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Title:

The influence of habitat availability and landscape structure on the distribution of wood cricket (*Nemobius sylvestris*) **on the Isle of Wight, UK**

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1.1 Abstract

Little information is available regarding the landscape ecology of woodland invertebrate species with limited dispersal ability. An investigation was therefore conducted within woodland fragments in an agricultural landscape for the flightless wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK. The current pattern of distribution of the species, established during a field survey, was related to measures of habitat availability and habitat isolation/fragmentation. Results revealed that wood cricket populations were patchily distributed and mainly found in relatively large mature woodland fragments situated closely (<50 m) to another occupied site. Although the occurrence of wood cricket was related to fragment area, isolation, habitat availability and woodland age, a logistic regression model revealed that presence of the species was most accurately predicted by fragment isolation and area alone. These results highlight the vulnerability of relatively immobile woodland invertebrate species, such as wood cricket, to the potential negative impacts of habitat fragmentation.

Keywords: woodland; forest; habitat availability; fragmentation; landscape scale; invertebrate; insect; wood cricket; *Nemobius sylvestris*; Isle of Wight.

1.2 Introduction

In recent years, many habitats and species have been subjected to increasing anthropogenic pressures. Activities such as agricultural intensification and exploitation of natural resources have resulted in substantial habitat loss and fragmentation (e.g. Forman and Godron 1986; Andrén 1994), which are increasingly being recognised as principal drivers of biodiversity loss worldwide (Hanski 1998; Fahrig 2003). These effects are typically evident at the landscape scale, with many landscapes now being characterised by a mosaic of different agricultural land use types with fragments of native habitat embedded within them (e.g. Peterken 2000; Newton 2007).

In fragmented landscapes, the distribution and abundance of species is commonly influenced by the quality and amount of habitat available within individual habitat fragments, and the spatial configuration of fragments within the landscape (Andrén 1994; Fahrig 2003). In terrestrial environments, the factors most commonly examined in relation to patterns of species diversity at the landscape scale are measures of fragment or patch area and connectivity. A substantial body of literature is now available documenting the influence of these factors (Andrén 1994; Mazerolle and Villard 1999; Bennett 1999, 2003; Ewers and Didham 2006; Bailey 2007). Many studies have recorded a positive relationship between species diversity and fragment area and a negative relationship between diversity and the degree of isolation, consistent with island biogeography theory (MacArthur and Wilson 1963, 1967). However, these relationships vary in their precise response and degree of significance among and within different taxonomic groups, primarily because of variation in habitat specialisation and the level of permeability of the matrix for different groups of organisms (MacArthur

and Wilson 1967; Andrén 1994; Mazerolle and Villard 1999; Bennett 1999, 2003; Magura et al 2001; Lövei et al 2006).

Landscape-scale studies on individual species also indicate the importance of patch area and connectivity as key variables influencing the distribution of individual species at the landscape scale, as shown in studies on mammals (Andrén 1994; Mazerolle and Villard 1999; Bennett 1999, 2003) and birds (Andrén 1994; Mazerolle and Villard 1999). However, most previous investigations have focused on species with relatively high dispersal ability (Andrén 1994; Bellamy et al 1996; Crooks and Sanjayan 2006; Bailey 2007). Very few studies have assessed the factors influencing the distribution of relatively immobile species within fragmented wooded landscapes, raising questions about the general applicability of results obtained to date (Andrén 1994; Mazerolle and Villard 1999; Bailey 2007). In particular, relatively immobile invertebrates have been neglected by previous landscape ecology research (Mazerolle and Villard 1999; Bailey 2007). Understanding the impact of habitat fragmentation on this group of species is of particular importance, as many have highly restricted distributions and are considered as priorities for conservation action; they may also be especially vulnerable to fragmentation impacts (Ranius 2002; Buse et al 2007; Matern et al 2007; NBN Gateway 2007). Those investigations undertaken to date have focused primarily on beetles, and have revealed differing responses to fragmentation based on variation in the degree of habitat specialisation (Rukke and Midtgaard 1998; Ranius 2000; Rukke 2000). In general, the habitat availability within individual patches was found to be a strong predictor of the distribution of such species at the landscape scale (Petit and Burel 1998; Rukke and Midtgaard 1998; Ranius 2000; Rukke 2000).

No previous study has examined the effects of fragmentation, together with within-patch habitat availability and fragment age, on the landscape-scale distribution of a relatively immobile woodland invertebrate species. This investigation therefore examined the effects of patch area, isolation, habitat availability and patch age on the incidence of such a species within woodland fragments in a predominantly agricultural landscape. The study was performed on wood cricket (*Nemobius sylvestris*) on the Isle of Wight, United Kingdom. Wood cricket is a non-flying cricket species that is strongly associated with native broadleaved (i.e. deciduous) woodland, typically dominated by oak (*Quercus spp.*) (Richards 1952). The species is characteristic of relatively open areas within woodlands representing a transition between closed- and open-canopy habitat, and generally can be found along wooded edges, tracks and rides, and within clearings (Richards 1952). Like all Orthoptera and the majority of insects, wood cricket need warmth for their development (Marshall and Haes 1988). Presence of permanently open, sunny woodland edge habitat is therefore important for the persistence of the species within the landscape. The insects live on the ground and need a well-developed leaf litter layer that acts as shelter, a primary food source and as breeding ground (Gabbutt 1959). Presence of deciduous tree species within the canopy and/or understorey of woodland stands is therefore essential to create suitable habitat for this species. In Europe, the species is widely distributed from the Mediterranean countries through to central Europe (Marshall and Haes 1988). In the UK, the species reaches its northern limit and can only be found at three main locations in southern England, namely the New Forest (Hampshire), South Devon and on Isle of Wight (Marshall and Haes 1988; NBN Gateway 2007). In the UK, wood cricket is classified as 'Nationally Scarce' and designated as a 'Species of Conservation Concern' (NBN Gateway 2007).

This study addressed the following aims: (1) to determine the landscape-scale distribution of wood cricket on the Isle of Wight (UK), which was largely unknown at the outset of this investigation (NBN Gateway 2007); (2) to test the relationships between wood cricket presence/absence and (*a*) patch area, (*b*) isolation (i.e. Euclidean distance), (*c*) edge habitat availability and (*d*) patch age; and (3) to develop a deterministic model for wood cricket presence within habitat patches. Based on the general findings of previous fragmentation research and the known biology of the species, it was hypothesised that wood cricket would be more likely to be present in woodlands that: (*1*) are large rather than small (because large woodlands are likely to include more edge habitat); (*2*) are spatially aggregated rather than isolated (because wood cricket is flightless, limiting its dispersal ability); (*3*) have a relatively large perimeter and are relatively complex in shape (because woodland edges are their preferred habitat), (*4*) provide a high amount of permanent edge habitat, and (*5*) are relatively long-established (because wood cricket need permanent woodland habitat conditions to persist).

1.3   Methods

1.3.1   Study area

A survey was carried out in the woodlands of the Isle of Wight (UK) situated between 50° 39' N, 1° 35' W and 50° 40' N, 1° 04' W (Figure 1). The total surface area of the Isle of Wight is 388 km² (estimated in ArcGIS 9.1 (ESRI, Redlands, California, USA)). Total woodland area is currently 51.2 km² (5120 ha) covering 13% of the island (Figure 1). The landscape matrix is dominated by urban and agricultural land with woodland

patches distributed across the island. Of the total woodland area, 32% is classified as woodland still retaining ancient woodland characteristics of which 17% is classified as ancient semi-natural woodland (ASNW) and the remaining 15% as planted ancient woodland sites (PAWS) (i.e. planted with non-native, mainly coniferous, tree species). The remaining woodlands are secondary in origin or are plantations (Smith and Gilbert 2003).

#Figure 1#

1.3.2   Survey methods

The survey was carried out between mid-July and mid-September 2005. Wood cricket is known to be associated with deciduous woodlands as its preferred habitat. Therefore, the focus of the survey was on the northern part of the Isle of Wight where the majority of deciduous woodland fragments are located. The following selection criteria were used for the survey. All mature deciduous woodlands with at least 50% native species cover in the canopy that were larger than 5 ha in extent were included in the survey. A random sample of smaller woodlands was also surveyed. When wood cricket was found within a woodland fragment, all neighbouring areas of woodland were also surveyed. All woodland fragments were surveyed with the same intensity relative to their size (ha).

The survey was focused on adult wood crickets. Individuals were located by sound recognition of stridulating males, following the method of Proess and Baden (2000). Male wood cricket produce a very distinctive sound by stridulation, which is not readily confused with any other species (Proess and Baden 2000). Presence of wood cricket

was confirmed by visual observation wherever possible. To optimise detection success the surveys were carried out on days with a mean daytime temperature of ≥15°C. Individual woodlands were each systematically surveyed focusing on the woodland perimeter and internal edges such as rides and clearings. When individuals were encountered, each location was recorded using a hand-held GPS device (Garmin III GPS V, Garmin (Europe) Ltd, Romsey, UK).

1.3.3   Habitat variables and GIS analysis

A digital map based on the National Inventory of Woodland and Trees (NIWT) (Smith and Gilbert 2003) was used within the software package ArcGIS 9.1 (ESRI, Redlands, California, USA) to create a base map, in which the different woodland habitat types present on the Isle of Wight were differentiated (Figure 1). The original map was adapted by reducing the original stand classification to three main woodland habitat stand type classes, namely 'mixed', 'broadleaved' and 'coniferous'. 'Mixed' included stands with a mixture of broadleaved and coniferous species with both groups occupying at least 20% of the canopy. 'Broadleaved' and 'coniferous' stands were defined as each respectively having an overall dominance of at least 80% within the canopy.

From the base map, two woodland sample maps were constructed, which were used in further analyses. The first sample (Sample 1) included all the woodlands that were surveyed, which were each classified according to the three woodland habitat stand-type classes. With this classification, a single woodland could therefore be divided into several individual woodland 'units', each representing a different stand type. This

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resulted in a sample including 215 separate woodland 'units', which were each classified as one of three stand type categories namely broadleaved (n_b = 115), coniferous (n_c = 44) and mixed (n_m = 56). For the second sample map (Sample 2), the separate woodland 'units' (Sample 1) were aggregated within the boundaries of each single woodland fragment to represent the precise digitised woodland fragments as they occur on the Isle of Wight. Fragment boundaries were defined either by neighbouring agricultural land (grassland or arable) or by distinct anthropogenic/natural landscape features (urban fringes, roads, railway lines, rivers and steams (> 1 m wide)). As the species is flightless, these landscape features were assumed to potentially form barriers to movement of wood cricket. This resulted in a sample size of 147 individual woodland fragments for 'Sample 2'. 'Sample 1'was used to test for differences in wood cricket presence between the different woodland habitat stand types and 'Sample 2' was used for all other analyses. The separate classifications were checked for accuracy against digitised, orthorectified aerial photographs using imagery from The GeoInformation Group (© 2007) available in Google Earth (3.0, Google Inc., Silicon Valley, California, USA) and Getmapping Plc (© 1998, Hartley Wintney, Hampshire, United Kingdom).

Wood cricket presence/absence was related to patch variables that were computed by analysing the sample maps in ArcGIS. 'Sample 1' and 'Sample 2' were used to calculate for each individual woodland fragment the total area (ha), perimeter (m) (i.e. circumference), and two shape measures, namely the fractal dimension index (FRAC) and the shape index (SHAPE) using FRAGSTATS 3.3 (for more details see McGarigal et al 2002). In this case, area can be related to the total amount of woodland habitat present, and perimeter, FRAC and SHAPE to the amount of edge habitat that is available for each individual woodland fragment.

For quantifying the degree of isolation between woodland fragments, a Euclidean distance measure (i.e. nearest occupied neighbour distance) was computed. The distance from the edge of each surveyed woodland to the edge of its nearest occupied neighbour was measured in a straight-line using measurement tools in ArcGIS. This measure was performed separately for both the inhabited and uninhabited woodlands. For the individual woodlands (Sample 2), woodland age was derived using a digital map produced from the inventory of ancient woodland sites for the United Kingdom (Ancient Woodland Inventory; see Spencer and Kirby 1992). This map was used to differentiate between ancient (i.e. woodland established before 1600 AD) and secondary woodland (i.e. woodland established after1600 AD). All woodlands including ancient woodland characteristics within its boundary were classified as 'Ancient'. All other woodlands were classified as 'Secondary'. Only woodland fragments over two hectares in area were included in the analysis, following the original inventory criteria (Spencer and Kirby 1992). This resulted in a sample size for 'Sample 2' of $n = 115$ (40 secondary, 75 ancient).

Finally, for each woodland fragment the total amount of permanent edge habitat was measured as a measure of habitat availability for wood cricket. This measure was computed by adding the perimeter distance to the total distance of permanent edges present within the boundaries of the woodland fragments. Permanent edges within woodlands were defined as clearly visible tracks, paths, roads and railway lines within the boundary of the woodland as detected on orthorectified aerial photographs derived from the GeoInformation Group (© 2007) available in Google Earth (3.0, Google Inc., Silicon Valley, California, USA). These permanent linear features within woodlands

and the woodland perimeter are considered to provide permanent suitable edge habitat for wood cricket. The total distance of these features were calculated with measurement tools available in Google Earth and ArcGIS.

1.3.4   Statistical data analysis

The individual habitat variables were tested to identify relationships with wood cricket presence using SPSS 12.0.1 for Windows (SPSS Inc., Chicago, Illinois, USA). The values for the separate variables were first explored using descriptive statistics within SPSS. This included testing for normality (Kolmogorov-Smirnov test) and producing boxplots for the individual variables to visualise the range and variation in values of measurements made for both 'presence' and 'absence' locations. All variables were found to be not normally distributed.

To explore the relationships between wood cricket presence and woodland area, woodland perimeter, fractal dimension index (FRAC), shape index (SHAPE), distance to nearest wood cricket inhabited woodland and habitat availability (i.e. permanent edges), Mann-Whitney U tests were performed. Additionally, the effect size (r) for each individual variable was calculated ($= z$ / square root n), in this case indicating the strength of association of each variable with wood cricket presence/absence. For exploring the relationships between wood cricket presence and woodland age (using Sample 2) and stand type (using Sample 1), chi-square tests of association were performed. In addition, for woodland age, the odds ratio for wood cricket presence was calculated to examine the likelihood of wood cricket presence in ancient woodland compared to secondary woodland. Finally, a Spearman rank correlation test was

undertaken to examine correlations between the measured variables. To explore the underlying relationships among the group of related variables, a principal components analysis (PCA) was also conducted. Finally, based on Euclidean nearest occupied neighbour distance of all the woodland fragments, all individual response variables were tested for spatial autocorrelations using the autocorrelation test (Box-Ljung test) available in SPSS. For all response variables, autocorrelations were calculated to the 3rd order.

Several logistic regression methods were used to examine the relative influence of the different habitat variables on distribution of wood cricket at the landscape scale. For these analyses, combinations of the continuous variables Area, Perimeter, Permanent edge, FRAC, SHAPE, Distance and Age were used. Three outlying cases were excluded from 'Sample 2' ($n = 147$) resulting in a sample size of $n = 144$, with 113 'absent' and 31 'present' woodlands. These three woodland fragments were excluded, because they were situated in areas where the survey of the surrounding woodlands was not completed. All individual variable responses were explored using the 'Enter' function within SPSS. Only the significant variables ($P < 0.05$) were used to build subsequent models using different variable combinations again by using the 'Enter' function.

The following selection criteria were used to choose the most powerful and realistic model: (1) to avoid an effect on the outcome of the logistic regression analyses, response variables included in the models had to be spatially uncorrelated and all individual correlations (r values) between the variables included had to be < +/- 0.2, (2) all individual tests for significance had to be met ('model fit test' ($P < 0.05$), 'Hosmer & Lemeshow model fit test' ($P > 0.05$) and 'Wald test' ($P < 0.05$)), (3) all B values had to

indicate the correct sign of the relationship (+/-), and (4) the 95% confidence interval for Exp(B) was not allowed to include the value of 1, which indicates no effect. The best-fitting model was then selected based on the highest scores for 'effect size' (R^2_N) and 'Hosmer & Lemeshow model fit test' scores. SPSS output interpretation for logistic regression analyses followed Tabachnick and Fidell (2001).

1.4   Results

1.4.1   Landscape scale distribution

#Figure 2#

Of the total woodland area (5123 ha) present on the Isle of Wight, 2346 ha (45.8%) was surveyed. Of this surveyed woodland area, 1018 ha (43.4%) sustained wood cricket populations (Figure 2). A total of 147 different woodland fragments were surveyed ranging from 0.13 to 396 ha in surface area with a mean of 15.6 +/- 3.71 ha. Of the 147 woodland fragments that were surveyed, 32 fragments supported wood cricket populations where the remaining 115 fragments did not. This survey further indicated that wood cricket has a patchy distribution on the island (Figure 2). Wood cricket shows a wide distribution over the northern part of the island, but the species was found to be absent from several major woodland areas, which were found to be mainly dominated by mixed stands of trees.

1.4.2   Analysis of the independent variables

#Table 1#

In both 'Sample 1' and 'Sample 2', no spatial autocorrelations were present within the response variables (autocorrelation coefficient < +/- 0.136, Box-Ljung: $P > 0.194$, for all variables). Further analysis performed on 'Sample 1' ($n = 215$) testing for association between wood cricket presence/absence and stand type revealed that there was no significant difference between the three stand type categories (Pearson Chi-Square: $\chi^2 = 2.283$, df = 2, $P = 0.319$). Therefore, further analyses focused on 'Sample 2' ($n = 147$). In Table 1, a summary of the independent Mann-Whitney U test results are presented. Nearest occupied neighbour distance showed the highest effect size (r) and significance (P) values related to wood cricket presence (Table 1), indicating a negative effect on wood cricket presence of increasing distance between woodland fragments. Furthermore, the variable indicating the level of habitat availability (Permanent edge) showed a relatively strong relationship with wood cricket presence compared to the other variables (Table 1). Finally, fractal dimension index (FRAC) was not significantly related to wood cricket presence (Table 1).

#Figure 3#

In Figure 3, a series of individual boxplots are presented. The median distance between inhabited woodland fragments ($n_1 = 32$) was found to be significantly less than the median distance between unoccupied woodland fragments ($n_2 = 115$) and their nearest neighbouring woodland inhabited by wood cricket (Figure 3a, Table 1). The median distance between occupied woodlands was 50 m (Figure 3a), indicating that fragments more distant from each other were likely to be effectively isolated. The majority (57%)

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of occupied woodland fragments were found to lie within 50 m of each other (Figure 4).
Furthermore, the majority (82%) of unoccupied woodlands were found to be located
more than 200 m away from occupied locations. Further exploration of the pattern of
occupancy revealed that only four locations on the Isle of Wight included aggregations
of occupied woodland fragments. All other locations (14) consisted of only one
occupied woodland fragment, indicating that most populations at the landscape scale are
effectively isolated from each other.

The median value of permanent edge (i.e. habitat availability), woodland perimeter,
shape index and woodland area was found to be significantly higher for woodland
fragments in which wood cricket was present than for woodland fragments where wood
cricket was absent, although this was not the case for the fractal dimension index
(FRAC) (Figure 3b – f, Table 1).

#Figure 4#

#Table 2#

In accordance with the initial hypothesis on the influence of woodland age, the chi-
square test showed that wood cricket was more likely to be present in woodland
fragments with ancient characteristics than in woodlands of secondary origin (Table 2).
Furthermore, the odds ratio indicated that wood cricket is four times more likely to be
present in ancient woodland than in secondary woodland (Table 2).

#Table 3#

The exploration (PCA) of the correlated variables revealed that the underlying relationships could be captured by three components with eigenvalues exceeding 1, explaining 46.2% (axis 1), 24.7% (axis 2) and 16.4% (axis 3) of the variance respectively. The pattern and structure matrix for the PCA further revealed that axis 1 was highly positively related to Area, Permanent edge and Perimeter (all > 0.922). Axis 2 was highly positively related with FRAC and SHAPE (> 0.948), and axis 3 was positively related to Distance (0.780) and negatively related to Age (-0.735). This indicates each of these groups of variables explain different parts of the variance in the data set.

1.4.3   Logistic regression analysis

Several logistic regressions were undertaken to build a predictive model and to identify the key variables explaining the variation in presence/absence of wood cricket between woodlands. In Table 4, a summary of the most realistic models based on the selection criteria described above are displayed. For these analyses, seven variables were explored with logistic regression, five of which passed the significance test (Wald test: $P < 0.05$; Table 4). These five variables were further used to build a (biological) realistic deterministic model based on the initial selection criteria. After the exploration of the SPSS output for the separate models, for 'Sample 2' ($n = 144$) the best-fitting total model included the variables Distance and Area (Table 4). This model met all selection criteria showing that: (1) no spatial autocorrelations were present and all individual correlations (r) between the variables included were < +/- 0.2 (Distance vs. Area: $r = -0.03$, $P = 0.760$; see Table 3); (2) all individual tests for significance were

met ('model fit test' ($P < 0.05$), 'Hosmer & Lemeshow Model fit test' ($P > 0.05$) and 'Wald test' ($P < 0.05$)) (Table 4); (3) all B values indicated the correct sign of the relationship (+/-) based on the boxplots presented in Figure 3, and (4) the 95% confidence interval for Exp(B) did not include the value of 1 (Table 4).

#Table 4#

Distance to the nearest occupied woodland was the strongest predictor variable, explaining 20% of the variation (Nagelkerke $R^2 = 0.20$; Table 4). For woodland area the explained variation was slightly less (Nagelkerke $R^2 = 0.18$; Table 4). The combined 'Effect size' of distance and area explaining wood cricket presence/absence in the total model was 35% (Nagelkerke $R^2 = 0.35$; Table 4).

#
Figure 5#

Figure 5 shows a 3D representation of the total model showing the probability for wood cricket presence predicted by woodland distance to the nearest occupied woodland and woodland area together. This graph indicates that wood cricket presence is most likely in large woodland fragments situated in close proximity to each other.

1.5   Discussion

The effects of habitat fragmentation on biodiversity have been measured in a variety of ways (Pascual-Hortal and Saura 2006), including impacts on species diversity (e.g. Mazerolle and Villard 1999) and species occurrence (e.g. Vos and Stumpel 1995; FitzGibbon et al 2007). Isolation measures such as Euclidean distance between one habitat fragment and its nearest neighbour have been widely used in this context, mainly because these measures require the least amount of information to obtain them (Calabrese and Fagan 2004). However, such measures are often found to be poor predictors of species presence (e.g. Ranius 2000; Rukke 2000). In the current study, another Euclidean distance measure was used, measuring the distance between all individual fragments to its nearest occupied neighbour. Here, a strong negative relationship was revealed between wood cricket presence and distance to the nearest inhabited woodland fragment. This measure has been used in two previous studies on woodland invertebrate species, which revealed similar relationships. Chardon et al. (2003) observed a similar response for a relatively mobile butterfly species associated with woodland edge habitat, and Petit and Burel (1998) for a ground-dwelling flightless woodland generalist carabid beetle. These results indicate that distance to the nearest occupied neighbour is a useful measure to detect effects of fragmentation and isolation acting on mobile and relative immobile woodland invertebrates at the landscape scale.

Fragments sustaining wood cricket populations were mainly found in close proximity to each other, whereas more distant isolated woodlands tended to be uninhabited. A likely explanation for this is that greater isolation may reduce the interactions between individual populations, making isolated populations more prone to extinction (Hanski and Gilpin 1997). The median distance between occupied woodlands was found to be 50 m, suggesting that wood cricket is highly dispersal limited at the landscape scale.

This implies that the distances between habitat fragments in the landscape studied have a large negative effect on the probability of wood cricket being present. This is understandable given the physical characteristics of the species, being relatively small and flightless (Richards 1952). These results highlight the strong negative effect of fragmentation at the landscape scale on the persistence of this species within individual woodland fragments.

Positive relationships between patch area and presence/absence of individual species have been documented in a number of fragmented landscapes (e.g. Kindvall and Ahlén 1992; Rukke and Midtgaard 1998; Walker et al 2003). For wood cricket, a similar relationship was found: with an increase in woodland fragment area, wood cricket was more likely to be present. Few other studies of relatively immobile woodland invertebrates are available for comparison. The only study examining the effects of fragmentation on the distribution of an immobile ground-dwelling woodland invertebrate at the landscape scale was on the flightless carabid beetle *Abax parallelepipedus* (Petit and Burel 1998), which did not test the relationship between the presence of the species in the woodlands that were surveyed (20 occupied, 10 unoccupied) and the size of these fragments. However, as the species was also found in very small woodlots and hedgerow intersections, this relationship was thought unlikely to be significant (S. Petit (INRA, France), personal communication). The positive relationship recorded here for wood cricket between fragment area and presence is therefore a unique result for an immobile woodland species at this scale of investigation. This result indicates that this relationship may be generally applicable to both mobile and immobile woodland species. However, to support this contention, this relationship needs to be tested for a wider range of relatively immobile woodland species.

Patch area can be considered as a measure of potential habitat available to a species. However, it has been shown previously that presence of woodland invertebrates within a patch is often better predicted by measures of species-specific habitat availability, informed by the ecology of the species (Rukke and Midtgaard 1998; Rukke 2000). In the current investigation, the amount of permanent edge habitat was a strong positive predictor for wood cricket presence within woodland fragments (Table 1, Figure 3b). However, in this case, all measures related to edge habitat availability (Perimeter, SHAPE, FRAC and Permanent edge) were highly positively correlated with fragment area (see Table 3), making the relative influence of these factors difficult to elucidate. Patch area is often used as a measure of habitat availability in fragmentation studies (Fahrig 2003). In the case of wood cricket, a decrease in fragment area will also negatively influence edge habitat availability, consequently decreasing the likelihood of wood cricket being present. These results therefore indicate that decreases in the area of individual woodlands (i.e. habitat loss) will negatively influence the persistence of wood cricket populations at the landscape scale.

Simple models using patch characteristics and distance measures have often been used to predict species presence within fragmented landscapes (Fahrig and Jonsen 1998; Mazerolle and Villard 1999; Debuse et al 2007). However, responses often vary between and within different taxa (e.g. Fahrig and Jonsen 1998; Herrando and Brotons 2002; Barbaro et al 2005). For constructing models predicting presence/absence of a species, logistic regression is often used (e.g. Ranius 2000; Rukke 2000). For wood cricket this method produced a predictive model indicating that distance to the nearest occupied neighbouring woodland and woodland area were the most important variables

explaining wood cricket presence at the landscape scale. Chardon et al. (2003) found similar results using similar variables for the occurrence of Speckled wood butterfly (*Pararge aegeria*) which is recognised a woodland edge generalist species. However, for this species the habitat area was found to be more important than occupied nearest neighbour distance. The difference in outcome between their study and the current investigation is possibly due to the smaller spatial scale used, and the higher mobility of the butterfly species compared to wood cricket. For relatively mobile invertebrate species, distance between habitat patches is probably less important as a determining factor for presence than total habitat area/availability within patches.

The results also have implications for understanding metapopulation structure in the species, an aspect not investigated previously. Metapopulation theory is based on the concept that species are distributed among discrete fragments or patches of habitat, with movement of individuals between them, and suggest that while local populations may be unstable, equilibrium can occur at the regional scale (Hanski 1999). Much research has focused on the original or 'classical' metapopulation theory, which considers a metapopulation as a `population of populations', where extinction and colonisation of populations are in a dynamic balance (Hanski 1998). This version of the theory has been widely explored in relation to relatively mobile invertebrate species such as butterflies (Hanski 2004). For relatively immobile species such as wood cricket, other conceptions of metapopulations such as 'patchy populations' are likely to be more realistic, as scope for recolonisation following extinction is likely to be limited (Harrison 1994; Harrison and Taylor 1997). Similarly to habitat-specialist beetle species (Driscoll 2005), the results of this study suggest that individual woodlands function as distinct islands operating as more-or-less closed systems within the agricultural matrix. Extinctions

within fragments that are further away than 50 m from another populated fragment are therefore likely to be permanent. However, the pattern of occupancy also suggests that in some areas where the level of fragmentation is low (i.e. woodlands are in close proximity to each other and major landscape barriers are lacking), interactions between fragments are occurring. This further suggests that in these specific areas a functional form of metapopulation dynamics between woodlands may exist. Interestingly, the current results (Figure 4) support one of the assumptions on which metapopulation models are typically based, namely the exponential decline in dispersal probability with increasing distance between two patches (Drechsler et al 2003).

Further research is required to examine the occurrence of metapopulation structure within wood cricket, and whether the results obtained here are generally applicable to relatively immobile woodland invertebrate species. If so, it may be possible to develop generalised approaches to their conservation and management, which is urgently required given that many species of conservation concern are characterised by limited dispersal ability. In the case of wood cricket, further research is also required to determine the relative permeability of different land cover types to movement of the species, and whether features such as roads and watercourses act as barriers to its movement, as assumed here. Understanding of such processes would enable the effectiveness of landscape-scale approaches to habitat management to be evaluated, with respect to both wood cricket and other species with similar ecological characteristics.

Acknowledgements

Table 1: Mann-Whitney U test for the relation between wood cricket presence/absence and six independent variables analysed through separate tests. Distance = nearest occupied neighbour distance; Permanent edge = total amount of edge habitat; SHAPE = Shape index; FRAC = Fractal dimension index. n = number of woodland fragments: wood cricket present n_1 = 32 and absent n_2 = 115; U = Mann-Whitney test statistic; z = test statistic given by SPSS when performing a Mann-Whitney U test and is used to test for a significant difference (P) between two groups; P = probability or significance level; r = effect size.

Mann-Whitney U test	n	U	z	P	r
Distance	147	714.0	-5.29	0.000	0.44
Permanent edge	147	1061	-3.65	0.000	0.30
Perimeter	147	1107	-3.44	0.001	0.28
Area	147	1199	-3.01	0.003	0.25
SHAPE	147	1321	-2.44	0.015	0.20
FRAC	147	1470	-1.74	0.082	0.14

Table 2: Contingency tables for woodland age related to wood cricket presence and subsequent Pearson Chi-square tests of association. Odds indicate the likelihood for wood cricket being present in secondary (4/36 = 0.1) or ancient woodland. Odds ratio indicates the likelihood for wood cricket being present in ancient woodland compared to presence in secondary woodland (0.4/0.1= 4.0).

Contingency table		Wood cricket			
		Absent	Present	Total	Odds
Age	Secondary	36	4	40	0.1
	Ancient	52	23	75	0.4
	Total	88	27	115	
Pearson χ^2	n	χ^2	df	P	Odds ratio
Age	115	5.10	1	0.024	4.0

Table 3: Spearman rank correlation between the independent variables. $n = 147$, $r =$ correlation coefficient, $P =$ significance or probability value. SHAPE = Shape index; FRAC = Fractal dimension index. Correlation coefficients $r > 0.50$ are displayed in bold.

Spearman correlation		Area	Perimeter	SHAPE	FRAC	Distance	Permanent edge
Perimeter	*r*	**0.93**	.				
	P	0.000	.				
SHAPE	*r*	0.44	**0.71**	.			
	P	0.000	0.000	.			
FRAC	*r*	0.24	**0.54**	**0.97**	.		
	P	0.003	0.000	0.000	.		
Distance	*r*	-0.03	-0.08	-0.16	-0.17	.	
	P	0.760	0.311	0.048	0.039	.	
Permanent edge	*r*	**0.94**	**0.99**	**0.68**	**0.51**	-0.08	.
	P	0.000	0.000	0.000	0.000	0.360	.
Age	*r*	0.41	0.29	0.01	-0.09	-0.15	0.30
	P	0.000	0.000	0.951	0.302	0.064	0.000

Table 4: Summary of the logistic regression analyses. Model: variables included in the logistic regression model. Model performance: summary of model performance tests. Model fit test: tests if the model fits the data ($P < 0.05$ = good model fit). Hosmer & Lemeshow model fit test: tests if the model fits the data ($P > 0.05$ = good model fit). Classification table (%): indicates percentage of cases correctly classified by the model. Effect size: indicates the amount of explained variation by the model (Nagelkerke R^2; range $0 - 1$). Variables in the equation: indicates the usefulness of the individual variables included in the model. Wald test: tests contribution of the individual variables to the model ($P < 0.05$ = significant contribution). B (with Standard Error): indicates the direction of the relationship between the individual variables and wood cricket presence (- negative, + positive). Exp. (B) (with 95% Confidence Interval): indicates the odds ratio for wood cricket presence per unit increase of the individual variable (values below 1 indicate a decrease and above 1 an increase).

Logistic regression model		Model performance										Variables in the equation								
		Model fit			Hos. & Lem. Model fit test			Classification table (%)			Effect size	Wald test							95% C.I. Exp(B)	
Variables	n	χ^2	df	P	χ^2	df	P	Absent	Present	Total	Nagelkerke r^2	z	df	P	B	S.E.	Exp (B)		Lower	Upper
Distance	144	36.41	2	0.000	11.57	8	0.171	96	26	81	0.35	8.506	1	0.004	-0.002	0.001	0.998		0.997	1.000
Area												8.449	1	0.004	0.052	0.018	1.053		1.017	1.091
Constant												8.363	1	0.004	-1.040	0.360	0.353			
Distance	144	19.83	1	0.000	39.16	8	0.000	100	0	79	0.20	8.764	1	0.003	-0.001	0.000	0.999		0.998	1.000
Constant												2.610	1	0.106	-0.450	0.279	0.637			
Area	144	17.39	1	0.000	14.04	8	0.081	97	23	81	0.18	11.38	1	0.001	0.054	0.016	1.055		1.023	1.089
Constant												44.26	1	0.000	-1.984	0.298	0.138			
Permanent edge	144	16.58	1	0.000	4.481	8	0.811	97.3	12.9	79.2	0.17	11.86	1	0.001	0.000	0.000	1.000		1.000	1.001
Constant												39.26	1	0.000	-2.243	0.358	0.106			
Perimeter	144	15.05	1	0.000	5.032	8	0.754	97.3	16.1	79.9	0.15	11.97	1	0.001	0.001	0.000	1.001		1.000	1.001
Constant												36.85	1	0.000	-2.337	0.385	0.097			
SHAPE	144	4.412	1	0.036	9.586	8	0.295	100.0	0.0	78.5	0.05	4.485	1	0.034	0.765	0.361	2.148		1.059	4.359
Constant												14.34	1	0.000	-2.697	0.712	0.067			

Figure 1: The woodland fragments on the Isle of Wight. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith and Gilbert, 2003).

Figure 2: Distribution of wood cricket (*Nemobius sylvestris*) on the Isle of Wight. The black patches represent woodlands where wood cricket was present, the dark grey patched represent woodlands where wood cricket was absent, and the white patches represent woodland fragments that were not surveyed.

Figure 3: Boxplots ($n = 147$, with wood cricket present $n_1 = 32$ and absent $n_2 = 115$) illustrating the ranges and median (horizontal black line) for woodland fragments where wood cricket was 'Absent' or 'Present' in relation to (a) Euclidean distance from each surveyed woodland to its nearest occupied neighbour (medians: 715.0 m, 50.00 m), (b) length of permanent edge (medians:1241 m, 2785 m), (c) length of woodland perimeter (medians: 1202 m, 2418 m), (d) woodland area (medians: 5.138 ha, 9.469 ha), (e) shape index (medians: 1.583, 1.886) and (f) fractal dimension index (medians: 1.086, 1.107). Identical letters indicate a non-significant difference (a – a), different letters indicate a significant difference (a – b) ($P < 0.05$, Mann-Whitney *U* test).

Figure 4: Frequency distribution for Euclidean nearest occupied neighbour distance between the individual woodland fragments. The x-axis represents the distance to the nearest occupied woodland in meters (m) divided in intervals (i.e. interval 25 represents all woodlands between 0-25 m from each other, 50 between 25-50 m etc.). The y-axis

indicates the percentage of occupied ($n = 32$) (black bars) and unoccupied ($n = 115$) (white bars) woodlands in each interval.

Figure 5: Predicted probability graphs for wood cricket presence in woodland fragments related to distance to the nearest occupied neighbour and woodland area. The curve was calculated with the following probability equations using the B values from Table 4:

$$P(y) = \frac{e^{-1.040 + (-0.002)(\text{Distance}) + (0.052)(\text{Area})}}{1 + e^{-1.040 + (-0.002)(\text{Distance}) + (0.052)(\text{Area})}}$$
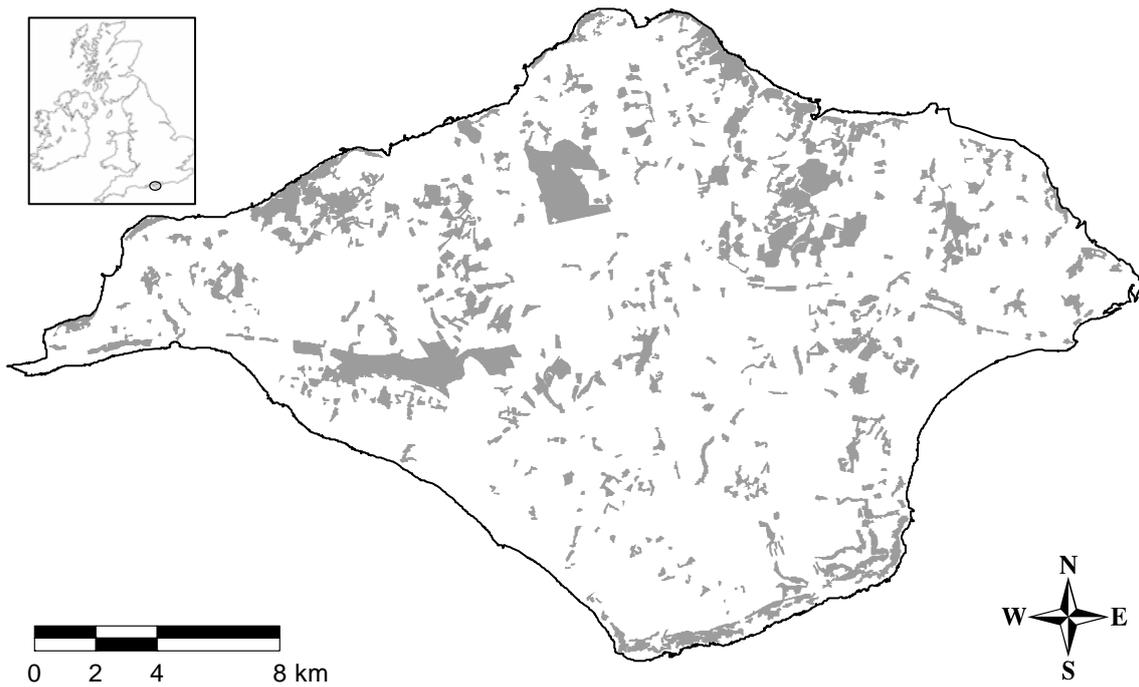
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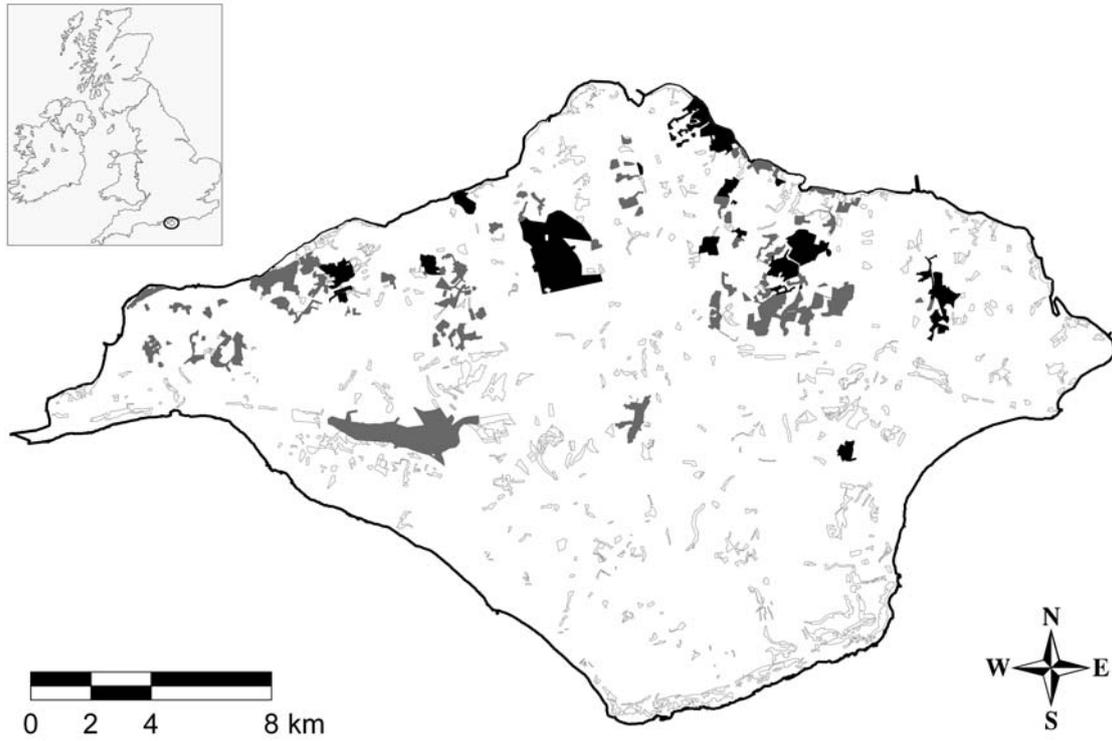
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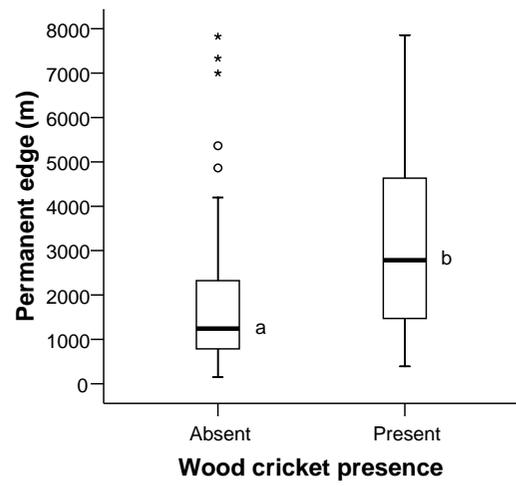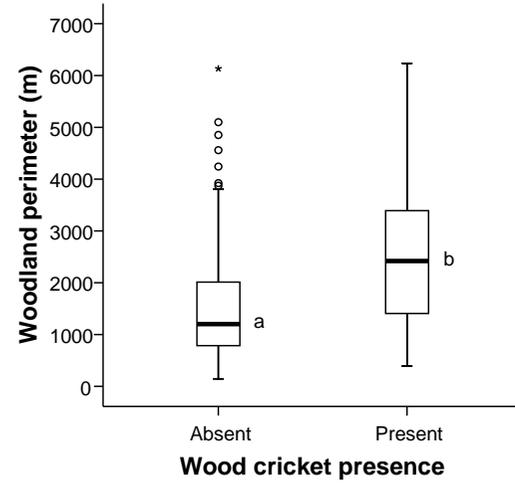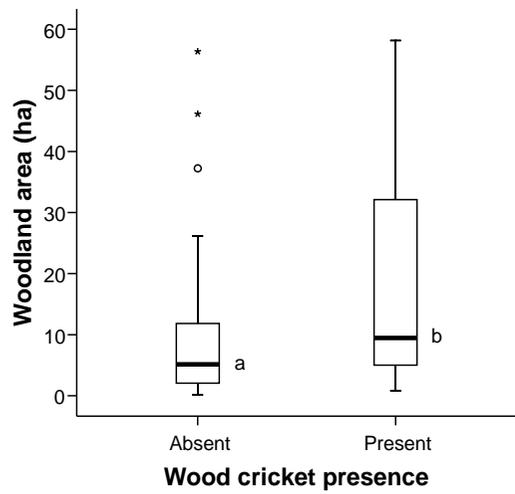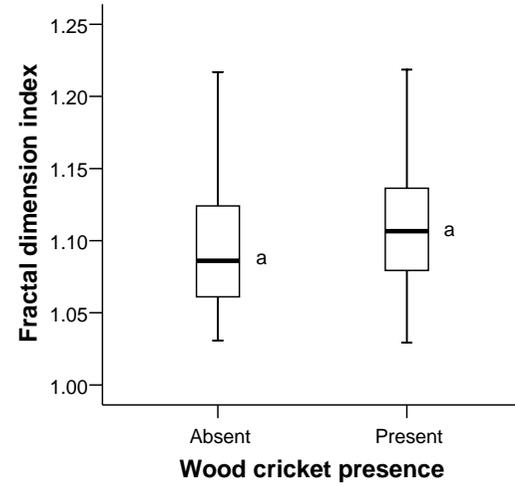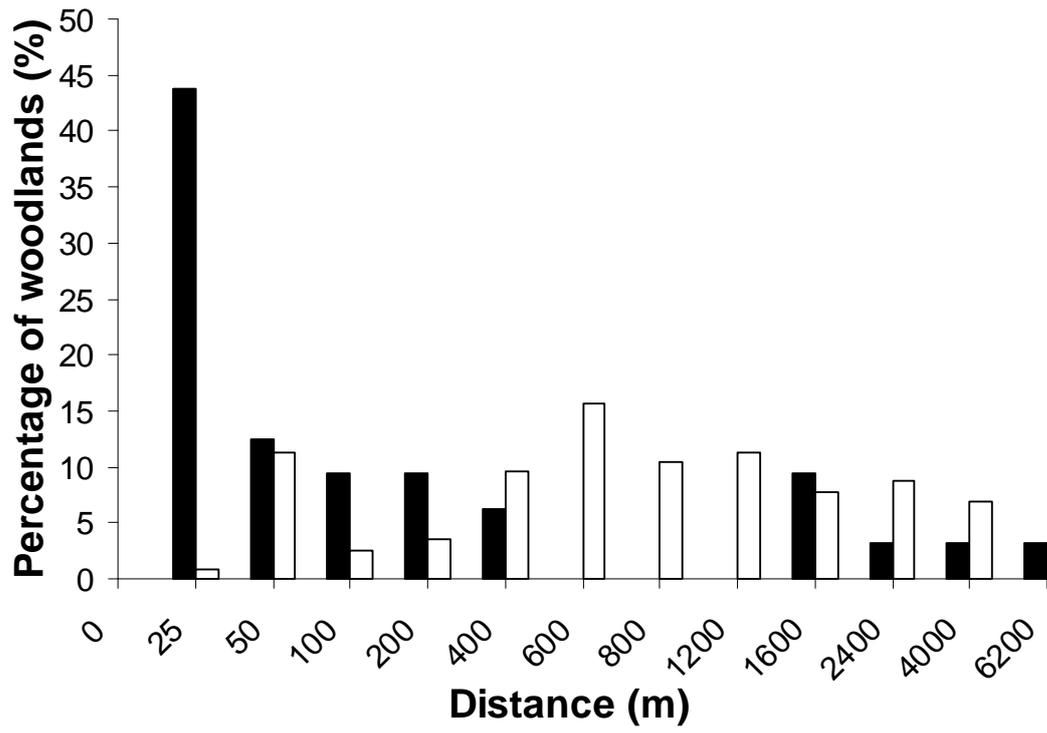
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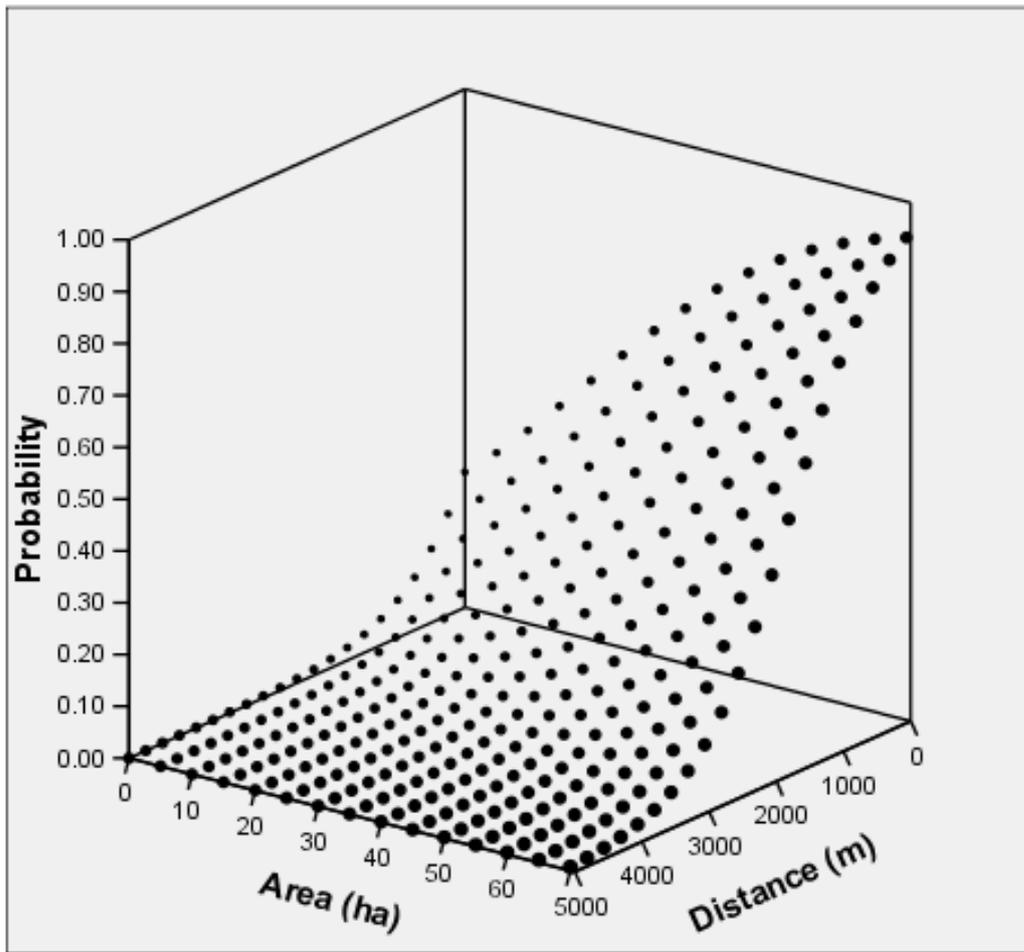
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Figure 5 (see attached file: Figure 5.tif)

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