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RESEARCH ARTICLE

Living on the edge: quantifying the structure of a fragmented forest landscape in England

Terhi Riutta · Eleanor M. Slade · Michael D. Morecroft · Daniel P. Bebber · Yadvinder Malhi

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Abstract Forest ecosystems have been widely fragmented by human land use, inducing significant microclimatic and biological changes at the forest edge. If we are to rigorously assess the ecological impacts of habitat fragmentation, there is a need to effectively quantify the amount of edge habitat within a landscape, and to allow this to be modelled for individual species and processes. Edge effect may extend only a few metres or as far as several kilometres, depending on the species or process in question. Therefore, rather than attempting to quantify the amount of edge habitat by using a fixed, case-specific distance to distinguish between edge and core, the area of habitat within continuously-varying distances from the forest edge is of greater utility. We quantified the degree of fragmentation of forests in England, where forests cover 10 % of the land area. We calculated the distance from within the forest patches to the nearest edge (forest vs. non-forest) and other landscape indices, such as mean patch size, edge density and distance to the nearest neighbour. Of the total forest area, 37 % was within 30 m and 74 % within 100 m of the nearest edge. This highlights that, in fragmented landscapes, the habitats close to the edge form a considerable proportion of the total habitat area. We then show how these edge estimates can be combined with ecological response functions, to allow us to generate biologically meaningful estimates of the impacts of fragmentation at a landscape scale.

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T. Riutta (✉) · Y. Malhi
Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford OX1 3QY, UK
e-mail: terhi.riutta@ouce.ox.ac.uk

E. M. Slade
Wildlife Conservation Research Unit, Department of Zoology, University of Oxford, Tubney House, Abingdon Road, Tubney, Abingdon OX13 5QL, UK

E. M. Slade
Spatial Foodweb Ecology Group, Department of Applied Biology, University of Helsinki, Latokartanonkaari 5, PO Box 27, 00014 Helsinki, Finland

M. D. Morecroft
Natural England, Cromwell House, 15 Andover Road, Winchester SO23 7BT, UK

D. P. Bebber
Department of Biosciences, University of Exeter, Stocker Road, Exeter EX4 4QD, UK

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Introduction

Fragmentation and habitat loss have been identified as major threats to forest biodiversity and ecosystem functioning (Saunders et al. 1991; Laurance et al. 2002; Watts 2006; Hambler et al. 2011). Forest fragmentation results in smaller habitat patches, and changes in ecological responses, which vary with distance to the edge, termed 'edge effects' (Saunders et al. 1991; Harper et al. 2005; Fletcher et al. 2007). Fragmentation affects biodiversity, population dynamics and ecological processes through changes in habitat quality, reduced habitat area and reduced connectivity between patches (for reviews, see Saunders et al. 1991; Harrison and Bruna 1999; Fahrig 2003). However, the responses of species and processes to habitat fragmentation vary widely and are often idiosyncratic and dependent upon management and disturbance history (Ewers and Didham 2006a, 2007; Laurance et al. 2007).

Most edge effects, particularly abiotic ones, such as increased light levels, higher and more variable temperatures, and increased evapotranspiration, occur within 100 m of the forest edge (Chen et al. 1995; Didham and Lawton 1999; Laurance et al. 2002 and references therein; Herbst et al. 2007). However, these effects are process- and species-specific as well as scale-dependent. Deleterious effects on processes or populations may occur only within the first few metres from a fragment edge (Ewers and Didham 2006b) or they may extend several hundred metres (Laurance et al. 2002; Slade et al. 2013) or as far as several kilometres (Laurance 2000; Ewers and Didham 2008). Thus, the spatial and temporal scales most relevant for the species or process in question need to be taken into account (Murcia 1995). In addition, defining and quantifying the depth of edge influence is not a simple task, as discussed by Didham and Lawton (1999). Therefore, rather than attempting to quantify the amount of edge habitat by using some semi-arbitrary species- or process-specific distance to distinguish between edge and core, we suggest distance to the edge be treated as a continuous variable.

There is a wealth of literature documenting ecological responses to forest fragmentation (e.g. Murcia 1995; Fahrig 2003; Ries et al. 2004; Ewers and Didham 2007; Laurance et al. 2007; Banks-Leite et al. 2010). However, only a few studies extrapolate the responses to fragmentation measured at study site scales to the landscape level (but see Laurance and Yensen 1991; Bowers et al. 1996; Sisk et al. 1997; Robinson et al. 2009; Ewers et al. 2010; Lafortezza et al. 2010). One reason for this may be that it is difficult to find quantitative estimates on the degree of forest fragmentation at regional or global scales, despite the importance this has for management and conservation strategies (Ries et al. 2004). Such estimates can be generated using GIS to inform fragmentation studies (McGarigal and Cushman 2002), and biological response functions can then be combined with fragmentation maps to assess the impact of fragmentation at a landscape scale (Ewers et al. 2010; Lafortezza et al. 2010).

Temperate forests are the most fragmented forest biome in the world and the forests in Europe are the most fragmented of all the continents (Wade et al. 2003). In the UK, forest area has declined from around 75 % of the land area 6,000 years ago, to approximately 15 % 900 years ago and to less 6 % in the 1940s, but has increased to 13 % today (Peterken 1993; Watts 2006; UK National Ecosystem Assessment 2011; Forestry Commission 2012). Within England, forests represent 10 % of the land area (Forestry Commission 2012). Even with the increase in recent decades, this still lies well below the European average of 37 %, and much of this recent afforestation has been in the form of coniferous production forest, which comprises 26 % of the forest area in England (Forestry Commission 2012). Although forest species diversity is now recovering, with the increase in forest area (UK National Ecosystem Assessment 2011), the past habitat loss has been one of the main drivers of species extinctions in the UK (Hambler et al. 2011). A recent review of forestry in the UK recommends a renewed commitment to increasing forest area (Independent Panel on Forestry 2012). At the same time, a major goal of current conservation policy is to increase the resilience and coherence of ecological networks (Lawton et al. 2010; Defra 2011). Quantitative information on the degree of fragmentation and on the amount of edge-influenced habitat will help evaluate the landscape-scale effects of forest fragmentation on biodiversity and ecosystem functioning, which are often only measured at a study site scale. Moreover, such information is important when designing the planting of new forest areas, to maximize their benefits as part of a functioning network.

The objective of this paper was to quantify the degree of forest fragmentation and the amount of edge-influenced forest habitat in England. Edge, in this case, is defined as a border between forest and non-forest. Although the quantitative results are specific to England, the study also illustrates the impact of fragmentation on landscape indices in an extremely fragmented landscape in general. Specifically, we aimed to:

(1) Quantify the amount of habitat at different distances from the forest edge, treating the distance from the edge as a continuous variable, therefore overcoming the problem of using a case-specific forest edge vs. forest core dichotomy.
(2) Quantify landscape indices, such as forest patch size distribution, connectivity and patch shape.
(3) Simulate the impact of a 10 % increase in forest area on the landscape indices.

Fragmentation statistics generated in this paper can be used for quantifying the landscape scale impact of fragmentation on biodiversity, population dynamics, dispersal and colonisation, and on ecosystem processes such as primary productivity and nutrient cycling. We illustrated the use of the data with two examples (moth abundance and tree stand transpiration), which combined ecological response functions and fragmentation statistics.

Methods

Forest patch datasets

Two datasets were used in this study: (i) all forest patches and (ii) ancient woodlands, which are defined as having had a continuous forest cover since at least 1600 AD (Spencer and Kirby 1992). *Dataset 1, all forest patches*, was based on the Forestry Commission data on forest patches in England, available in vector format (Forestry Commission, National Forest Inventory—England, © Crown copyright and database right 2011. All rights reserved. Ordnance Survey Licence number 100021242. Available to download at http://www.forestry.gov.uk/datadownload). In this dataset, patches are defined by forest type categories (Interpreted Forest Type in the dataset). Therefore, each continuous forest area in the dataset may comprise more than one patch if the tree species composition within the forest varies. To analyse the general forest landscape, all internal boundaries between different forest types within continuous forest areas were removed. Thus, continuous forest areas are described as single patches, even if they consist of several forest types. After removing the internal boundaries, patches $\geq$2 ha were extracted for the analysis. This cut-off limit was chosen for computational reasons and because the small patch data was not as accurate and comprehensive as the large patch data.

The data on all forest patches was analysed for forests overall (all types combined) and by four forest types: broad-leaved forests, including coppiced areas (proportion of broad-leaved trees >80 %); coniferous forests (proportion of coniferous trees >80 %); mixed forests (proportion of both broad-leaved and coniferous trees $\geq$20 %); and areas of sparse tree cover, comprising young forests, shrublands and felled patches. The analyses carried out by forest type included patches <2 ha, as long as these patches were within a larger, $\geq$2 ha forest area.

Patches <2 ha make up 6.8 % of the total forest area in England, but 75 % of the total number of patches (Watts 2006). To assess the importance of the small patches to the overall landscape metrics, all patches <2 ha were checked, and if necessary, digitised on orto-rectified Google Earth images in five sample 10 km × 10 km areas in the Upper Thames catchment area in Southern England (Fig. 1). The landscape metrics were then calculated for those areas both including and excluding the small patches. Patches that were partly outside of the chosen sampling areas were included if >50 % of the patch area was within the sampling area. Four of the sampling areas were selected randomly and one was placed around Wytham Woods, a well-studied forest (Butt et al. 2009; Savill et al. 2010), from where data are available to estimate the landscape scale effect of fragmentation on ecological processes.

Dataset 2, ancient woodlands, was based on the Ancient Woodland Database (© Natural England copyright 2013. Contains Ordnance Survey data © Crown copyright and database right 2013). Ancient woodlands cannot be considered "virgin forests", having been affected by human activities for centuries,

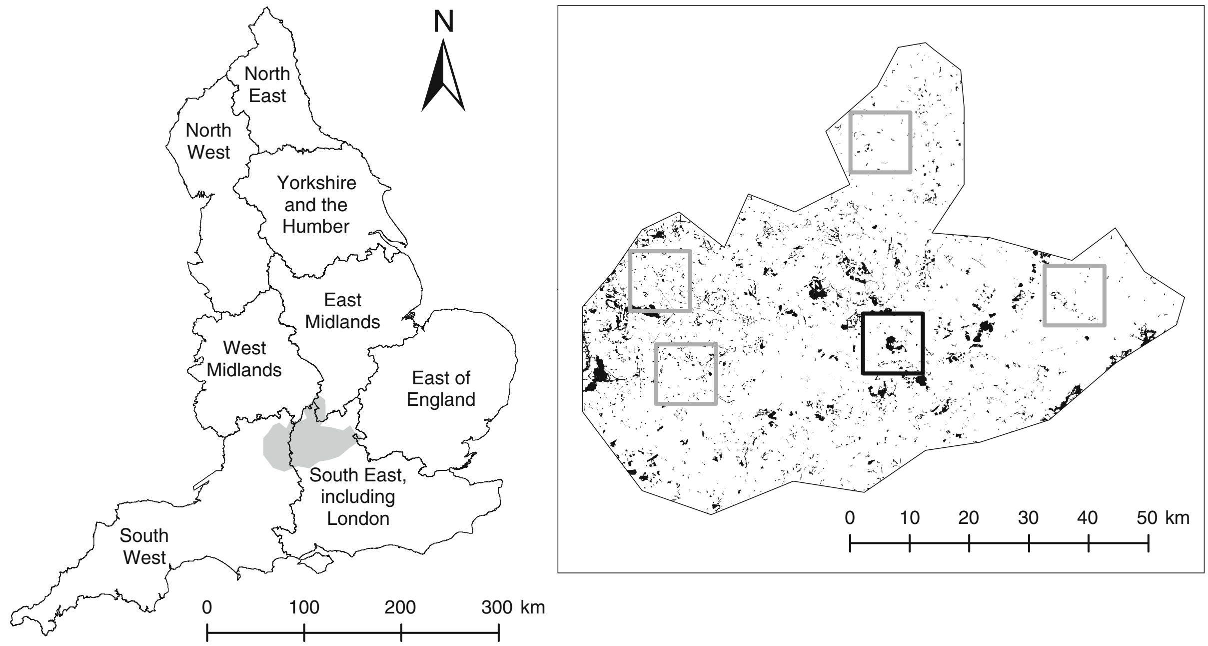

Fig. 1 Regions of England, and the Upper Thames catchment area (*grey area* in the large map; *inset*), within which five 10 km × 10 km sub-areas (*rectangles in the insert*) were selected for assessing the importance of forest patches <2 ha on the results. Data from the sub-area marked with the *black rectangle* was used for combining fragmentation statistics with ecological response functions (see text and Fig. 3). Source of the regional boundaries: 2001 Census, Output Area Boundaries. Crown copyright 2003. Crown copyright material is reproduced with the permission of the Controller of HMSO. Forest patches ≥2 ha in the inset are based on information supplied by the Forestry Commission, National Forest Inventory—England, © Crown copyright and database right 2011. Ordnance Survey Licence number 100021242

but they have specialist species that rarely occur in woods of recent origin, and are thus one of the most important ecosystem types for conservation in England (Peterken 1993; Rackham 2008). Although ancient woodlands have had a continuous tree cover since at least 1600 AD, they may have been managed and allowed to regenerate naturally, or the original tree cover might have been replanted, often with conifers. In the database, ancient woodlands are divided into two categories: ancient and semi-natural woodlands (ASNW), and ancient replanted woodlands. We analysed the data separately for all ancient woodlands and for ASNW. For the analysis of all ancient woodlands, internal boundaries within continuous ancient woodland areas were removed and patches ≥2 ha extracted for the analysis. The analyses for ASNW included patches <2 ha, as long as these patches were within a larger, ≥2 ha ancient woodland area.

Landscape indices

To characterise the landscape, we calculated landscape indices (see e.g. Riitters et al. 1995; Hargis et al. 1998; Cushman et al. 2008) in four ways: (i) for continuous forest patches consisting of any, possibly several, forest types, (ii) by the four different forest types described above (broad-leaved, coniferous, mixed, sparse tree cover), (iii) for ancient woodland patches, and (iv) for ANSW patches. The indices calculated were:

- Total area.
- Number of patches.
- Mean and median patch size.
- Mean and median shape index of the patches, calculated for each patch as the perimeter of the patch divided by the minimum perimeter of a patch of the same size (i.e. the circumference of a circle of equivalent area).

- Edge density, which is the sum of the total length of the forest edge (forest vs. non-forest) divided by the total land area, calculated for all forest and by forest type.
- Average distance from within each patch to the nearest open edge (an edge between forest and non-forest), calculated as the mean of all the 10 × 10 m pixels within the patch. The mean and median for the landscape was taken from the patch-wise results.
- Mean and median maximum distance to the open edge. Maximum distance was calculated separately for each patch and the mean and median for the landscape was taken from the patch-wise results.
- Mean distance (edge to edge) to the nearest patch of the same category (i.e. to the nearest continuous forest patch of any type, to the nearest patch of the same forest type, to the nearest ancient woodland patch, and to the nearest ASNW).

The current forest policy in England is to increase the forest area from 10 to 12 % of the land area by 2060 (Defra 2013). To reflect a realistic shorter-term objective, we simulated the influence of an increase in forest area from 10 to 11 % of the land area in two ways: (i) New patches, the size and shape distribution of which matched the existing patches, were created in random locations. New patches were created until the total forest area was increased by 10 %. (ii) The area of randomly sampled existing patches was increased by 10 % by creating a buffer around the patch, the width of which depended on the area of the patch. Existing patches were randomly chosen and buffered until the total forest area was increased by 10 %. In case the new or enlarged patches overlapped with an existing patch, only the non-overlapping areas were included. The landscape metrics were then re-calculated for the two simulated forest landscapes, including both the original and the new or enlarged patches.

In addition to the landscape metrics, we created a continuous surface of distance to the nearest open edge (an edge between forest and non-forest) from within the forest patches to examine in more detail the magnitude of forest edge habitat (the definition of which is not be pre-determined, but is flexible and chosen later, depending on the species or ecosystem process being examined) in England. The main analyses concentrated on the edge between forest and non-forest land. For broad-leaved forests and ASNW, the most important forest types for biodiversity, we also examined the edges bordering coniferous or sparsely treed areas, because a change in forest type may form an important boundary for specialist species. The pixel size used in this analysis was 10 m × 10 m. To allow a numerical comparison of the edge habitat distribution and magnitude between different forest types, a hyperbolic curve (Eq. 1) was fitted separately for each forest type:

$$y = a \times dist/(1 + b \times dist) \quad (1)$$

where y is the cumulative proportion of the forest area, $dist$ is the distance to the nearest edge from within the forest patch, a/b denotes the asymptotic maximum of y and $1/b$ denotes the distance at which 50 % of the asymptotic maximum is reached. The curves were fitted using SigmaPlot 12.0.

The emphasis of the study was on the country scale data. However, the analyses were also carried out by different regions (Fig. 1) to assess the variation within England.

Combining ecological response functions and landscape characteristics

To illustrate the potential applications of the data, landscape metrics were combined with ecological response functions. We chose one example related to an ecosystem process and one related to biodiversity, both from Wytham Woods (51°46′N, 001°20′W) in southern England, and used the five sampling areas in Fig. 1 to show how the maps can be used to quantify ecological processes at the landscape scale. The ecosystem process example was the transpiration of broad-leaved tree stands at varying distances from the edge (Herbst et al. 2007). The biodiversity example was a study on how distance from the edge influences the abundance of forest specialist moths (Slade et al. 2013). Both processes showed a clear edge effect, and the response functions (process vs. distance from the edge) were used to evaluate the effect at a landscape scale.

All GIS analyses were carried out in ArcGIS, versions 9.3, 10.0 and 10.1.

Results

Forest patches ≥2 ha covered 9 % of the total land area of England. Although patches <2 ha were not

Table 1 Patch characteristics of forest patches $\geq$2 ha in England

Forest type	Forest area (ha) and proportion of total forest area (%)	Number of patches	Mean (median) patch size (ha)	Mean (median) shape index[a]	Edge density (km km^{-2})[b]	Mean (median) distance to the nearest open edge (m)[c]	Mean (median) maximum distance to the nearest open edge (m)[d]	Mean (median) distance to the nearest patch of the same type (m)
All forest	1,168,110 (100 %)	71,230	16.4 (4.4)	2.02 (1.82)	142	29 (24)	84 (65)	230 (130)
Broad-leaved	694,860 (59 %)	103,090	6.7 (2.8)	1.96 (1.79)	132	33 (25)	84 (65)	160 (60)
Coniferous	306,000 (26 %)	35,380	8.6 (2.3)	1.60 (1.46)	38	59 (39)	124 (85)	350 (130)
Mixed	42,250 (4 %)	19,780	2.1 (1.3)	1.52 (1.43)	11	75 (31)	97 (51)	620 (310)
Sparsely treed	125,000 (11 %)	33,530	3.7 (1.5)	1.88 (1.56)	24	51 (27)	99 (65)	430 (160)
All ancient woodlands	350,013 (29 %)	21,639	16.2 (6.5)	1.82 (1.64)	38	63 (44)	152 (110)	380 (150)
ASNW[e]	199,850 (17 %)	21,135	9.5 (4.7)	1.83 (1.64)	29	73 (43)	151 (108)	400 (160)
All forest, 10 % new patches[f]	1,280,350 (110 %)	72,340	17.7 (4.4)	1.81 (1.71)	140	29 (24)	82 (65)	240 (150)
All forest, 10 % buffer[g]	1,284,870 (110 %)	70,990	18.1 (4.4)	1.95 (1.76)	135	29 (24)	83 (65)	220 (120)

In the ‘All forest’ category, forest type is not taken into account: each patch may comprise more than one type. See Fig. S1 in the Online Supplementary Material for examples of distributions

[a] Calculated for each patch as the perimeter of the patch divided by the minimum perimeter of the patch of same size (i.e. circumference of a circle of equivalent area)

[b] Mean for the landscape; total edge length in the landscape (by forest type) divided by the total land area

[c] Average distance to the edge calculated separately for each patch, as a mean of all the 10 $\times$ 10 m pixels within the patch, and the landscape mean and median taken from the patch-wise results

[d] The longest possible distance to the edge calculated separately for each patch and the landscape mean and median taken from the patch-wise results

[e] Ancient and semi-natural woodlands, which is a sub-category of ancient woodlands. Ancient woodlands comprise two categories: ASNW and ancient replanted woodlands

[f] Simulation, where new patches were created in random locations, until a 10 % increase in total forest area was reached. The size and shape distribution of the new patches mirrored those of the existing patches

[g] Simulation, where the area of randomly chosen existing patches was increased by 10 %, until a 10 % increase in total forest area was reached

Table 2 Landscape metrics in the five sample areas in Upper Thames region (Fig. 1), including and excluding forest patches <2 ha

	Forest area (ha) and proportion of total forest area (%)	Number of patches	Mean (median) patch size (ha)	Mean (median) shape index[a]	Edge density (km km^{-2})[b]	Mean (median) distance to the nearest open edge (m)[c]	Mean (median) maximum distance to the nearest open edge (m)[d]	Mean (median) distance to the nearest patch (m)
Patches <2 ha included	2022 (100 %)	450	4.5 (2.1)	1.66 (1.45)	97	21 (18)	56 (49)	290 (200)
Patches <2 ha excluded	1807 (89 %)	224	8.1 (4.0)	1.84 (1.62)	76	28 (24)	77 (66)	350 (210)

[a] Calculated for each patch as the perimeter of the patch divided by the minimum perimeter of the patch of same size (i.e. circumference of a circle of equivalent area)

[b] Mean for the landscape; total edge length in the landscape divided by the total land area

[c] Average distance to the edge calculated separately for each patch, as a mean of all the 10 × 10 m pixels within the patch, and the landscape mean and median taken from the patch-wise results

[d] The longest possible distance to the edge calculated separately for each patch and the landscape mean and median taken from the patch-wise results

included in the country-wise analysis, the patch size distribution was highly skewed towards small patches, with mean and median patch sizes of 16 and 2 ha, respectively (Table 1). The other indices were also skewed towards small values (distributions shown in Fig. S1 in the Online Supplementary Material). In an average forest patch, the maximum possible distance to the edge was 84 m. Continuous forest patches typically consisted of more than one forest type; the number of continuous forest patches comprising any forest type was 71,230, whereas the sum of the patches by individual forest type was 191,780. The mean patch size of coniferous forests was larger than those of the other types. The distance to the nearest patch of the same type was smallest for the broad-leaved patches. Based on the shape index, the broad-leaved patches had slightly more complex shapes than the other forest types. Ancient woodlands had a slightly lower mean patch size but a higher median patch size, and longer average and maximum distance to the edge than forests in general. ASNW, however, had markedly lower mean and median patch size than all ancient woodlands or all forests overall. The mean distance to the nearest patch of the same type was longer for ancient woodlands than for forests in general.

The hypothetical 10 % increase in forest area increased the mean and median patch sizes (Table 1). These changes were more pronounced when the area of the existing patches was increased, compared with the creation of new patches in random locations. The new or enlarged patches often connected several existing patches. Therefore, the total number of patches was only slightly higher (in case of new random patches) or slightly lower (in case of enlarged patches) compared with the original landscape.

Based on the sample from the Upper Thames area (Fig. 1), inclusion of the small patches (<2 ha) in the analyses decreased the mean and median patch size, as would be expected (Table 2). The small patches had less complex shapes than the patches ≥2 ha, resulting in a lower mean shape index. The amount of forest edge in the landscape increased by 28 % (edge density, km of forest edge per square km of land area) and the distance to the nearest patch decreased when the small patches were include in the analyses.

Edge-influenced areas formed a considerable proportion of the total forest area (Fig. 2a; Table 3). Thirty-seven percent of the forest area was within 30 m (equivalent of the height of the tallest canopy

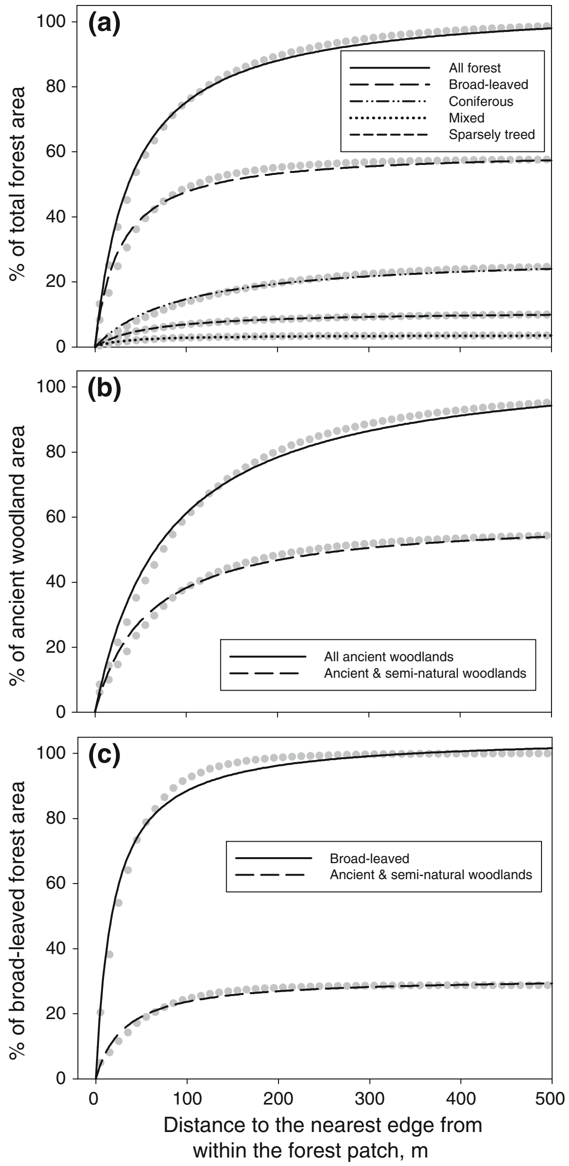

Fig. 2 Cumulative percentage of **a** forest area by forest type and **b** ancient woodland area as a function of the distance to the nearest non-forest edge from within the forest patch; **c** broad-leaved and ancient and semi-natural woodland area as a function of the distance to the nearest coniferous, sparsely treed forest or non-forest edge, from within the forest patch. Hyperbolic curves (Eq.1; Table 3) were fitted to the data

trees; zone of the most pronounced microclimatic effects) and 74 % was within 100 m (the extent of most microclimatic effects) of the nearest open edge. Only 2 % of the total forest area was >500 m from the nearest edge. The longest distance to the edge in the whole country was 1.4 km, in a conifer plantation on the border of the North East and North West regions (Fig. 1) (Kielder Forest in Northhumberland). Ancient woodlands had slightly less edge habitat than forests overall: 28 and 62 % of the area was within 30 and 100 m of the nearest open edge, respectively (Fig. 2b; Table 3). ASNW made up a higher proportion of the total ancient woodland area in the categories closer to the edge than the ancient replanted areas. Taking internal (broad-leaved forest vs. forest of different type) boundaries into account, >90 % of the total broad-leaved forest area was within 100 m from the edge (Fig. 2c). Hyperbolic curve (Eq. 1; Table 3) was overall the best fit to characterise the cumulative area–distance to the edge relationship, out of the many saturating functions tested. From approximately 150–200 m onwards, a simple power function ($y = ax^b$) would also have fitted the data, indicating scale invariance at these larger distances.

Regional (Fig. 1) differences in the landscape metrics and edge distribution were relatively small (Fig. S2, Online Supplementary Material), with the exception of the North East, where 30 % of the total forest area was >500 m from the edge and the mean patch size (29.4 ha) was markedly higher than elsewhere, reflecting the large scale planting of conifers in the region.

We used two examples to illustrate how fragmentation maps can be combined with ecological response curves to generate biologically meaningful estimates of the impacts of fragmentation on ecosystem processes and biodiversity. First, forest stand transpiration increases towards the forest edge (Herbst et al. 2007; Fig. 3). Assuming no edge effect, the estimate for the stand transpiration in the landscape in Fig. 3 was 327 mm over the growing season. However, if the edge effect was taken into account, the mean stand transpiration in the landscape was 428 mm (30 % higher), or 436 mm (33 % higher), if patches <2 ha were included.

As the second example, the abundance of forest specialist moths markedly decreases towards the forest edge (Slade et al. 2013; Fig. 3). Based on the response curve, areas >200 m from the forest edge can be considered core areas that support the maximum number of individuals (100 %). In the landscape in Fig. 3, only 9 % of the forest area was >200 m from the edge. Taking the edge effect into account, the distance weighted average number of moths in the landscape was 49 % of the number of individuals observed in the forest core areas.

Table 3 Parameters *a* and *b* (and their standard errors), coefficient of determination (R^2), standard error of the estimate (SEE) and significance of the regression (*p* value) of Eq.1, fitted separately for each forest type

Forest type	*a*	*b*	R^2	SEE	*p* value
All forest	2.60 (0.04)	0.025 (0.0004)	0.99	1.31	<0.0001
Broad-leaved	2.24 (0.07)	0.037 (0.0012)	0.97	1.32	<0.0001
Coniferous	0.30 (0.01)	0.011 (0.0003)	0.98	0.74	<0.0001
Mixed	0.12 (0.01)	0.032 (0.0010)	0.98	0.08	<0.0001
Sparsely treed	0.19 (0.01)	0.017 (0.0002)	1.00	0.12	<0.0001
All ancient woodlands	1.40 (0.03)	0.013 (0.0033)	0.99	1.91	<0.0001
ASNW[a]	1.05 (0.02)	0.017 (0.0005)	0.99	1.19	<0.0001
Broad-leaved, with internal boundaries	5.52 (0.22)	0.052 (0.0023)	0.97	2.42	<0.0001
ASNW, with internal boundaries	0.99 (0.04)	0.032 (0.0015)	0.97	0.042	<0.0001

[a] Ancient and semi-natural woodlands, which is a sub-category of ancient woodlands

Discussion

It is well known that the forest area in England, and in the whole of the UK is low, and comprises mainly small, isolated fragments (for a detailed analysis on the patch size distribution, see Watts 2006). However, what has not been previously quantified is how much of this forest area is edge influenced. This study is the first to specifically quantify the magnitude of the forest edge in England, and to our best knowledge, such analyses have not been carried out for any other country. The results show that even when the small forest patches (<2 ha) are excluded, half of the total forest area, and 45 % of the ancient woodland area in England lies within 60 m of the nearest open edge—just two or three canopy tree heights. This has implications on biodiversity and ecosystem functioning. For example, edge effects on forest microclimate, such as soil and air temperature, relative humidity and soil and litter moisture typically extend to between 30 and 100 m (Kapos 1989; Matlack 1993; Young and Mitchell 1994; Chen et al. 1995; Didham and Lawton 1999; Davies-Colley et al. 2000). Therefore, approximately 40 to 75 % of the forest area in England is edge-influenced in terms of microclimate, which will in turn have an effect on ecosystem processes, such as soil fauna activity (Simpson et al. 2012) and litter decomposition (Riutta et al. 2012). If we use the (admittedly, somewhat subjective) cut-off limit of 100 m as the division between edge and core, then edge habitat prevails (74 % of the total forest area), and has prevailed for centuries, in England. The magnitude of the edge habitat is even more pronounced, if the internal edges between forest types are taken into account: in case of broad-leaved forests, >90 % of their total area is within 100 m of the nearest open edge, or an edge bordering coniferous or sparsely treed forests.

To our best knowledge, this approach of treating the distance to the nearest edge as a continuous variable has not been used before as a measure of habitat fragmentation in landscape ecological studies. One of the factors that complicate efforts to 'scale up' edge responses is the lack of a definition of forest edge and core habitat, and how far an edge extends into a patch (Ries et al. 2004; Ewers and Didham 2006b). Treating edge as a continuous variable is thus advantageous when quantifying edge effects: It is more flexible than a predefined division into edge and core habitats, because it is not process or species-specific. Therefore, the continuous distance to the edge surface, and the resulting numerical data, can be used for multiple purposes. The amount of the edge and core habitat can be easily derived from this data for any case-specific definition of edge and the core. This data can also be flexibly used for upscaling any ecological response as a function of distance to the edge. Such an approach has been advocated as the best method to assess and compare the effects of fragmentation between different studies, taxa and ecosystems (Ewers et al. 2010). Moreover, developing models and methods to upscale ecological data from local to landscape level to improve predictions and management decisions has been listed as one of the key future directions in biodiversity research (Cardinale et al. 2012). Recent studies suggest that responses to edge effects may be more important than responses to changes in habitat area *per se* and may underlie many of the observed

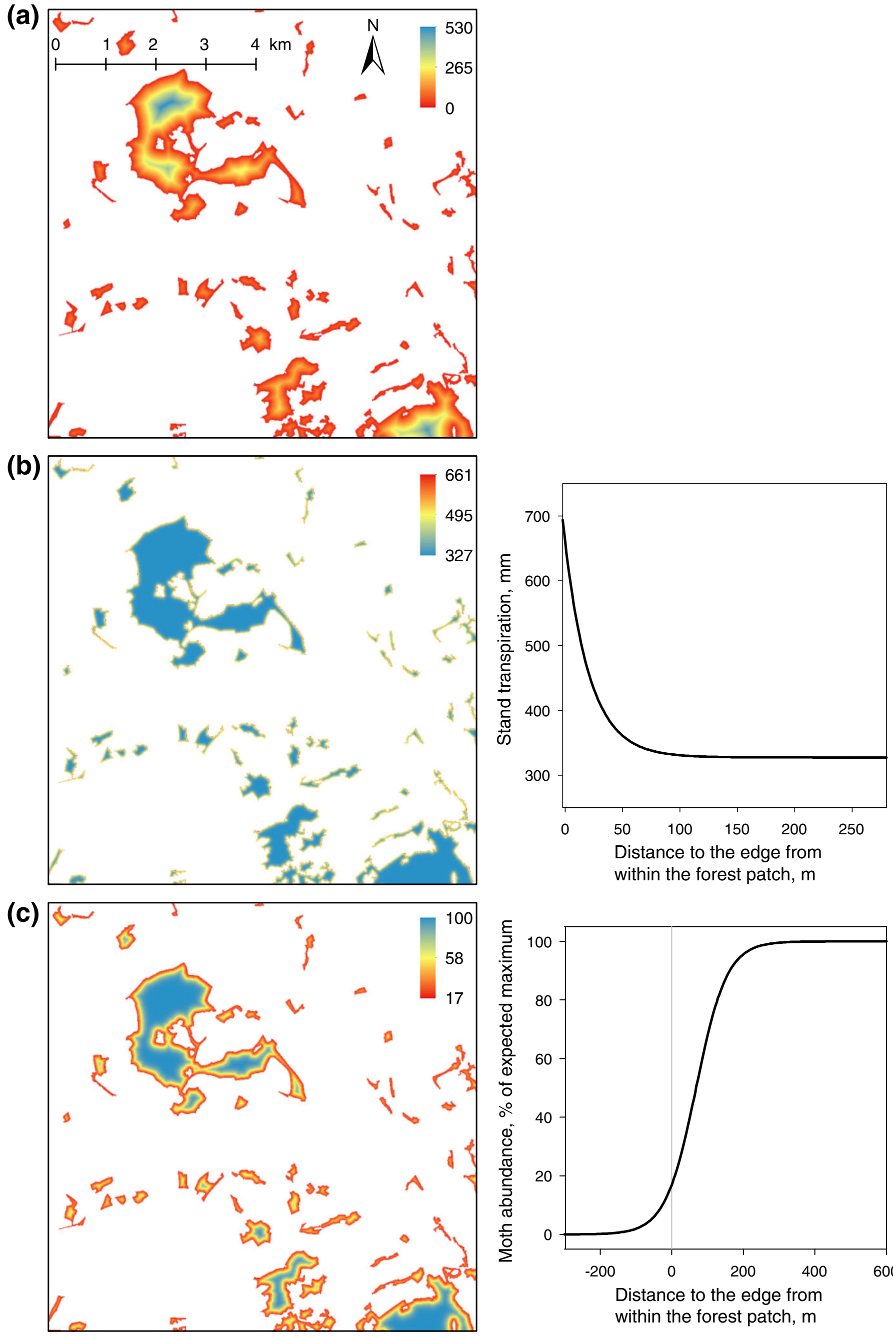

Fig. 3 Examples of combining ecological response functions with fragmentation maps. **a** Forest patches ≥2 ha in one of the sample areas in the Upper Thames catchment area (see Fig. 1, *black square* in the *inset*). *Colours* indicate distance to the nearest edge (forest vs. non-forest) from within the forest patch (m). **b** Transpiration (mm) of a broad-leaved stand as a function of distance to the edge, response curve estimated based on Herbst et al. (2007). **c** Abundance (% of the number of individuals found in forest core area) of forest specialist moths as a function of distance to the edge (data from Slade et al. 2013). Map of the forest patches are based on information supplied by the Forestry Commission, National Forest Inventory—England, © Crown copyright and database right 2011. Ordnance Survey Licence number 100021242

species–area relationships (Ewers et al. 2007; Fletcher et al. 2007; Banks-Leite et al. 2010). Therefore, being able to quantify the amount of habitat at various distances from the edge becomes increasingly important.

Forest studies, unless they are explicitly addressing edge effect or fragmentation, tend not to take place at the very edge of the forest, particularly if the sampling design is not random. However, given that 17 % of the total forest area in England is within 10 m from the nearest forest edge, even when patches <2 ha are excluded, every sixth study site or sampling plot should be within this distance to be representative of the landscape. Whether this is the case in the UK forest literature is difficult to evaluate, but we venture a guess that the areas close to the edge are undersampled. This is likely to be especially true for studies requiring intensive monitoring plots, complex experiments or large structures that are not feasible to replicate in large numbers (or at all), such as forest carbon cycling plots (see e.g. Heinemeyer et al. 2007; Fenn et al. 2010) or canopy walkways. Because edge effects are often non-linear (Murcia 1995; Ewers et al. 2007) and strongest within the first 10–20 m from the edge (Young and Mitchell 1994; Chen et al. 1995; Didham and Lawton 1999; Ewers and Didham 2008) the landscape scale estimates are particularly sensitive to the values from this zone. As the examples used in this study illustrate, the estimates for an ecosystem process or species abundance can be widely different depending on whether the data has been collected only in forest interior or whether it includes forest edges. Even with a relatively short depth of edge influence, like the stand transpiration example in this study (60 m), the landscape scale estimates changed by 30 %, when the edge effect was taken into account.

The effects of climate change on forests may be exacerbated in fragmented landscapes for at least two reasons: Firstly, the microclimate in forest edges and small fragments is already more extreme, more variable (Chen et al. 1993; Didham and Lawton 1999; Davies-Colley et al. 2000; Riutta et al. 2012) and likely to experience bigger changes than the forest core area, being more exposed and lacking the buffer created by the surrounding forest. As a result, the future temperature and moisture conditions in the edges and small fragments are more likely to fall outside the temperature or moisture niche of a species, especially during extreme events, or temperature or moisture may become a limiting factor for an ecosystem process, such as photosynthesis or decomposition. Therefore, larger patches are likely to be more resilient. Secondly, climate change induces shifts in species' geographic ranges and habitat networks (Berry et al. 2002; Opdam and Wascher 2004), but the configuration of the landscape, such as patch size distribution and connectivity, may limit the species' ability to disperse and recolonize. Therefore, the effect of climate change on metapopulation ecology should be examined in the context of spatially explicit landscapes (Opdam and Wascher 2004).

Large scale planting of trees can effectively change the characteristics of the forest landscape. This can be seen in the North East region, which has a markedly higher mean patch size and a smaller proportion of the edge-influenced forest area than the other regions in England, due to large areas of conifer plantations. However, in this case the plantations consist mostly of non-native conifers (predominantly Sitka spruce). Therefore, they are of low conservation value, despite their large patch size, and targets for restoration when situated in ancient woodland sites (HMSO 1995; Hall and Kirby 1998; JNCC and Defra 2012). The simulations carried out in this study showed that a 10 % increase in forest area had a relatively small impact on the fragmentation indices if the increase happened in random places. The changes were bigger when the increase was in a form expansion of existing patches rather than creation of new patches. Recent simulations have shown that in highly fragmented habitats the effect of fragmentation on metapopulation dynamics is more effectively reduced if habitat fragments are in clusters rather than randomly distributed across the landscape (Rybicki and Hanski 2013). Therefore, if the goal is to maximise the patch size and connectivity, the efforts to increase the forest area should take place in targeted locations, rather than randomly, taking into account the characteristics of the landscape.

Conclusion

We suggest that using a distance to the edge from within the forest patch as a continuous variable and quantifying the distribution of the forest area along the distance gradient is a useful way to characterise habitat fragmentation. In England, 37 % of the total forest area was within 30 m and 74 % within 100 m of the nearest edge, highlighting the importance of taking edge effects into account in ecological studies in this type of landscape.

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