models in conservation planning has been questioned (e.g. Moilanen and Nieminen, 2002; Calabrese and Fagan, 2004; Fagan and Calabrese, 2006) as their simplicity was found not to be adequate compensation for a lack of accuracy (Moilanen and Nieminen, 2002). Incorporating more species-specific dispersal information within buffer-radius models could potentially improve their performance and increase their value for supporting decision making (Calabrese and Fagan, 2004). There is therefore a need to evaluate different buffer-radius approaches informed by actual species data with respect to their level of accuracy for predicting functional habitat networks within real landscapes.

This paper provides a comparative analysis of buffer-radius modelling approaches used in forest conservation management to identify forest habitat networks in a fragmented landscape. This study used empirical data for a model species, wood cricket (*Nemobius sylvestris*), which has been the subject of detailed field-based research. Previous empirical studies on this insect has focused on its (1) distribution and occurrence at the landscape scale, (2) habitat requirements and (3) dispersal ability through different habitat and landscape features (Brouwers and Newton, 2009a, b; Brouwers *et al.*, 2009; Brouwers and Newton, in press). This research indicated that wood cricket is an 'edge specialist', generally found on the margins of forest fragments, and displaying limited movements into surrounding landscape features (i.e. it is matrix sensitive). In comparison with other forest-related insects, the species is considered to be a poor-to-moderate disperser (Brouwers and Newton, 2009c; Brouwers and Newton, in press), able to disperse up to 60 m through forest habitat during the entire life cycle (Morvan *et al.*, 1978). Movement through non-forest vegetation, such as grasslands, was found to be restricted. Wood cricket was able to cross small watercourses but generally avoided crossing linear landscape features such as roads, which therefore represent possible dispersal barriers (Morvan and Campan, 1976; N.C. Brouwers, personal observation). These empirical data combined with field observations of the species were used to parameterize and build alternative buffer-radius network models and to compare the model outcomes.

This study aims to address the following objectives: (1) to investigate the influence of data availability on the model outcomes; (2) to compare the alternative network models, informed by empirical data, in predicting patch occupancy for wood cricket on the Isle of Wight (UK) and (3) to conduct a sensitivity analysis of the various parameters used in the network models.

Materials and methods

Study area

The Isle of Wight (UK) was used as the basis for this study as it represents a highly fragmented landscape, typical for much of lowland England, with forest fragments situated within a predominantly agricultural matrix. The total surface area of the Isle of Wight is ~380 km^2, with forest covering ~50 km^2 or 13 per cent of the island area. Of the total forest area, 32 per cent is classified as forest still retaining ancient characteristics, of which 17 per cent is classified as ancient semi-natural woodland (i.e. pre-1600 AD native broadleaf woodland) and the remaining 15 per cent are planted ancient woodland sites (i.e. pre-1600 AD woodland that was converted/planted with non-native, mainly coniferous, tree species). The remaining forest areas are of more recent origin (i.e. post-1600 AD native woodlands) and/or are plantations (Smith and Gilbert, 2003). On the Isle of Wight, several forest restoration schemes have been carried out, including targeted landscape-scale habitat creation schemes aiming to enlarge and join ancient woodlands (Quine and Watts, 2009).

Survey data

In 2005, a landscape-scale survey was undertaken on wood cricket targeting individual forest fragments on the Isle of Wight. A total of 147 individual fragments were surveyed of which 32 were occupied by wood cricket populations, while the remaining 115 fragments were unoccupied at that particular time (Brouwers and Newton, 2009b). Fragment boundaries were defined either by neighbouring agricultural land (grassland or arable) or by distinct anthropogenic/natural landscape features (urban fringes, tarmac roads, railway lines, rivers and watercourses) (Brouwers and Newton, 2009b). These data combined with field data and observations gathered in 2006 and 2007 on the habitat preferences (Brouwers and Newton, 2009a) and dispersal ability of wood cricket (Brouwers and Newton, 2010; Brouwers and Newton, in press; N.C. Brouwers, personal observation) were used to run and evaluate the alternative buffer-radius modelling approaches.

Modelling

In this study, three scenarios were developed to generate potential habitat networks for wood cricket on the Isle of Wight using a Euclidean and a least-cost buffer-radius approach. These three scenarios utilized increasing amounts of empirical data in order to investigate the influence of data availability on the model outcomes. The first scenario required the least amount of input data and used a simple Euclidean distance buffer approach, based on recorded maximum dispersal distance (Scenario 1). This approach creates an equidistant buffer around each forest fragment following the contours of its boundary. The areas that overlap are merged, each representing a potential habitat network where movement of the target species is believed to occur. The other two scenarios that were developed utilized least-cost distance approaches, which require, besides the maximum dispersal distance, additional data on the dispersal ability of the species through the different landscape features. This approach uses a buffer based on the maximum dispersal distance, weighted by the underlying permeability of the surrounding land cover. In this case, permeable land cover features will extend or stretch the buffer, whereas more hostile landscape features will contract or reduce the buffer extent. As with the previous method, areas that overlap are merged and treated as potential habitat networks. Scenarios 2 and 3 differed by the detail of the surrounding land cover utilized, as detailed below.

The network analysis was conducted by a custom-made least-cost network extension within ArcGIS, developed by Forest Research under the banner of BEETLE (Watts *et al.*, 2005). This tool maps the potential network for a species within a landscape based on its maximum dispersal distance and the predicted ability of a species to move through different landscape features (Watts *et al.*, 2005).

Four digitized land cover maps were used to generate the habitat networks for the three different scenarios. 'Map 1' represented all forest habitats on the Isle of Wight and was derived from the National Inventory of Woodland and Trees (Smith and Gilbert, 2003). 'Map 2' was compiled using data included in Map 1 and Ordnance Survey digital data (OS MasterMap, Ordnance Survey, Southampton, UK), excluding roads, inland water bodies and watercourses intersecting the forest habitat. 'Map 3' combined the forests included in Map 1 with Land Cover Map 2000 (LCM2000, CEH, Wallingford, UK) digital data for the Isle of Wight. The LCM2000 dataset defines all the different land cover types on the Isle of Wight based on a computer classification of satellite scenes, obtained mainly from Landsat satellites with a resolution of 25 × 25 m (CEH Monks Wood, Huntingdon, England). 'Map 3' therefore represented all forest habitats and all other land cover features represented in the LCM2000 dataset, including semi-natural landscape features, grassland, arable, estuaries and urban developed land. 'Map 4' combined the edited forests included in Map 2 with LCM2000(CEH) and the OS MasterMap data for roads, small inland water bodies and watercourses, respectively. Map 4 therefore included all landscape features represented in Map 3 but also included the separate features for roads, inland water bodies and watercourses. All maps were compiled using general editing features available in ArcGIS (9.1) (Table 1).

Based on the maximum dispersal distance observed for wood crickets (Morvan *et al.*, 1978; N.C. Brouwers, personal observation), for all three scenarios a buffer distance (i.e. maximum dispersal distance) of 60 m was used (Table 2). For Scenario 1, an equidistant buffer was created around the forest fragments included in Map 1. For Scenarios 2 and 3, the permeability of each feature was calculated by dividing the buffer distance by the assigned cost value (see Table 2). These cost values were based on empirical data and field observations of wood cricket gathered over the course of 3 years of intensive study (Brouwers and Newton, 2009a, b; Brouwers *et al.*, 2009; Brouwers and Newton, in press). Scenario 2 calculated forest habitat networks within the landscape without the influence of roads, inland water bodies and watercourses combining Map 1 and Map 3 (Table 1). Scenario 3 included the influence of roads, inland water bodies and watercourses combining Map 2 and Map 4 to generate the potential forest habitat networks (Table 1). Additionally, the model built in Scenario 3 included all the combined knowledge on the dispersal ability of the study species and can therefore be considered as the most informed model in terms of predicting functional forest habitat networks for wood cricket. For each scenario, after the buffers were created around each forest fragment, all forests overlapping or touching each other were defined as an individual network. All predicted habitat networks that were created with these scenarios therefore contained one or more distinct forest fragments that are currently present within the landscape of the Isle of Wight.

Model comparison

Differences between the model scenarios were based on variation of data used to run and build the models. The amount of data that were used increased with each successive model scenario (i.e. Scenarios 1–3, respectively). To investigate the influence of data availability using the three model scenarios (objective 1), the differences between the model outcomes were evaluated with the following comparative analyses.

Table 1: Summary of the landscape features that were included in the maps that were used for the different scenarios

	Scenario 1	Scenario 2	Scenario 3
Maps used	Map 1	Maps 1 and 3	Maps 2 and 4
Landscape features	Included	Included	Included
Forest	Yes	Yes	Yes
Arable and urban developed land	No	Yes	Yes
Semi-natural landscape features and grassland	No	Yes	Yes
Estuaries	No	Yes	Yes
Roads, inland water bodies and streams	No	No	Yes

Table 2: Summary of the input values used for the individual scenarios

	Scenario 1		Scenario 2		Scenario 3	
Buffer distance	60		60		60	
Landscape feature	Cost	Perm.	Cost	Perm.	Cost	Perm.
Forest	1	60	1	60	1	60
Arable and urban developed land			30*	2	30*	2
Semi-natural landscape features and grassland			2*	30	2*	30
Estuaries			60*	1	60*	1
Roads, inland water bodies and streams					60*	1

Buffer distance and permeability are in meters. Perm.: permeability = buffer distance/cost. Cost values indicated with an asterisk were primarily based on field observations.

Analysis one

To test for differences in the total number of networks that were generated for all the forest fragments on the Isle of Wight, chi-square 'goodness of fit' tests were performed. Between each scenario, the total number of networks that were generated was tested against expected values of equal size.

Analysis two

To test if the surface area of the networks that were generated differed between the scenarios, individual Mann–Whitney *U* tests were performed to test for differences in the median network size between each scenario.

Analysis three

To reveal if differences in the scenarios were shown for networks with known presence/absence for wood crickets, differences between the outcomes of the scenarios were further tested using a subsample of the forest fragments that were surveyed in 2005 ($n = 147$). For these tests, the networks that included a surveyed forest were included in the analyses. Differences in the number of surveyed networks between the scenarios were tested against expected values of equal size using chi-square 'goodness of fit' tests.

Analysis four

To compare the alternative scenarios in predicting patch occupancy for wood cricket on the Isle of Wight (UK) (objective 2), only networks including occupied forests were considered. In this case, the number of unoccupied forests included in the occupied networks was compared and tested against expected values of equal size using chi-square 'goodness of fit' tests.

Analysis five

For each scenario, the network area of occupied and unoccupied networks was compared using Mann–Whitney *U* tests. This test was performed to confirm earlier findings on the positive effect of patch and network size on species and wood cricket presence (MacArthur and Wilson, 1967; Brouwers and Newton, 2009b).

Sensitivity analyses

To test how sensitive the models were to variations in the input variables, a series of sensitivity analyses were conducted (objective 3).

Analysis six

First, to compare the influence of the buffer distance (i.e. dispersal distance), simulations applying distances in the range of 5–500 m were used to generate networks for the three different scenarios. The differences between the scenarios were compared by plotting the number of networks that were generated against buffer distance.

Analysis seven

Scenario 3 incorporates the highest amount of empirical data related to the dispersal ability of the study species (see Materials and Methods, Modelling) and can therefore be considered likely to be the most accurate in terms of predicting functional forest habitat networks. Where a certain amount of expert knowledge was used to assign the cost values to the different landscape features that were incorporated in the maps to generate the networks, a further series of sensitivity analyses were conducted for Scenario 3. For these analyses, the cost values that were primarily based on field observations were varied for the four main groups of non-forest habitat (see Tables 2 and 3). For all these series, the total number of networks generated was compared with the original number generated under Scenario 3 and tested against expected values of equal size using chi-square 'goodness of fit' tests. All statistical tests mentioned in the analyses were performed using SPSS 14.0 for Windows (SPSS Inc., Chicago, IL).

Results

Model comparison

Based on the variation of input data used to run and build the model scenarios, the following differences were found when comparing the model outcomes (objective 1). A larger number of networks were generated with consecutive scenarios (1–3) (Figures 1 and 2). Where the Euclidean buffer-radius approach (Scenario 1) generated one network, the least-cost buffer-radius Scenarios 2 and 3 generated 5 and 10 networks for the same area, respectively (see Figure 2), indicating an increased degree of forest fragmentation.

Analysis one revealed that for each successive scenario, a higher number of networks were generated (Table 4), indicating a higher level of predicted fragmentation of forest habitat between consecutive scenarios (i.e. with increasing

Table 3: Input values used for the sensitivity analyses for the least-cost buffer Scenario 3

	Series 1	Series 2	Series 3
Landscape feature	Cost	Cost	Cost
Forest	1	1	1
Arable and urban developed land	30	30	3, 6, 30
Semi-natural landscape features and grassland	2	1, 2, 6	2
Estuaries	30, 40, 60, 120, 600	60	60
Roads, inland water bodies and streams	30, 40, 60, 120, 600	60	60

The buffer distance used was 60 m.

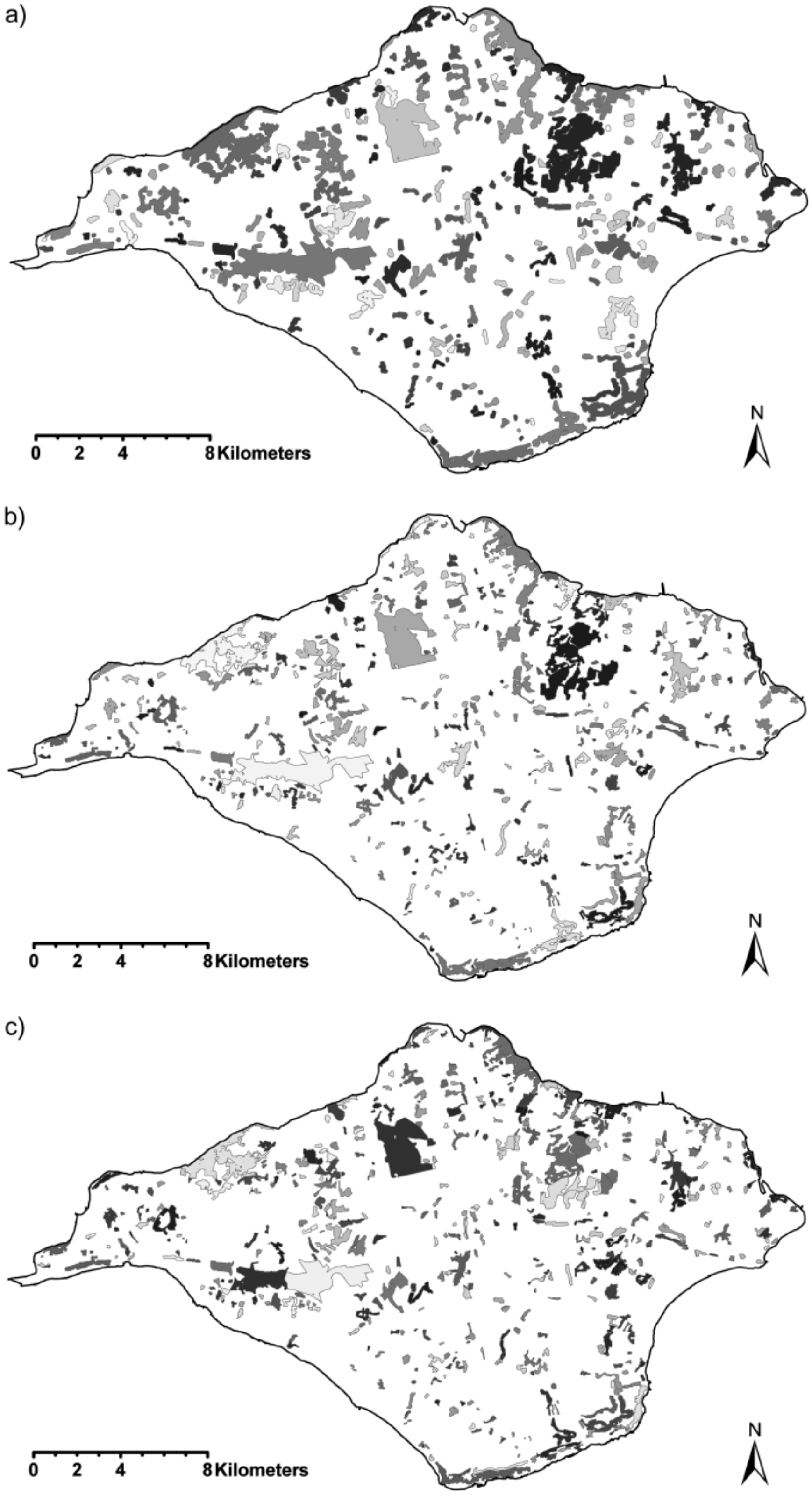

Figure 1. The predicted forest habitat networks on the Isle of Wight generated by the Euclidean buffer-radius approach (a) Scenario 1 ($n = 284$); and the least-cost buffer-radius approach (b) Scenario 2 ($n = 391$) and (c) Scenario 3 ($n = 532$). The patches with different shades of grey represent the individual forest networks.

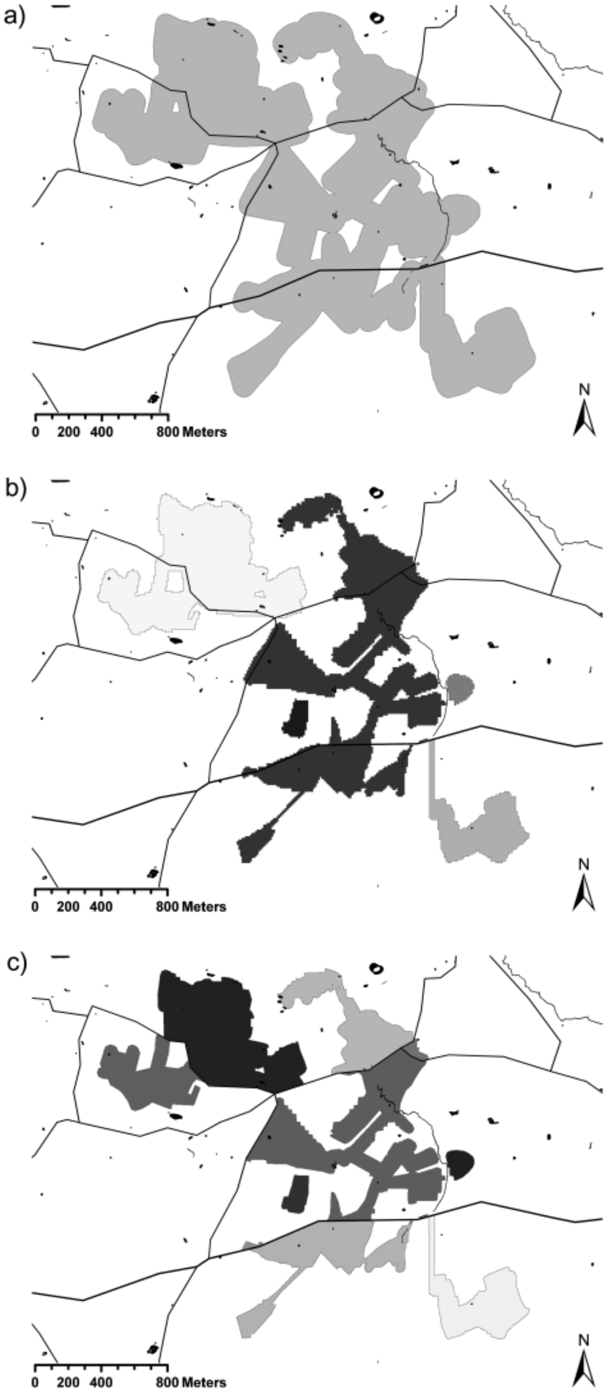

Figure 2. Detail showing the break-up of a forest network when using an increasing amount of input data (Scenarios 1–3, (a)–(c), respectively). The different shades of grey indicate individual networks. Lines represent roads and small watercourses, and dark dots indicate inland water bodies.

detail of digital data and knowledge of the dispersal ability of the model species used). Furthermore, analysis two revealed that the total network area decreased with each consecutive scenario (see Figure 3), indicating a decreasing amount of habitat availability within individual habitat networks between consecutive scenarios. Further results of the analyses comparing the model outputs of the three different scenarios are presented in Table 4. When considering the subsample of networks including a surveyed forest, analysis three showed that each successive scenario generated a higher total number of networks (Table 4). For all unoccupied and occupied networks, each successive scenario also generated a higher total number (Table 4). Together these results indicated that the amount of detailed species data that were used in the model scenarios had a significant influence on the outcome of the simulations.

To compare the alternative network models further, tests were performed to examine their ability to predict patch occupancy for wood cricket on the Isle of Wight (UK) (objective 2). When specifically considering the subsample of occupied networks, analysis four revealed that the number of surveyed unoccupied forests decreased with each successive scenario (with $n = 32$ for surveyed occupied forests) (Table 4). The number of surveyed unoccupied forests included in the occupied networks was found to be significantly higher in Scenarios 1 compared with Scenarios 2 and 3, but there was no difference between Scenarios 2 and 3 (Table 4). Furthermore, percentage of patch occupancy within the predicted occupied networks increased with the successive scenarios used (Table 4). This indicates that for the model species, the least-cost buffer approach outperforms the Euclidean buffer approach in predicting patch occupancy within fragmented landscapes.

Additionally, analysis five showed that for each scenario, occupied networks were found to be larger than unoccupied networks (Mann–Whitney U test: Scenario 1, median occupied = 125.07 ha, median unoccupied = 14.81 ha, $U = 78.000$, $z = -3.094$, $P = 0.002$; Scenario 2, median occupied = 51.45 ha, median unoccupied = 7.05 ha, $U = 189.000$, $z = -3.523$, $P < 0.001$; Scenario 3, median occupied = 25.60 ha, median unoccupied = 8.16 ha, $U = 479.000$, $z = -2.411$, $P = 0.016$), confirming previous findings (Brouwers and Newton, 2009b). This indicates that wood crickets are most likely to be found in areas within the landscape where forest cover is high (see relatively large networks; Figure 1).

Altogether, these analyses indicate a significant improvement in the performance of buffer-radius models when more detailed information on the dispersal ability of the model species and supporting data on environmental data are used.

Sensitivity analyses

To address objective 3, a series of sensitivity analyses of the various parameters used in the network models were performed. Analysis six revealed that the number of networks generated by Scenarios 1–3 decreased with increasing buffer distance (Figure 4). Overall, the Euclidean buffer approach (Scenario 1) showed the highest sensitivity for changes in the buffer distance used. The number of individual networks showed a rapid exponential decrease with increasing buffer distance (Figure 4). Compared with the least-cost buffer approach (Scenarios 2 and 3), this indicates

Table 4: Summary of the differences between the numbers of forest habitat networks generated by the different scenarios used in this study

	Scenario 1	Scenario 2	Scenario 3
Number of networks for all forest fragments	284**	391**	532**
Number of networks for all surveyed fragments	43*	69*	97*
All unoccupied networks	30*	52*	75*
All occupied networks	13	17	22
Number of occupied fragments included	32	32	32
Number of unoccupied fragments included	59*	36*	24
Percentage of occupied fragments included	35	47	57

$^*P < 0.05$; $^{**}P < 0.001$, based on chi-square test of number of networks between consecutive scenarios.

that small inaccuracies in estimating dispersal distances for a species can result in a significant underestimation of the number of functional networks and an overestimation of the level of connectivity for forest habitat when using a Euclidean buffer approach. When including more detail in the digital data for the least-cost approach (Scenarios 2 and 3), by including linear features (i.e. roads and watercourses) in Scenario 3, the sensitivity for buffer distance was higher compared with Scenario 2 at low values but comparable at higher values (Figure 4). This indicates that when including more detail, such as small linear features functioning as dispersal barriers, the accuracy of the estimated dispersal distance becomes increasingly important to model outcomes.

To test the sensitivity of the most detailed and realistic model scenario (Scenario 3) that was used in this study, the influence of the permeability of the three main groups of non-forest landscape features was tested by varying the cost values for these groups (see Materials and Methods, Analysis seven). In sensitivity Series 1, decreasing the permeability of estuaries, roads and inland water bodies and watercourses from 1 m (cost 60) to 0.1 m (cost 600) did not change the total number of networks that was generated ($n = 532$; Table 5). Increasing the permeability of these features from 1 to 1.5 m (cost 40) significantly decreased the number of networks (Table 5). These results indicate a high sensitivity of the least-cost method when slightly decreasing the cost value (i.e. slightly increasing the permeability) of narrow linear landscape features. Furthermore, excluding minor roads as landscape features within the analysis revealed that significantly fewer networks were generated than when minor roads were included (chi-square: $n_{\text{incl minor}} = 532$, $n_{\text{excl minor}} = 457$, $\chi^2 = 5.688$, df = 1, $P = 0.017$; Table 5). This indicates that including the influence of minor roads had a large effect on the outcome of Scenario 3. For sensitivity Series 2, increasing the permeability of the semi-natural landscape features and grassland from 30 m (cost 2) to 60 m (cost 1) decreased the number of networks significantly (Table 5). Decreasing the permeability of these features from 30 m (cost 2) to 10 m (cost 6) did not significantly increase the number of networks (Table 5). Both results indicate a moderate effect of these features on the outcome of Scenario 3. For sensitivity Series 3, increasing the permeability of arable and urban developed land from 10 m (cost 6) to 30 m (cost 2) did not significantly decrease the number of networks generated (Table 5). This indicates a minor effect of these features on the outcome of Scenario 3.

Together these sensitivity analyses indicate that the empirical data that are used for simulations with buffer-radius approaches need to be accurate to prevent significant over- or underestimations of the predicted level of connectivity/fragmentation in forested landscapes.

Discussion

The study presented here demonstrated that the amount of input data used had a major influence on the degree of accuracy that was achieved in predicting functional habitat networks within forested landscapes. Accurate parameterization of buffer-radius models can be very demanding in terms of the amount of resources and time required to collect the species-specific information that is needed (Fagan and Calabrese, 2006). Typically, there is a lack of detailed information available on species-specific dispersal, and for this reason, simple buffer-radius approaches are often favoured over more data intensive models (Calabrese and Fagan, 2004; Fagan and Calabrese, 2006). This often results in simple measures and modelling approaches being used to make 'informed' decisions in landscape conservation management and planning (Calabrese and Fagan, 2004). Simplicity should, however, not be favoured over accuracy (Moilanen and Nieminen, 2002) as inaccurate model predictions could have major implications for planning and decision making. Our study showed that the amount and accuracy of input data significantly influenced the outcomes of buffer-radius modelling approaches and that least-cost buffer outperformed the simple Euclidean buffer approach in predicting functional forest habitat networks for the model species in the forested landscape on the Isle of Wight. Our study further highlights the risk of underestimating the level of forest fragmentation when the simplicity of the buffer-radius approach is favoured over accuracy. This indicates that the choice of the buffer-radius model and the amount of input data used will have considerable implications for the level of accuracy that is achieved when making decisions in terms of forest habitat management.

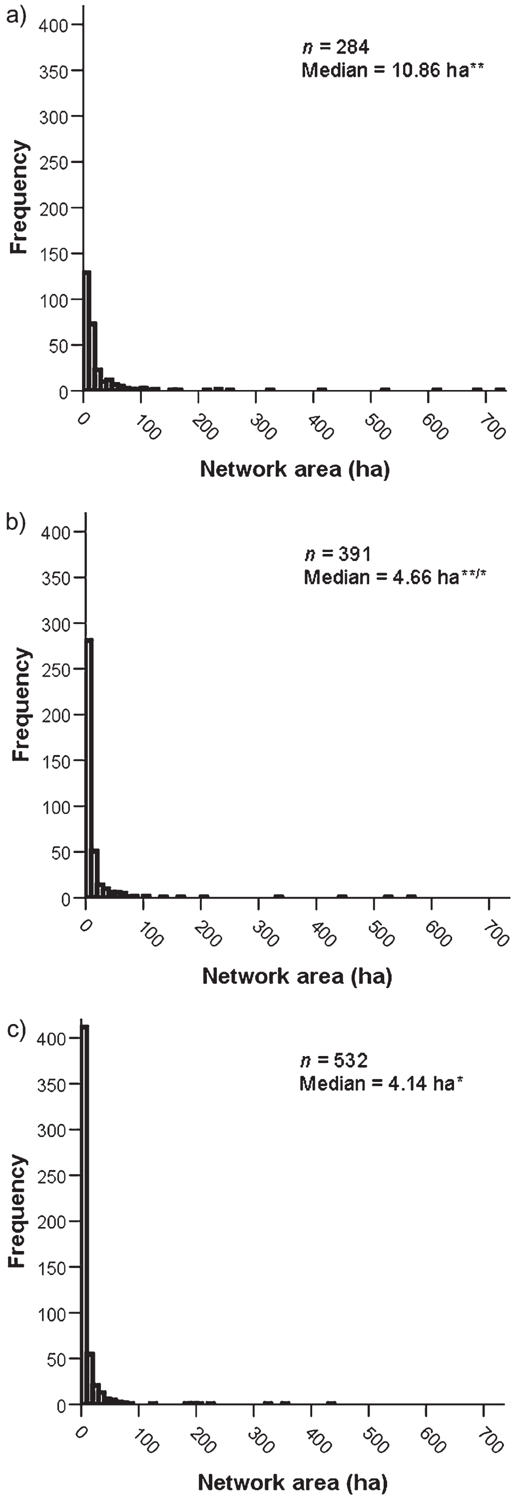

Figure 3. Frequency table for the predicted forest habitat networks generated by Scenarios 1, 2 and 3 ((a), (b) and (c), respectively) grouped by network surface area. Graphs show an increase in number of small networks, a decrease in number of large networks, and an overall decrease in the size of the networks when increasing the amount of input data. $*P < 0.05$; $**P < 0.001$, based on Mann–Whitney *U* test of median network area between consecutive approaches.

Forest habitat within landscapes is often fragmented, and forest fragments are often separated from each other by different landscape features (e.g. Quine and Watts, 2009). The surrounding matrix has been found to have a considerable impact on the dispersal of species when moving between habitat fragments (Forman, 1995; Turner *et al.*, 2001). This was also found for the model species used in this study. The Euclidean buffer-radius approach (Scenario 1) ignores the surrounding matrix habitat completely when simulating habitat networks for species. However, the least-cost approach does incorporate the species response to the matrix (Watts *et al.*, 2005). Intuitively, the Euclidean approach can therefore be considered as a poorer predictor of functional habitat networks than the least-cost buffer-radius modelling approach that was used here (Scenarios 2 and 3). Our study showed that least-cost buffer outperformed simple Euclidean buffer in predicting presence and absence for the model species, indicating the higher level of predictive power of least-cost buffer-radius approaches. This supports earlier indications of poorer performance of simple connectivity measures compared with more complex measures that found least-cost distance to be a better predictor for patch occupancy than Euclidean distance (Moilanen and Nieminen, 2002; Chardon *et al.*, 2003). This emphasizes the importance of incorporating the matrix habitat in connectivity models, achieving a higher level of predictive accuracy. Adopting least-cost modelling approaches should therefore become the new standard to assist in landscape conservation and planning.

Some evidence is available that landscape or structural connectivity increases when forested areas are specifically targeted in conservation initiatives that focus on increasing the degree of habitat connectivity (Quine and Watts,

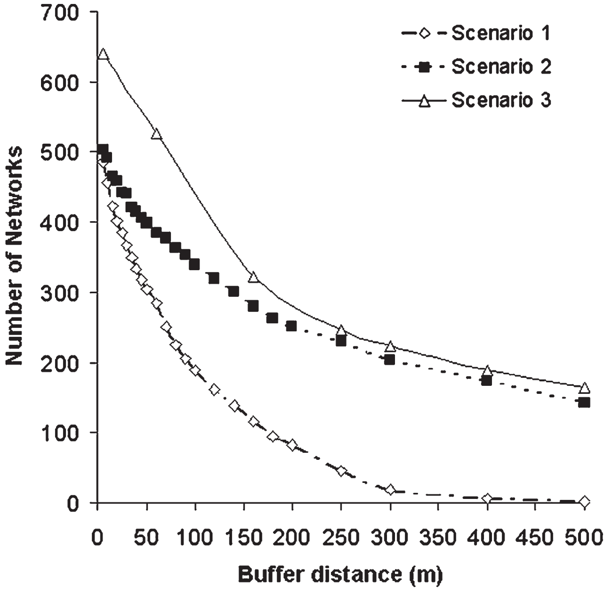

Figure 4. The number of predicted forest habitat networks generated by Scenarios 1–3 with increasing buffer distance (in metres).

Table 5: Results of the individual sensitivity analyses for Scenario 3.

Series 1		Series 2		Series 3	
Cost	Networks	Cost	Networks	Cost	Networks
30	432	1	462*	2	512
40	433*	2	532*	3	519
60 (excluding minor roads)	457*	6	595	6	532
60	532*				
120	532				
600	532				

Series 1 varied the cost values for estuaries, roads, inland water bodies and watercourses. Series 2 varied the cost values for semi-natural landscape features and grassland. Series 3 varied the cost values for arable and urban developed land. Networks indicate the number of forest habitat networks generated with each model run.

*$P < 0.05$, based on chi-square test of number of networks between consecutive cost values.

2009). However, landscape/structural connectivity is measured from a human perspective (Lindenmayer and Fischer, 2006) and does not measure the actual or functional habitat connectivity for species living in the landscape (Crooks and Sanjayan, 2006; Fagan and Calabrese, 2006). Furthermore, whether targeted conservation initiatives, like creating habitat networks, are benefiting species living in forest habitat remains largely untested (Bailey, 2007; Boitani *et al.*, 2007). The difficulties of measuring the effectiveness of such initiatives for specialized forest-dwelling species mainly lies in the fact that newly created habitat corridors that connect existing habitat fragments need time to develop, before they offer functional connectivity. In the case of forest habitat, meeting the specific habitat requirements of specialized species can take several decades of forest development (Beier *et al.*, 2008). In the UK, forests continue to be the focus of ongoing conservation management involving habitat restoration and expansion (Forestry Commission, 2006). The structural connectivity between habitat networks for forest invertebrates similar to wood crickets was found to have increased during a recent targeted forest restoration scheme on the Isle of Wight (Brouwers *et al.*, 2009; Quine and Watts, 2009). For wood cricket itself, the restoration scheme was successful in increasing structural connectivity in three of four areas where wood cricket was known to be present (Brouwers *et al.*, 2009). However, long-term monitoring of species migration and dispersal will be a key to evaluate the actual effectiveness of these schemes in terms of increasing functional habitat connectivity for forest species.

Sensitivity analyses of forest modelling approaches are needed to determine how useful such approaches are for stakeholders involved in conservation management and planning, particularly when available input data are mainly based on expert opinion, as is often the case (Beier *et al.*, 2008, 2009; He, 2008; He *et al.*, 2008; Humphrey *et al.*, 2009). In this study, using buffer-radius models, all scenarios and both approaches were found to be highly sensitive to the buffer distance that was used. This buffer distance was directly related to the maximum dispersal distance observed for the target species of interest. However, for most species accurate estimates for maximum dispersal distance are lacking and are difficult to obtain (Turchin, 1998; Ranius, 2006). These are therefore often necessarily estimated using expert opinion instead of empirical evidence (e.g. Humphrey *et al.*, 2009). However, if dispersal estimates are inaccurate, this can have considerable consequences for the model predictions of buffer-radius approaches, as shown in this study. Additionally, Humphrey *et al.* (2009) specifically highlight the need for sensitivity analyses of the cost values used for the matrix features surrounding forest habitat fragments in least-cost buffer-radius modelling approaches. A sensitivity study on a least-cost model used for corridor design revealed that the model predictions informed by expert opinion were generally robust to variations in the cost values used (Beier *et al.*, 2009). However, our study showed that small variations in the cost values and exclusion of certain anthropogenic features such as small roads had a significant impact on the number of functional forest networks that were predicted. The study of Beier *et al.* (2009) examined seven relatively mobile mammal species and one bird species, whereas our study considered a relatively immobile (i.e. small flightless) invertebrate species, which may explain the difference in results obtained. Additionally, variation in the accuracy of the digitized remote-sensed land cover datasets that were used could also have been influential (Driezen *et al.*, 2007; Gillespie *et al.*, 2009; Newton *et al.*, 2009b). Such an effect was shown in a case study measuring habitat connectivity using three different remote-sensed datasets for woodland (Gillespie *et al.*, 2009), which found considerable differences between the model outcomes. Our sensitivity analyses indicate that inaccuracies in the input data can have a considerable impact on the predictions of buffer-radius models. This highlights the fact that output maps generated with buffer-radius models should be interpreted with caution, particularly when input values are used based on expert knowledge alone.

It is increasingly being recognized that conservation initiatives should adopt a community- or ecosystem-based approach rather than examine single target species (e.g. Vos *et al.*, 2001; Fagan and Calabrese, 2006; Beier *et al.*, 2008). Some of the approaches that have been explored in this context are the use of umbrella species (Fagan and Calabrese, 2006; Beier *et al.*, 2009) or the focal species approach (Eycott *et al.*, 2007; Beier *et al.*, 2008, 2009;

Humphrey *et al.*, 2009). These approaches are aimed at encapsulating the characteristics of a broad range of species linked with a certain habitat. The dispersal values used are assumed to be representative for a range of species (Eycott *et al.*, 2007); however, the validity of this approach remains largely untested. In this study, dispersal characteristics of wood crickets were used to perform the modelling simulations. Wood crickets were found to display similar dispersal rates to a range of other relatively specialized forest species, representing a large group of flightless ground-dwelling insects that spend most of their life cycle in forest habitat (e.g. carabid beetles) (Brouwers and Newton, 2009c; Brouwers and Newton, in press). This suggests that the most informed and realistic model (Scenario 3) that was developed in this study can be used as a tool for predicting functional forest habitat networks within the landscape and used for guidance in directing conservation initiatives for this type of species.

Based on empirical evidence and expert knowledge of the model species, the most realistic scenario used in this study was the least-cost buffer-radius model including the influence of roads and watercourses (Scenario 3). With this scenario, patch occupancy of the species within occupied networks was accurately predicted for 57 per cent of the forest fragments that were included. In a metapopulation study, using ecological scaled landscape indices within a metapopulation model, Vos *et al.* (2001) found that patch occupancy was a good indicator of metapopulation viability. Using empirical data for a range of species, including two Orthoptera species, Vos *et al.* (2001) found a metapopulation viability threshold at 50 per cent patch occupancy within the landscape. The least-cost model (Scenario 3) therefore suggests that for wood cricket, viable metapopulation structures exist within the predicted occupied habitat networks. This conclusion would not have been reached with the less detailed alternative models that were developed (i.e. Scenarios 1 and 2). Compared with these models, this indicates the greater ability of the detailed model (Scenario 3) to indicate more precisely the areas where functional metapopulation communities are likely to occur in the wider landscape for wood cricket and similar species, making it more useful for forest managers and practitioners.

The overall success of forest conservation lies in adopting a multi-scale and multi-management strategic approach (Lindenmayer and Franklin, 2002). This research showed that for making informed decisions, least-cost buffer approaches could potentially be a valuable tool to assist and support forest and landscape conservation management and planning. It also showed that collection of field data is highly necessary to generate valuable output and for the validation of these kind of models. However, where the availability of these data (i.e. species-specific as well as land cover data) is generally limited and the quality often poor, least-cost modelling approaches should be used with caution. Therefore, least-cost buffer-radius approaches should be used as an indicative rather than prescriptive tool within the existing management toolset. Further modelling efforts should focus on incorporating real data of multiple species taxa to improve their overall usefulness in assisting and supporting landscape conservation and planning.

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Conflict of interest statement

None declared.

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