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Research paper

The incidence function model as a tool for landscape-scale ecological impact assessments

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ABSTRACT

Landscape-scale approaches to assessing the impact of land-use change on species' persistence are necessary because species depend on processes acting at varying scales, yet existing approaches to ecological impact assessment tend only to be site-based. A further major criticism of current ecological impact assessments is that they tend to be qualitative. Here we develop methods that apply the Incidence Function Model (IFM) in real urban planning contexts, by generating repeatable and comparable quantitative measures of ecological impacts. To demonstrate the methods for a case study (Nottingham, UK), we estimated landscape-scale measures of species' persistence that indicate metapopulation viability. We based these on Nottingham's landscape when urban developments were recently proposed, then adjust the land cover to include the proposed developments, and also for two projected landscapes where 10% and 20% of the original natural or semi-natural land cover is lost. We find that the IFM shows promise as a tool for quantitative landscape-scale ecological impact assessment, depending on the size of the impact. We detected minimal differences in the species' viability measures between the original and post-development landscapes. This suggests that for small (around 2%) cumulative losses of natural/semi-natural space, current site-based approaches are sufficient. However, when the cumulative effect of continued development was modelled by increasing the losses of natural/semi-natural land cover to 10–20% of existing cover, the impact on many of the species studied was more substantial. This indicates that a landscape-scale approach is necessary for larger, prolonged and cumulative habitat losses.

1. Introduction

Increasing human population and industrialisation are leading to an increase in the numbers of people living in urban areas. In 2015, 54% of the global population lived in cities (The World Bank, 2017). The rising populations put increasing pressure on our cities, and the habitats and species contained within. However, urban green spaces provide a range of benefits to humans and biodiversity conservation (Aronson et al., 2017). Conservation of biodiversity is often in conflict with social and economic goals, such as city development (Ng Mei Sze and Sovacool 2013). Nature conservation is frequently listed as a key issue in land-use conflicts (von der Dunk, Grêt-Regamey, Dalang, & Hersperger, 2011). It is increasingly recognised, however, that conservation needs to be integrated with social and economic issues (Brown 2002). It is therefore necessary that urban planning be strategic at a landscape scale such that the increased need for development is met while having the least impact on the natural environment (Mörtberg, Balfors, & Knol, 2007).

Protection for non-designated natural areas is available in the form of ecological impact assessments (EcIAs), which are parts of environmental impact assessments (EIAs). EIAs have been integrated into policy in many countries with varying levels of success (Wathern, 2013), and in some cases the information provision has been found to be insufficient (Drayson, Wood, & Thompson, 2015). An EcIA is a process which identifies, quantifies and evaluates the potential impacts of actions, such as developments, on ecosystems and their component species (Treweek, 1999). In Europe, EIAs are subject to the Environmental Impact Assessment Directive (Official Journal of the European Union, 2011) and also the Strategic Environmental Assessment (Official Journal of the European Union, 2001), though these are not compulsory for all developments. Additionally, EcIAs tend to only to consider impacts on protected and priority species. Many non-protected species are nevertheless currently showing decline (Hayhow et al., 2016; Defra, 2013), and there are strong arguments for also investigating impacts on non-priority species and habitats.

A site-based approach to EcIA is argued to be insufficient (Mörtberg et al., 2007). The spatial configuration of habitat is an important factor in species persistence (Opdam, Verboom, & Pouwels, 2003). Increasingly it is recognised that an understanding of landscape pattern and

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process is necessary to identify the impacts of land-use change on species, and that planning decisions need to be taken at a landscape scale (Hobbs, 1997; Mörtberg et al., 2007). As a result, it is crucial that a method for assessing landscape-scale impacts of urban development on species persistence be available. Landscape-scale approaches have been developed to identify habitat expansion areas (McHugh & Thompson 2011), but it is also necessary to analyse the effects of habitat conversion at a landscape scale.

We propose that the incidence function model (IFM; Hanski, 1994) is an appropriate method to simulate the impacts of changes in the urban landscape on species persistence. The IFM is most applicable in highly fragmented landscapes (Hanski, 1999) where suitable habitat consists of small, discrete patches. Urban areas generally contain many small patches of remnant, managed and unmanaged habitat (McKinney, 2002). Unlike classical metapopulation models, the IFM is spatially realistic – it takes as an input the size and locations of the patches – which means it can be used to investigate the impact of the removal of patches within real landscapes (Hanski, 1994). The IFM also has the advantage of less-intensive data requirements than other such models: it can be parameterised using a snapshot of species occurrence (Etienne, ter Braak, & Vos, 2004; Hanski, 1999). Patch occupancy models, including the IFM, have previously been tested for the purpose of comparing the impact of different landscape configurations on the persistence of focal species (for example Heard, McCarthy, Scroggie, Baumgärtner, & Parris, 2013; Wahlberg, Moilanen, & Hanski, 1996).

In this paper, we aim to develop measures of landscape-scale species' persistence which are comparable between landscapes, for the purpose of investigating the ecological impacts of proposed developments. We demonstrate that the IFM has potential as a tool for aiding EcIAs. We provide a proof of concept using the case study of Nottingham City with respect to urban development proposals put forward in 2005. We compare outputs of simulations for the original landscape (contemporary with the development plans), the landscape adjusted by removing habitat as specified by the proposed developments, and two projected future landscapes with further losses of 10% and 20% cover of natural and semi-natural broad habitat types.

2. Methods

2.1. Study site and data

We used the Nottingham City unitary authority as the case study area, and included a 2 km buffer to allow for dispersal from outside. Nottingham is a fairly typical medium-sized urban area (area 74.61 km^2, population c. 305,680) in the East Midlands of England. Nottingham is characterised by remnant woodland and grassland habitat within the city boundary, a greater proportion of freshwater than comparable urban areas, and surrounded by a higher proportion of arable land in the peri-urban areas.

We obtained maps of the proposed developments for the Nottingham City unitary authority from the Nottingham Local Plan (Nottingham City Council, 2005a). These proposed developments are those that have since been approved in the strategic plan and include residential, employment and mixed use. Maps were downloaded from the Nottingham City Council website for the North Side (Nottingham City Council, 2005b) and South Side (Nottingham City Council, 2005c). The study site and locations of proposed developments are shown in Fig. 1. We used Land Cover Map 2007 data (Morton, Rowland, Wood, Meek, Marston, Smith, & Simpson, 2011) for information about the spatial configuration and classification of habitat patches at the time when the developments were proposed.

We used a suite of indicator species to investigate the impacts of development on landscape-level species persistence. The species chosen had a range of habitat specialisms and dispersal abilities. Only species with dispersal distance < 10 km were included because longer-dispersing species have been shown not to be suitably dispersal limited to model metapopulation dynamics at the scale of this study (Graham, Haines-Young, & Field, 2015). We recommend that only species with a dispersal distance approximately $\leq \sqrt{studyarea(km^2)}$ be included. Therefore, species with a longer dispersal distance are more appropriate for analysis of larger study areas (e.g. regional, rather than city scale). The species, their specialisms, habitat associations and dispersal abilities are given in Table 1.

For each of the landscapes under comparison, we created modified maps which reflect the species' habitat requirements shown in Table 1. So that patches were portrayed in the way species use them, rather than how they are viewed by humans, we dissolved all artificial boundaries in the LCM 2007 data. The artificial boundaries were those which would be considered boundaries by humans, but not by the species using the habitats, that are caused by differing land ownership, separation of similar habitat types, and paths and roads ≤3 m wide.

Species occurrence data for bird species were provided by Nottinghamshire Birdwatchers and the amphibian data were downloaded from the National Biodiversity Network Gateway using the R package 'rnbn' (Ball & August, 2013). The resolution of the species' data (2 km x 2 km) is coarser than that required as input to the model (patch-level occupancy), so we employed a downscaling technique. For each grid cell reported as occupied, we assigned species' occupancy to patches by area-weighted sampling, a method which was found to produce the most realistic species occupancies after simulation with the IFM (Graham et al., 2015). Within each occupied 2 km x 2 km cell, patches are randomly allocated occupancy with a higher probability the larger the patch. The proportion of patches occupied within a cell is equal to the proportion of 2 km x 2 km cells occupied in the landscape. To account for the uncertainty in the downscaling method, a set of 200 starting conditions of species' occurrences was created using this method. These species' occupancy patterns are the input data to the IFM.

2.2. Developments and projected loss landscapes

To create a 'developments' layer, we georeferenced the Local Plan maps to match the LCM 2007 data using ArcMap 10.0, then digitised the proposed developments. The developments layer was overlaid on the LCM 2007 data and any corresponding non-urban or suburban polygons were updated to urban to simulate the effect of development.

For further comparison, and to investigate the effects of cumulative developments over time, we created two additional landscape maps: projected maps of 10% and 20% habitat loss. These maps were created based on the idea that development acts as a contagion on the landscape, and that natural spaces closest to development are more vulnerable (Laurance, 2008). We methodically removed patches defined as terrestrial habitat (i.e. any patch falling in the classes listed in Table 1 except freshwater) in order of distance to the nearest development (closest first) until 10% and 20% of original habitat cover had been removed (see Fig. 2 for maps of these projected future landscapes).

2.3. Model simulation

The incidence function model (IFM, Eq. (1)), a stochastic patch occupancy model developed by (Hanski, 1994), allows long-term predictions of metapopulation persistence in a network of habitat patches to be made through estimation of colonisation and extinction rates. The occupancy of a patch i is given by J_i where J_i is a balance of colonisations (C_i) and extinctions (E_i).

$$J_i = \frac{C_i}{C_i + E_i - C_i E_i} \tag{1}$$

The extinction probability is calculated following the assumption that the number of individuals is directly proportional to the area of the patch they occupy. Extinction is affected by population size, so E_i can therefore be expressed as a function of A_i:

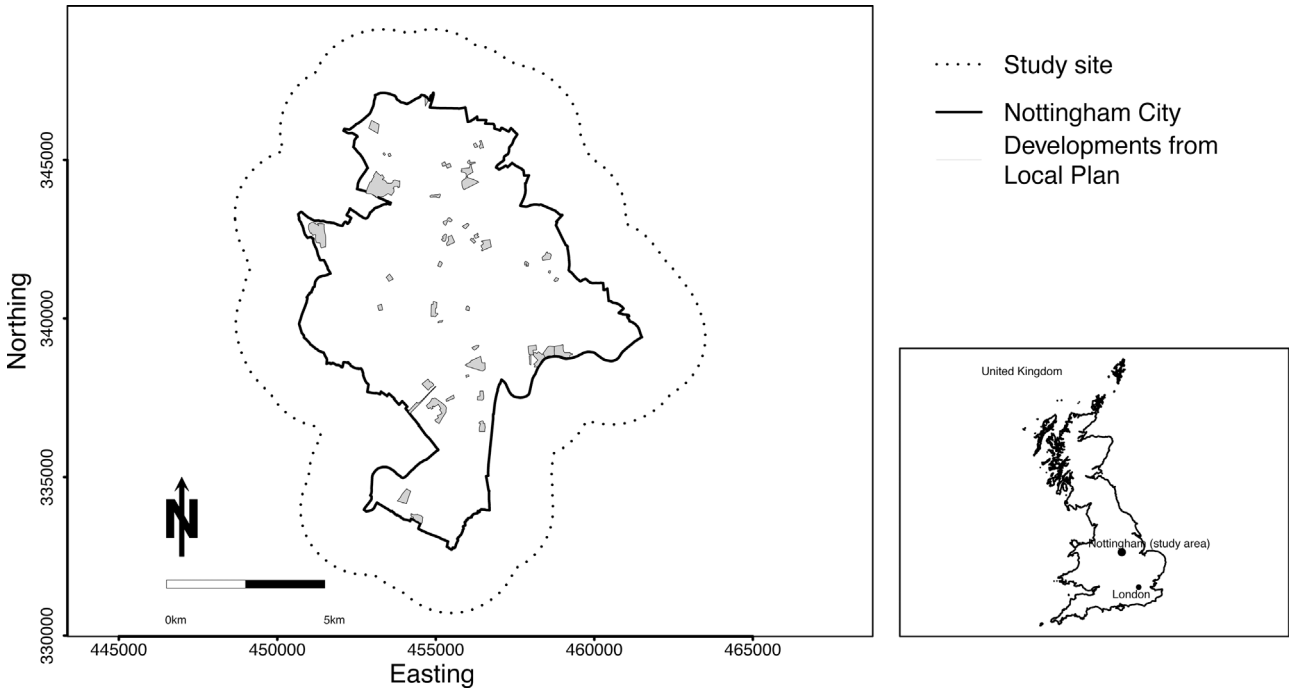

Fig. 1. Study site of Nottingham with 2 km buffer showing locations of the proposed developments from the Local Plan. Inset map shows the location of Nottingham within Great Britain.

Table 1
Broad habitat type (based on LCM 2007), mean natal dispersal distance and minimum habitat requirement for each species. LCM classes: 1. Broadleaved woodland, 2. Coniferous woodland, 3. Arable and horticulture, 4. Improved grassland, 5. Rough grassland, 6. Neutral grassland, 8. Acid grassland, 9. Fen, marsh and swamp, 10. Heather, 11. Heather grassland, 16. Freshwater.

Species	Common name	Dispersal (km)	LCM class	Min. area (ha)
Turdus merula	Blackbird	3.300	1, 2, 3, 4, 5, 6, 7, 8	0.02
Prunella modularis	Dunnock	2.100	1, 2, 3, 4, 5, 6, 7, 8	0.02
Carduelis chloris	Greenfinch	4.200	1, 2, 3	0.25
Emberiza calandra	Corn bunting	4.000	3, 4, 5, 6, 8	2.50
Passer montanus	Tree sparrow	8.000	1, 2, 3	0.12
Emberiza citrinella	Yellowhammer	8.400	3, 5, 10, 11	0.03
Garrulus glandarius	Jay	3.500	1, 2	0.32
Poecile palustris	Marsh tit	0.885	1	2.10
Rana temporaria	Common frog	1.000	1, 2, 3, 4, 5, 6, 8, 9, 16	0.02
Bufo bufo	Common toad	0.700	1, 2, 5, 6, 8, 9, 16	0.02

$$E_i = min\left[\frac{u}{A_i^{\,x}}, 1\right] \tag{2}$$

Here, u and x are species specific parameters, and patch i is currently occupied. The critical patch size, below which a species cannot survive in the patch, is given by $u^{\frac{1}{x}}$ (all patches $\leq u^{\frac{1}{x}}$have extinction probability 1). Parameter x represents the extent to which a species' survival is dependent on patch size (larger x represents weaker dependence).

The colonisation probability is a function of patch connectivity S_i (Eq. (4)). Species-specific parameter y represents the level of connectivity required by a species to achieve colonisation.

$$C_i = \frac{S_i^2}{S_i^2 + y^2} \tag{3}$$

Finally, connectivity is a function of the distance from patch i to patch j, the occupancy and area of patch j (p_j and A_j respectively) and the species' mean natal dispersal ability, $\frac{1}{\alpha}$. Mean natal dispersal distance is derived from the literature.

$$S_i = \sum_{j=1}^{n} e^{-\alpha d_{ij}} p_j A_j \tag{4}$$

Parameters u, x and y are estimated from the data. For each species, we estimated the parameters of the IFM by fitting eight years of species patch occupancy data to a logistic regression model derived from the above equations (Eq. (5)) for each of the 200 downscaled occupancy configurations.

$$logit(J_i) = \beta_0 + 2log(S) + \beta_1 log(A) \tag{5}$$

Here $\beta_0 = -log(uy)$ and $\beta_1 = x$. Parameter u is estimated by assuming that for the smallest of all occupied patches, $E_i = 1$, then solving Eq. (2) for u. This value is then substituted into $\beta_0$to solve for y. We calculated the Nagelkerke pseudo-$R^2$to assess model fit to the data.

Species' patch occupancies were simulated using the IFM (Eq. (1)) for 500 time-steps and 100 iterations using each of the 200 parameter combinations for the 10 species and 4 different landscapes. All simulations and analyses were performed in R v3.0.2 (R Core Team, 2014).

2.4. Assessing the impact of developments

From the output of the IFM, we calculated measures of metapopulation viability: minimum occupancy, occupancy at equilibrium and survival probability. The minimum occupancy was the lowest recorded proportion of suitable habitat across 500 time steps in a simulation; the mean was taken across the 100 replicates. The occupancy at equilibrium was the proportion of suitable habitat occupied at time step t = 175; again we took the mean of 100 replicates. This time step was chosen because it was the point at which most species had reached equilibrium under simulation of the original landscape. The survival probability was the proportion of the 100 replicates where the species was still present after 500 time steps had been simulated. Although we simulate occupancy in terms of time steps, the measures of persistence should be taken as indicators of metapopulation viability (or stability)

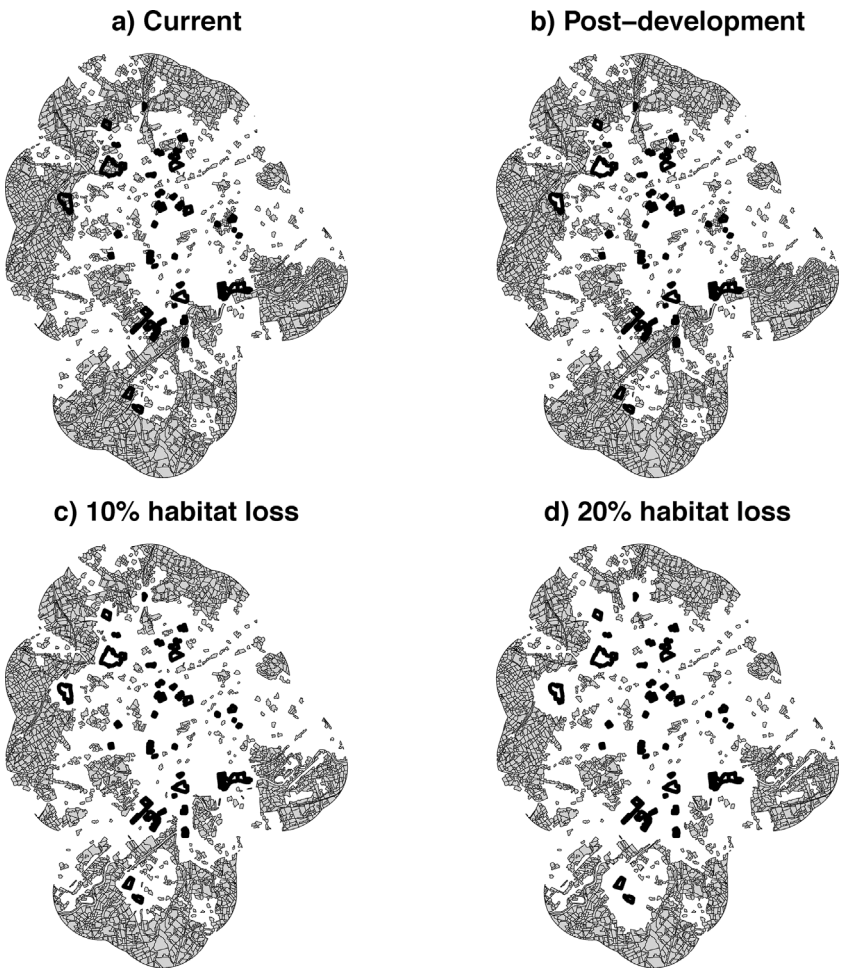

Fig. 2. Habitat configuration for the (a) current and (b) post development landscapes and the (c) 10% and (d) 20% habitat loss projections. Proposed developments are overlaid (bold lines).

rather than explicit predictions at a particular time step.

To assess the impact of proposed developments on species' landscape-level persistence, we compared the mean value of each of the measures of metapopulation viability of the current, post-development and projected landscapes. We focus on biological importance rather than statistical significance here because significance testing with simulated data provides artificially small p-values due to the large sample size, and breaks the assumption of hypothesis testing that a difference between groups is not known (White, Rassweiler, Samhouri, Stier, & White et al., 2014).

3. Results

3.1. Impact of proposed developments on land-cover configuration

The proposed developments for Nottingham City resulted in a 1.53% reduction in total habitat cover within the study site. It should be noted that while the study site includes the 2 km buffer, only developments within the city boundary were considered. For detailed information on the amount of each habitat type that was lost, see Table 2. This Table also shows the amount of each habitat type lost for the 10% and 20% habitat loss projections.

3.2. Model simulation

We estimated 200 sets of parameters x, u and y using logistic regression (see Appendix A for the explanation of these parameters and the logistic regression equation). The model was well fitting for all species (pseudo-$R^2 > 0.80$) except for *G. glandarius* (pseudo-$R^2 = 0.47$). The mean and standard deviations for these parameters are shown in Table 3.

The IFM simulations took a mean time of 1.71 h, with a minimum running time of 0.23 h for *P. palustris* under the landscape with 20% habitat loss and a maximum running time of 3.64 h for *T. merula* for the post-development landscape. The simulations were run on the University of Nottingham's High Performance Cluster (Intel Sandybridge E5-2670 2.6 GHz, 20 GB RAM allocated).

3.3. Impact of development on species

For most species, the reduction in occupancy is proportional to the amount of natural space lost at the scale of the city and the survival probability stays constant after the proposed developments. *E. citrinella* and *B. bufo*, however, both have more biologically significant reductions in minimum occupancy (−5.06% and −14.25% respectively) and occupancy at equilibrium (−2.90% and −10.70%). Both these species, as well as *Poecile palustris* also saw reductions in survival probability under the proposed developments (−0.32%, −1.24% and −0.09% respectively, Table 4).

By expanding the habitat loss scenarios to 10% and 20% loss of natural space, we can evaluate the cumulative effect of developments. For the 10% habitat loss scenario we see departure from the proportional effect of habitat loss on species' persistence. This is particularly the case for occupancy at equilibrium for *Prunella modularis* (−12.57%), *E. calandra* (−19.99%), *Poecile palustris* (−73.62%) and *B. bufo* (−58.14%). Minimum occupancy also sees disproportionate reductions for *E. citrinella* (−14.49%), *Poecile palustris* (−93.05%) and *B. bufo* (−67.87%). *Poecile palustris* is particularly affected under 10%

Table 2
Percentage loss of each LCM 2007 terrestrial habitat type for the post-development landscape and the 10% and 20% projections.

LCM Class	Current (ha)	Post-development (% decrease)	10% habitat loss (% decrease)	20% habitat loss (% decrease)
Broadleaved Woodland	859.0	0.51	9.73	17.15
Coniferous Woodland	49.8	0.00	3.61	14.94
Arable and Horticulture	3902.3	1.70	7.53	17.88
Improved Grassland	2635.3	1.00	13.15	24.18
Rough Grassland	334.7	4.78	10.96	17.90
Neutral Grassland	195.7	1.37	13.87	19.39
Acid Grassland	4.7	0.00	0.00	0.00
Fen, Marsh and Swamp	4.1	0.00	0.00	28.71
Heather	28.2	0.01	5.52	13.96
Heather Grassland	16.1	43.64	62.94	62.94
Total	8029.9	1.53	9.98	19.96

Table 3
Means and standard deviations of parameter estimates and Nagelkerke pseudo-R^2 (measure of model fit) obtained for each of the 200 species occupancy starting conditions.

Species	Mean parameter values (SD)			Nagelkerke
	x	u	y	pseudo-R^2 (SD)
Turdus merula	0.69 (0.005)	0.07 (0.002)	2895.3 (31.1)	0.97 (0.00)
Prunella modularis	0.77 (0.008)	0.05 (0.002)	2524.3 (46.2)	0.98 (0.00)
Carduelis chloris	0.92 (0.046)	0.55 (0.062)	1566.1 (104.0)	0.91 (0.01)
Emberiza calandra	1.78 (0.068)	12.91 (1.790)	4852.2 (586.9)	0.99 (0.00)
Passer montanus	0.91 (0.032)	0.54 (0.185)	4936.9 (882.1)	0.91 (0.02)
Emberiza citrinella	0.45 (0.019)	0.23 (0.016)	2485.0 (130.1)	0.75 (0.03)
Garrulus glandarius	0.69 (0.035)	0.63 (0.032)	105.1 (4.5)	0.47 (0.03)
Poecile palustris	1.92 (0.090)	8.50 (0.831)	28.2 (2.0)	0.90 (0.02)
Rana temporaria	0.50 (0.003)	0.14 (0.002)	213.6 (1.4)	0.84 (0.00)
Bufo bufo	1.10 (0.051)	0.03 (0.008)	229.2 (40.2)	0.94 (0.01)

Table 4
Impact of development on species' persistence.

		% change			
Species	Persistence measure	Current	Post-development	10% loss	20% loss
Turdus merula	Minimum occupancy (ha)	6534.04	−1.32	−10.56	−21.46
	Occupancy at equilibrium (ha)	7736.68	−1.06	−10.22	−21.09
	Survival probability (over 500 years)	1.00	0.00	0.00	0.00
Prunella modularis	Minimum occupancy (ha)	5200.05	−1.43	−9.57	−21.17
	Occupancy at equilibrium (ha)	6866.40	0.26	−12.57	−26.48
	Survival probability (over 500 years)	1.00	0.00	0.00	0.00
Carduelis chloris	Minimum occupancy (ha)	3439.62	−1.05	−8.48	−20.43
	Occupancy at equilibrium (ha)	4571.40	−1.54	−8.61	−19.84
	Survival probability (over 500 years)	1.00	0.00	0.00	0.00
Emberiza calandra	Minimum occupancy (ha)	2775.76	−1.24	−9.17	−20.50
	Occupancy at equilibrium (ha)	4504.19	9.00	−19.99	−35.66
	Survival probability (over 500 years)	1.00	0.01	−0.02	−0.03
Passer montanus	Minimum occupancy (ha)	2415.30	−0.32	−7.10	−19.73
	Occupancy at equilibrium (ha)	4376.01	−1.42	−9.51	−22.34
	Survival probability (over 500 years)	1.00	0.00	−0.10	−0.17
Emberiza citrinella	Minimum occupancy (ha)	2164.13	−5.06	−14.49	−40.50
	Occupancy at equilibrium (ha)	3876.59	−2.90	−10.16	−26.68
	Survival probability (over 500 years)	0.99	−0.32	−0.85	−7.37
Garrulus glandarius	Minimum occupancy (ha)	383.78	−0.28	−9.28	−12.93
	Occupancy at equilibrium (ha)	825.10	−0.64	−11.86	−21.68
	Survival probability (over 500 years)	1.00	0.00	0.00	0.00
Poecile palustris	Minimum occupancy (ha)	7.48	−1.42	−93.05	−93.30
	Occupancy at equilibrium (ha)	47.48	−0.70	−73.62	−73.93
	Survival probability (over 500 years)	0.28	−0.09	−88.76	−88.76
Rana temporaria	Minimum occupancy (ha)	2196.18	9.62	−11.98	−40.32
	Occupancy at equilibrium (ha)	5049.74	3.11	−10.39	−28.34
	Survival probability (over 500 years)	0.98	0.50	−1.27	−4.35
Bufo bufo	Minimum occupancy (ha)	67.24	−14.25	−67.87	−90.17
	Occupancy at equilibrium (ha)	95.55	−10.70	−58.14	−80.97
	Survival probability (over 500 years)	0.98	−1.24	−13.51	−42.18

natural space loss, with the measure of survival probability dropping by 88.76%. Under the 20% natural space loss scenario, even more species see disproportionate reductions in their occupancy and survival probability. The 20% natural space loss scenario shows similar, but more exaggerated results.

4. Discussion

The IFM offers a method to generate quantitative measures of ecological sustainability which allow us to compare competing landscape management plans and to assess the impacts of developments on species persistence at a landscape scale. A major criticism of EcIA is that impacts are rarely quantified; our contribution is a method which allows estimation of such quantities in a repeatable and transparent way. In our proof of concept, we find that the size of the development is important for deciding whether a landscape-scale approach is appropriate. However, it should be noted that once cumulative effects of further development over time are taken into account, a landscape scale approach was always found to be most appropriate.

We found that a landscape-scale approach to ecological impact assessment is not necessary for relatively small losses of habitat; in this case < 2% cover of any natural or semi-natural land cover type. Although significant differences were found between the current and post-development landscapes, these differences were mostly small (Table 4). This suggests that current approaches to EcIAs are sufficient as long as the (total) amount of habitat lost remains small. It is also important to understand the cumulative effects of further developments, rather than just those on the immediate time horizon. To this end, we looked at the effects of 10% and 20% habitat loss on species' persistence. As the amount of habitat lost increases, more substantial impacts on species' occupancy and survival are seen and therefore a site-based approach is no longer sufficient. Similar research should be done in other landscapes and for other species to establish how general these findings are.

Metapopulation viability can be, and has been, estimated through a variety of measures; it is important, therefore, that we understand the implications of the measures in use. Examples of some such metapopulation measures are the number of patches occupied at equilibrium (Biedermann, 2000; Hanski, 1994), metapopulation extinction risk (Johansson, Ranius, & Snäll, 2013) or survival probability (Biedermann, 2000; Bulman, Wilson, Holt, Bravo, Early, Warren, & Thomas, 2007), minimum occupancy across the simulated time steps (Heard et al., 2013) and quasi-extinction, which is the proportion of replicates where the species occupancy is below a certain threshold (Heard et al., 2013). Here we calculated the survival probability, occupancy at equilibrium and minimum occupancy. For minimum occupancy and occupancy at equilibrium, occupancy was calculated as the proportion of the total available habitat occupied. Taking into account the size of the patches rather than just the number of patches gives an idea of the abundance of the species, because patch sizes are assumed to be proportional to population size (Hanski, 1994). The range of measures used here allows us to get a multidimensional view of ecological stability (Donohue et al., 2013) under landscape change, and also to capture the differing effects on a range of species.

Our results show that the appropriate measure to use depends on species' characteristics. For example, for species with high occupancy in the landscape, little information is obtained from the survival probability. When comparing using either minimum occupancy or occupancy at equilibrium, however, differences can be seen. For example, for *T. merula*, *P. modularis* and *C. chloris*, small differences can be seen in the proportion of habitat occupied as the amount of habitat decreases, but the survival probability remains at 1 for all landscapes. In contrast, for species with a low occupancy proportion in the landscape (*P. palustris*, *B.bufo*), examining the results for survival probability offers much more information. It is potentially relevant that these species also have the lowest dispersal capability, and poor dispersal has been linked to vulnerability to extinction (Tilman, Lehman, & Yin, 1997).

In addition to the choice of measure being dependent on species' characteristics, it is also important to note that the scale of study affects whether the IFM is appropriate to model the dynamics of a particular species. In our analysis, species with mean dispersal distance ≥10 km were omitted from the analysis because these species are not dispersal limited at the scale of study, a condition which must be met for a species to display metapopulation dynamics (Hanski, 1994). When we tested this, occupancies of species with mean dispersal distance ≥10 km were consistently over-predicted (100% occupancy for all such species, regardless of their initial occupancy, Graham et al., 2015). This is because of the spatial extent of the analysis. Species with longer dispersal distances are, however, less vulnerable to habitat fragmentation than poor dispersers (Garrard, McCarthy, Vesk, Radford, & Bennett, 2012). It is unlikely, therefore, that species with high dispersal ability would be affected by local developments unless the habitat lost is rare on a regional scale. In such a case the IFM could be used at a regional scale, where long-dispersing species are dispersal limited. This concurs with the idea that landscape sustainability assessments need to be performed on the appropriate spatial scale for the system under study (Opdam, Steingröver, & van Rooij, 2006).

Species that are rare in the landscape can also not be modelled using the IFM (Baguette, 2004). The reason is that there need to be at least 10 occupied patches in the study area to achieve accurate parameterisation (Hanski, 1999). As such, indicator species need to be chosen wisely; focal species should represent a wide range of habitat uses and dispersal abilities, and should be those which are sensitive to changes in their environment (Noss, 1990). In addition, the method presented herein should be used as part of a suite of decision-making tools, which should include assessments of impacts on rare species, such as a site-based EcIA.

A major criticism of EcIAs tends to be the lack of quantification, with impacts merely described rather than predicted or quantified (Geneletti, 2006; Karlson et al., 2014; Treweek, 1996). We have examined how the IFM can be used to quantify the impacts of development on species persistence at a landscape level, and therefore be useful for landscape-scale EcIAs. Caution should be taken when interpreting the results because they are based on a number of assumptions. The results should be interpreted as comparative assessments; for example, the new landscape configuration judged against the original landscape, or alternative modified landscapes judged against each other. Here, we have compared the ecological sustainability of the landscapes by comparing the results for each measure and species individually. Incorporating the results into multiple criteria decision analyses (MCDA) would allow the model to have greater utility as a decision support tool, and would have the additional benefit that non-ecological criteria could also be included in the analysis. Although an exact estimate of the size of the impact is difficult to obtain with any confidence, because of the uncertainty in parameter estimation for metapopulation models (Grimm et al., 2004), the measures obtained from the IFM give some indication as to the size of the impacts, which means that values are comparable. Further research into accurate parameterisation (for example Heard et al., 2013; Risk et al., 2011) will improve the estimates.

Current approaches to incorporating biodiversity into strategic planning and EcIAs tend to be based on habitat suitability mapping and species distribution modelling (Gontier, 2007; Mörtberg et al., 2007). Our approach allows for landscape connectivity to be incorporated into such an approach by including information about the spatial structure of the landscape and the dispersal abilities of the species under study. It is possible to combine the two approaches by including 'habitat quality', such as that derived from suitability maps, in the IFM by weighting the patch size by a quality measure; $\frac{Q_i A_i}{Q}$ where Q_i is the quality of the patch and Q is the maximum quality in the landscape (Hanski, 1994). Additionally, functional connectivity of the landscape can be included by bringing quality of the matrix into the model using least cost distance

(Adriaensen et al., 2003; Baguette & Van Dyck, 2007) in the connectivity measure. However, it has been found that such a substitution does not necessarily improve IFM performance (Moilanen & Hanski 1998). Alternatively a dynamic occupancy model could be used to directly incorporate patch-level covariates to estimate colonisation and extinction probabilities (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). This has the additional benefit that the detection process can be separately modelled and accounted for and therefore remove the need to discard 'low quality' data with low confidence in absences. Incorporating the results from habitat suitability mapping into a patch occupancy model in these ways could add value to these species' distribution modelling approaches to EcIA. The IFM allows for species dispersal behaviour, and the impacts of landscape connectivity to be incorporated into EcIAs to complement existing approaches. Because the IFM models the dynamics of the species over time, and bases these on local extinction and colonisation, the effect of extinction debt is also incorporated into the modelling approach. Extinction debt is the time delay between habitat loss and a species local extinction (Tilman, May, Lehman, & Nowak, 1994).

5. Conclusions

We have presented a method, based on the IFM, for landscape-scale ecological assessment. By simulating species' occupancies over many time steps, it is possible to derive quantities which represent species' persistence or metapopulation viability. These quantities are comparable between landscapes and therefore can be used to measure the ecological impact of a development or change in management practice. We found that the changes to the landscape need to be sufficiently large (in our case around 10% loss of natural/semi-natural space) for a landscape-scale approach to ecological impact assessment to be necessary. Further testing in other study areas will help to make this result more generalisable and provide important information about the conditions under which a site-based approach to ecological impact assessment is sufficient.

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