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Title:

Habitat requirements for the conservation of wood cricket (*Nemobius sylvestris*) on the Isle of Wight, UK

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1 Abstract

In the UK, wood cricket (*Nemobius sylvestris*) is a 'Species of Conservation Concern', being restricted to only three areas in southern England. Little information is available on the specific habitat requirements of this species. In 2006, a field investigation within three woodlands on the Isle of Wight was undertaken to identify its habitat preferences. Factors positively influencing wood cricket presence within woodlands included the presence of a well-developed leaf litter layer, relatively low ground vegetation cover and height, low canopy cover and relatively short distances between individual populations. Regression models identified the degree of isolation and variables describing vegetation structure as the main predictors for wood cricket presence within woodland fragments. The results of this study indicate the preference of wood cricket for open wooded edges. Conservation efforts for this species should focus on continuation of regular management activities aimed at providing permanent open edge habitat within woodlands, to maintain viable populations.

Keywords: woodland; forest; habitat requirements; conservation; wood cricket; *Nemobius sylvestris*; Isle of Wight; United Kingdom

2 Introduction

Much interest has focused recently on the role of landscape-scale factors in maintaining populations of species, particularly as a result of developments in metapopulation theory and landscape ecology (Hanski and Gilpin 1997; Gutzwiller 2002; Crooks and Sanjayan 2006). However, for the conservation of invertebrate species, factors acting at a local scale may often be equally important for the persistence of individual populations as habitat availability at the landscape scale, particularly for species with limited dispersal ability. Indications for this are found in habitat fragmentation studies that have been undertaken at a range of different spatial scales, revealing the relative importance of within-patch habitat compared to spatial measures such as patch size and isolation between habitat fragments (e.g. Rukke and Midtgaard 1998; Ranius 2000; Binzenhofer et al. 2005). For example, in a study on a burnet moth species in an abandoned agricultural landscape in Germany, Binzenhofer et al. (2005) found that presence of the species was mainly explained by total nectar plant cover (i.e. habitat availability) within patches, whereas no patch size or isolation effect between habitat patches was found. Two studies on beetles living in dead fungal fruiting bodies on trees revealed similar results, where fragment area and isolation were found to be less important explanatory variables for presence than the total amount of habitat (i.e. fungus fruiting bodies) available within the individual woodland stands (Rukke and Midtgaard 1998; Rukke 2000). Furthermore, in a study on an endangered longhorn beetle living on dead trees, Buse et al. (2007) revealed that variables measured at the tree level were better predictors of presence of the species than spatial measurements between trees. These examples indicate the overall importance of within patch (i.e. local scale) habitat availability in determining invertebrate presence and population persistence.

Detailed studies examining habitat factors influencing invertebrate populations are required to be able to determine habitat suitability and species-specific requirements within individual sites. Presence/absence studies are often used to analyse the responses of individual species to habitat variables (e.g. Rukke 2000; Binzenhofer et al. 2005). Variables often measured include habitat factors related to species-specific food availability, vegetation structure (e.g. canopy cover), abiotic conditions (e.g. sunlight availability) and isolation measures (e.g. nearest neighbour distance). Studies on grassland species have revealed positive relationships with food availability and negative relationships with habitat distance, but differing results for vegetation structure and related abiotic conditions (Binzenhofer et al. 2005; Strauss and Biedermann 2005; Heller and Gordon 2006). Studies specifically on woodland species have found similar relationships. Most such studies to date have focused

on endangered ground or tree related beetle species (Rukke and Midtgaard 1998; Rukke 2000; Siitonen and Saaristo 2000; Sroka and Finch 2006; Buse et al. 2007; Matern et al. 2007) and butterfly species (Thomas et al. 1992; Konvicka et al. 2007). These studies have similarly found positive relationships with measures of food availability (Rukke and Midtgaard 1998; Rukke 2000; Buse et al. 2007) and negative relationships with occupied nearest neighbour distance between habitat patches (Thomas et al. 1992; Rukke and Midtgaard 1998; Rukke 2000; Siitonen and Saaristo 2000; Buse et al. 2007). For canopy cover in most cases a negative relationship has been found (Rukke and Midtgaard 1998; Buse et al. 2007; Matern et al. 2007), however the influence of vegetation structure differs widely between species (Siitonen and Saaristo 2000; Sroka and Finch 2006; Buse et al. 2007; Konvicka et al. 2007; Matern et al. 2007; Sorvari and Hakkarainen 2007).

The research described here focused on wood cricket (*Nemobius sylvestris*) on the Isle of Wight, United Kingdom. Although wood cricket is relatively widespread in Europe (Brown 1978), in the UK it has the national status of a 'Species of Conservation Concern' (NBN Gateway 2007). In the UK, wood cricket reaches the northern limit of its European distribution. Populations of the species are restricted to the South of England at three main locations, the New Forest (Hampshire), South Devon and on the Isle of Wight (NBN Gateway 2007). On the Isle of Wight, populations are largely restricted to relatively large woodland fragments occurring in the northern half of the island (Brouwers and Newton 2008). The specific habitat requirements of the species are poorly understood, and existing knowledge is largely based on observational and anecdotal information (e.g. Richards 1952).

Wood cricket is a non-flying cricket species that is strongly associated with native broadleaved woodland, often dominated by oak (*Quercus spp.*) (Richards 1952). It is typically found in relatively open areas such as woodland clearings and edges of woodland tracks, footpaths, railway lines and woodland peripheries (Richards 1952; Morvan and Campan 1976; Beugnon 1980). Locally the species can reach high population densities (Gabbutt 1959). The insects live on the ground and prefer a well-developed leaf litter layer, which serves as shelter, a food source and as a breeding ground (Richards 1952; Brown 1978; Proess and Baden 2000). The species is considered to be omnivorous with the staple diet mainly being composed of dead leaf litter material (Gabbutt 1959; Koehler and Samietz 2006). However, to date no detailed study has been undertaken of the specific habitat requirements of the species in relation to its presence or absence within woodland stands.

To address this gap in knowledge, the distribution of wood cricket was investigated within three separate woodlands in relation to a range of habitat characteristics. In order to define

an appropriate approach to conservation management for this species it is critical to know its precise habitat preferences. Statistical modelling approaches are often used to determine the habitat variables that can be used to predict presence/absence of a species. This method has been implemented in a range of studies (Strauss and Biedermann 2005; Buse et al. 2007; Matern et al. 2007), however it has been noted that relatively few habitat modelling studies have been undertaken with rare and/or endangered species (Engler et al. 2004). Habitat models have also been identified as highly valuable for informing conservation management (Fleishman et al. 2002). Therefore, in this investigation, habitat suitability models based on logistic regression were developed in order to evaluate the relative importance of different habitat variables to provide a tool for assessing habitat suitability for wood cricket.

This study addressed the following aims: (1) to test the relationships between wood cricket presence/absence within woodlands and (a) ground habitat (i.e. leaf litter depth and volume), (b) vegetation structure (i.e. ground vegetation cover, vegetation height, canopy closure) and (c) isolation measures (i.e. Euclidean distance); and (2) to develop a deterministic habitat suitability model. Based on findings of habitat suitability studies on similar invertebrate species it was hypothesised that a positive relationship would be found between wood cricket presence and ground habitat availability (i.e. leaf litter) and a negative relationship would be found between presence and habitat isolation. Further hypotheses based on findings of previous research were that wood cricket would be more likely to be present when (1) ground vegetation cover was relatively sparse, and (2) canopy closure was relatively low.

3 Methods

3.1 Study area

In the summer of 2006, a field survey was carried out within three different woodlands located on the Isle of Wight, United Kingdom. The selected woodlands were Briddlesford copse (50° 42'40 N, 1° 13'23 W), Borthwood copse (50° 39'21 N, 1° 11'43 W) and Firestone copse (50° 43'00 N, 1° 12'54 W) (Fig. 1). All three woodlands are part of the anthropogenic landscape, bordering urban fringes but mainly agricultural land and are currently ungrazed by livestock.

Fig 1 approx. here

Briddlesford copse was surveyed between 20 - 29 July, Borthwood between 1 - 3 August and Firestone copse between 4 – 9 August. These sites were selected for study based on the fact that they (i) support relative widespread wood cricket populations within them, (ii) are similar in age and origin, (iii) are mainly dominated by broadleaf trees species and (iv) are larger than 20 ha in area.

All three woodlands retain ancient woodland characteristics (i.e. continuous woodland cover since 1600 AD) following the Ancient Woodland Inventory (see Spencer and Kirby 1992; English Nature 1998 - 2006). Briddlesford copse and Borthwood copse are predominantly classified as ancient semi-natural woodland sites (English Nature 1998 - 2006). Firestone copse is predominantly classified as an ancient replanted woodland site (English Nature 1998 - 2006). This woodland was heavily planted with coniferous tree species but retains its ancient woodland features for 66% of the total woodland area. The individual surface area of the selected woodlands is 49.9 ha for Briddlesford copse, 24.4 ha for Borthwood copse and 99.5 ha for Firestone copse (calculated in ArcGIS 9.1, ESRI, Redlands, California, USA). However, for Firestone copse, the focus of the survey was on the broadleaf-dominated areas that account for 26.2 ha of the total woodland area.

The Forestry Commission (South East England Forest District) manages Firestone copse. The main management aims adopted here are to integrate timber production, recreation and conservation by restoring the ancient characteristics of the woodland through removal of non-native mainly coniferous tree species and maintaining open woodland habitat through thinning. Briddlesford copse is managed by the People's Trust for Endangered Species

(PTES) (London, UK), a non-governmental conservation organisation (NGO). Their main management strategy aims to maximise biodiversity by maintaining open woodland habitat through extensive thinning and re-introduction of coppice rotation. The National Trust (Mottistone, Isle of Wight), another conservation NGO, manages Borthwood copse. Here, management focuses on facilitating public access and create a diverse habitat within the woodland by maintaining stands of different tree species and create permanent open woodland habitat through mowing, thinning and coppice rotation. The habitat of all three sites has been dynamic where management impacts and interventions have differed over time. However, similar management strategies and activities are currently being adopted to maintain biodiversity within these woodlands.

3.2 Survey methods

3.2.1 Sample design

The three individual woodlands were each divided into seven different strata. This stratification was based on observations on wood cricket habitat preference recorded during preliminary surveys completed in 2005 and 2006. The strata were: 'Ride' being woodland tracks and paths; 'Gaps' being areas without mature trees and/or overhead canopy situated within the boundaries of a woodland; 'Coppice with standards' being open coppiced areas with mature trees within them; 'Open canopy' being areas that were thinned and had an open canopy structure; 'Perimeter' being the edge of the woodland; 'Understorey' being a mature undisturbed woodland stand characterised by a closed canopy; and 'Occupied habitat' being locations where wood cricket was known to be present. To reduce the impact of errors in precision (e.g. using hand-held GPS), these strata were distinguished using a combination of data sources. A combination of high-resolution aerial photographs (Google Earth 3.0, Google Inc., Silicon Valley, California, USA), digital OS maps (Ordnance Survey MasterMap, Great Britain) and GPS (hand-held Garmin III GPS V, Garmin (Europe) Ltd, Romsey, UK) data points were used to identify and produce separate data layers in ArcGIS 9.1 (ESRI, Redlands, California, USA) for the different strata.

In order to obtain a similar sample size for both 'presence' and 'absence' locations, the following strategy was adopted. The six main woodland strata were sampled using a stratified random sampling design. Each of the strata were randomly sampled by generating random points using the Hawth's Analysis Tools (for ArcGIS, Version 3.24; (Beyer 2004)). The following criteria were used to establish presence or absence of wood cricket at each measurement site. A five-minute period was used to search and listen for wood cricket in a 3

m radius around the measurement location. The location was recorded as being occupied when a wood cricket was observed or heard (i.e. stridulating males following Proess and Baden (2000)).

The 'Occupied habitat' locations where wood cricket was known to be present based on a preliminary field survey, were thoroughly surveyed by walking through the area in a zigzag pattern. The locations where the individual measurements were taken were separated by a minimum distance of 10 m. If wood cricket was observed, a habitat measurement was taken at that exact location. If wood cricket was only heard (stridulating males), the location of the individual was determined by slowly moving towards it to pinpoint its location. This method is thought to be accurate enough to capture the overall preferred habitat because of the bimodal daily rhythm of movement the species shows during every 24 hour period (see Beugnon 1980).

The number of sample points was determined proportional to broadleaf dominated woodland area. This resulted in a total sample of $n_{Br} = 180$ with $n_{Br1} = 90$ present and $n_{Br2} = 90$ absent for Briddlesford copse (49.9 ha); $n_{Bo} = 100$ with $n_{Bo1} = 50$ present and $n_{Bo2} = 50$ absent for Borthwood copse (24.4 ha) and $n_F = 122$ with $n_{F1} = 61$ present and $n_{F2} = 61$ absent for Firestone copse (26.2 ha), resulting in a total sample size of $n = 402$ with $n_1 = 201$ present and $n_2 = 201$ absent locations for all woodlands together.

3.2.2 Habitat measurements

The measurements that were obtained were divided into two main groups. For habitat: ground surface measurements including all non-living habitat elements on the ground, such as leaf litter, and vegetation measurements including ground vegetation and canopy tree measurement. For distance: isolation measurements (i.e. Euclidean distance measures).

Table 1 approx here

A 1x1 m quadrat was used to perform the vegetation measurements. First, within the quadrat, the total ground vegetation cover was estimated visually (in %). Cover was also estimated for each of the main individual plant species present within the quadrat. Secondly the mean ground vegetation height and the height of the main individual plant species were measured (in cm) using a meter rule. Thirdly, measurements were taken recording leaf litter cover (in %) and leaf litter depth within the quadrat. Leaf litter depth (in cm) was measured by taking four separate measurements with a leaf litter probe in the middle of each of four

0.5 square meter sections within the quadrat. From the centre of the quadrat, canopy closure was measured using a spherical densiometer (Forest Densiometers, Bartlesville, US). This involved taking readings in North, East, South and Westerly direction (see Table 1).

Within ArcGIS, a series of Euclidean distance measurements were made between the individual quadrat measurement locations and different edge habitat within the woodlands. These measurements were made from the individual locations to: the nearest occupied permanent edge (being the perimeter of a woodland or an open ride edge where wood cricket was present); the woodland edge (being the outer edge of a woodland) and any edge (including edges of rides, within clearings and the woodland perimeter) (see Table 1).

3.3 Statistical data analysis

The individual habitat variables were tested for their relationship with wood cricket presence using SPSS (Version 14.0, SPSS Inc., Chicago, Illinois, USA). The values for the separate variables were first explored using descriptive statistics within SPSS, included testing for normality (Kolmogorov-Smirnov test). All variables were found not to be normally distributed. For examining the relationships between wood cricket presence and the individual computed habitat variables, Mann-Whitney *U* tests were performed. Additionally, the effect size (*r*) for each individual variable was calculated ($r = z / \text{square root } n$) in this case indicating the strength of association of each variable with wood cricket presence/absence (Pallant 2007). Furthermore, a Spearman rank correlation test was undertaken to examine correlations between the variables. Assessment of the correlations and effect size (*r*) was based on the guidelines of Cohen (1988) where values between $r = 0.10$ and 0.29 indicate a small correlation effect/effect size; $r = 0.30$ to 0.49 a medium effect and values $r = 0.50$ to 1.00 a large effect.

Several logistic regression methods were used to examine the relative influence of the different habitat variables for explaining the presence or absence of wood cricket within the woodlands. First, all individual variable responses were explored in order to determine their individual explanatory power using the 'Enter' function within SPSS. This function is used to build regression models by hand. Only the significant variables ($P < 0.05$) were used to build subsequent models using different variable combinations again by using the 'Enter' function.

The output that is generated by SPSS when analysing the individual models provides information on the performance of the total model and information on performance of the individual variables used within these models. For total model performance, SPSS produces

two 'goodness-of-fit' tests, a 'classification table' and information on 'effect size'. 'Goodness-of-fit' tests are designed to test how well the created models perform and fit the data. There is no universally preferred test for this purpose (Tabachnick and Fidell 2001), so SPSS performs a 'model fit test' and a 'Hosmer & Lemeshow model fit test'. However, in this case the 'Hosmer & Lemeshow model fit test' is considered to be more powerful than the 'model fit test' (Pallant 2007). The 'classification table' provides information on the percentage of cases (i.e. presence/absence locations) that are correctly classified by the model and the 'effect size' provides information on the amount of variation that is explained by the model. For the performance of the individual variables, SPSS uses the 'Wald test' to test the contribution of the individual variables to the predictive ability of the model. SPSS further generates B values (+ Standard Error) which are used as constants in the probability function (see Equation 1). This equation was further used to construct probability curves to display the relationships between the individual predictor variables and wood cricket presence.

Equation 1: Probability equation for wood cricket presence (from Tabachnick and Fidell, 2001). 'B' values are generated by SPSS for the individual variables that are included in the model.

$$P(y) = \frac{e^{a + \sum_{n=1}^x b}}{1 + e^{a + \sum_{n=1}^x b}}$$

$P(y)$ = probability of wood cricket being present

a = B value for the constant included in the model

b = B value * variable(s) included in the model

The B value further indicates the direction of the relationship between the individual predictor variables and the dependant variable (i.e. wood cricket presence). The final piece of information given is the Exp(B) (with 95% Confidence Interval) value which indicates the odds ratio for wood cricket presence per unit increase of the predictor variable. Further details on SPSS output interpretation for logistic regression analyses are provided by Tabachnick and Fidell (2001), Field (2005) and Pallant (2007). The following selection criteria were used to choose the most powerful and realistic model: (1) all individual correlations (r values) between the variables included had to be less than +/- 0.7 (following Strauss and Biedermann 2005), (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 $\text{Exp}(B)$ 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), 'Hosmer & Lemeshow model fit test' scores and the total percentage given in the 'classification table'.

4 Results

4.1 Analysis of the independent variables

The measurements undertaken in the field were used to compute 26 different variables. Mann-Whitney U test were performed to test the relationship between each habitat variable and wood cricket presence. Results of these tests indicated that 14 variables were found to have a significant influence on wood cricket presence (Table 1 and Table 2). The variable showing the strongest relationship with/and effect on wood cricket presence was the distance measure 'Euclidean distance to nearest occupied permanent edge', followed by vegetation variables 'South orientated canopy closure', 'Ground vegetation height' and 'Ground vegetation cover' (Table 2). Habitat measures based on leaf litter were found to be less important (Table 2).

Table 2 approx here

Overall, results indicated that wood cricket is more likely to be present at sites: (1) within a relatively short distance of edge habitat, (2) with relatively low percentages of canopy closure, (3) with relatively low measures of ground vegetation height (4) with relatively low percentages of vegetation cover, and (5) with a relatively thick leaf litter layer (see medians Table 2).). These results indicate the importance of nearby source populations, the availability of sunlight at ground level and to a lesser extent the availability of leaf litter for the persistence of the species within woodlands.

Table 3 approx here

A Spearman rank correlation test was performed to see if there were any associations between the variables that were examined. Four distinct correlated groups could be recognised based on a large effect size ($r > 0.50$) between all of the individual variables included. The first group included the 'Ground vegetation height', 'Cumulative ground vegetation cover', 'Ground vegetation cover' and 'Total vegetation cover' showing a high positive correlation with each other (range $r = 0.64 - 0.94$; Table 3). An exception in this group was the medium correlation between 'Total vegetation cover' and 'Ground vegetation height' ($r = 0.37$; Table 3). The second group included 'East-, South-, West-, East/South orientated canopy closure' and 'Canopy closure'. These five variables all showed a high positive correlation with each other ($r = 0.54 - 0.94$; Table 3). The third group included 'Leaf litter depth' and 'Leaf litter volume' that showed a very high positive correlation with each other ($r = 0.94$; Table 3). Finally the fourth group included 'Euclidean distance to nearest occupied permanent edge' and 'Euclidean distance to nearest permanent edge', which also showed a high positive correlation with each other ($r = 0.53$; Table 3). Euclidean distance to nearest occupied woodland edge was the only variable not correlated with any of the other variables.

Between these groups all canopy closure variables showed a medium negative correlation with 'Ground vegetation height', 'Cumulative ground vegetation cover' and 'Ground vegetation cover' ($r = -0.30 - -0.48$; Table 3), indicating a negative influence of canopy closure on ground vegetation development. The leaf litter variables both showed a moderate negative correlation with 'Ground vegetation cover' and 'Cumulative ground vegetation cover' ($r = -0.36 - -0.41$; Table 3) and a moderate positive correlation with 'Canopy closure' ($r = 0.32 - 0.34$; Table 3), indicating a positive influence of canopy closure on leaf litter presence.

4.2 Logistic regression analysis

Table 4 approx here

Several logistic regressions analyses were undertaken to build a predictive habitat model and identify the key variables explaining presence/absence of wood cricket within woodlands. For these analyses, twenty-six variables were initially included in the logistic regression. After the exploration of the SPSS output for the separate models, the best fitting (full) model explaining the highest amount of variation within the data included the variables 'Euclidean

distance to nearest occupied permanent edge', 'Ground vegetation height', 'South orientated canopy closure' and 'Cumulative ground vegetation cover' (Table 4). This model met all selection criteria (see Methods) showing that: (1) all individual correlations (r) between the variables included were less than +/- 0.7 (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 right sign of the relationship (+/-) based on the medians presented in (Table 2) and (4) the 95% confidence interval for $\text{Exp}(B)$ did not include the value of 1 (Table 4).

Fig 2 a-d approx here

Figure 2 shows the individual predictive probability response curves for wood cricket presence for the four variables included in the full model. All responses show a negative relationship with an increase in variable value, indicating a negative effect on wood cricket presence. The strongest response, similar to a negative-exponential response curve, was shown for 'Euclidean distance to nearest occupied permanent edge' (Fig. 2a), followed by more linear responses for 'Ground vegetation height' (Fig. 2b), 'Cumulative ground vegetation cover' (Fig. 2d) and 'South orientated canopy cover' (Fig. 2c). Fig. 3 shows bivariate response curves for the full model. With increasing values of 'South orientated canopy closure' and 'Cumulative (i.e. structured) ground vegetation cover', the probability of wood cricket presence decreased with increasing distance to the nearest occupied location and ground vegetation height (Fig. 3).

Fig 3 approx here

5 Discussion

The results of this study confirmed earlier observations indicating the preference of wood cricket for open wooded edges. Factors positively influencing wood cricket presence within woodland included the presence of a well-developed leaf litter layer, relatively low ground vegetation cover and height and relatively short distances between individual populations, supporting all of the initial hypotheses. Furthermore, the logistic regression model identified the degree of isolation and variables describing vegetation structure, but not leaf litter, as the main predictors for wood cricket presence within woodland fragments. None of these relationships have been defined previously for this species.

For invertebrates, habitat elements linked with different life-cycle stages have often found to be positively related with species presence (e.g. Rukke and Midtgaard 1998; Binzenhofer et al. 2005; Strauss and Biedermann 2005). For example, Rukke and Midtgaard (1998) found a strong positive relationship across three different spatial scales for presence of a fungus beetle and its specific breeding habitat. Wood cricket is known to pass most of its life-cycle in leaf litter, which is related to its breeding requirements (Brown 1978). Furthermore, although omnivorous, the staple diet of wood cricket was found to be components of dead leaf litter material (Gabbutt 1959; Koehler and Samietz 2006). Information available at the onset of this study suggested that leaf litter could be one of the primary factors determining wood cricket presence. Results of the current analyses revealed positive relationships between wood cricket presence and both leaf litter depth and volume. However, both variables only showed a small effect size in terms of predicting wood cricket presence (see Table 2). This might be due to the fact that wood cricket is omnivorous (Gabbutt 1959), which indicates that it is not entirely dependant on the presence of leaf litter as a food source over the course of its life-cycle. Therefore, leaf litter as a sole variable was found to be a poor predictor of wood cricket presence.

In general, sunlight availability has been shown to have a positive influence on diversity of a number of invertebrate groups (Greatorex-Davies et al. 1994; Rieske and Buss 2001). Ground-dwelling invertebrates generally favour sunlit conditions because of their thermophilic nature (e.g. Rieske and Buss 2001; Buse et al. 2007). The main vegetation variables influencing wood cricket presence were 'South orientated canopy closure', 'Ground vegetation height' and 'Ground vegetation cover'. These factors are often linked with sunlight availability, which has a strong effect on microclimatic conditions (e.g. Matern et al. 2007). Canopy closure and vegetation cover influence sunlight availability at ground level, and

therefore air temperature and humidity. Ground vegetation height appeared to be another successful predictor of wood cricket presence. Where ground vegetation was relatively high, wood cricket was less likely to be present. Relatively high measures of vegetation height combined with canopy closure and vegetation cover indicate an increase in the number of vegetation layers, which negatively influences sunlight availability at ground level, resulting in relatively low air temperatures. For wood cricket, these results highlight their preference for early succession and relatively open woodland habitat conditions, also confirming the thermophilic nature of the species (Proess and Baden 2000).

The factor most strongly influencing wood cricket presence within woodlands was distance to the nearest occupied permanent edge. Locations where wood cricket was found tended to be relatively close to these permanent habitat locations, indicating that more isolated suitable habitat locations were less likely to be inhabited. Similar results were found for three related beetle species (Rukke and Midtgaard 1998; Rukke 2000; Buse et al. 2007). Buse et al. (2007) found that host trees supporting a longhorn beetle community were more likely to be situated in close proximity of each other and isolated host trees were more likely to be uninhabited. Furthermore, in a study on a beetle species (*Bolitophagus reticulatus*) living in dead fungus fruiting bodies found on old/dying trees, again isolation had a negative influence on presence of the species in distinct habitat locations within woodlands (Rukke and Midtgaard 1998). On the basis of this relationship, Rukke and Midtgaard (1998) argued that this species demonstrates a habitat-tracking metapopulation structure (Harrison and Taylor 1997). Because of the successional dynamics of the habitat locations (i.e. fungus fruiting bodies on dying trees), for *B. reticulatus*, extinction was assumed more likely to be a consequence of the environment becoming permanently unsuitable than stochastic population fluctuations within permanent stable habitat locations (see Thomas 1994). Similar observations were made here for wood cricket. Repeated visits to the study sites in subsequent years (Brouwers, pers obs) indicated that, in the absence of deer and other grazing animals, coppice coups were rapidly recolonised by understorey vegetation and coppice regrowth, which was associated with a decline in wood cricket abundance and presence. Results of this study suggest that wood cricket is present only in early successional open woodland habitat with low vegetation cover. A metapopulation structure might therefore apply, with the rate of woodland regeneration determining the spatial dynamics of the populations within woodland. Together this indicates that this species needs regular natural disturbances and/or human interventions to provide the necessary open habitat conditions for it to persist. Historic differences in management might therefore also have had an influence on the current pattern of distribution of the species within the

surveyed woodlands. However, as this survey was undertaken during one moment in time, repeated surveys should be performed to test these suggestions.

The most powerful habitat suitability model identified here included an isolation measure and vegetation structure variables as the main predictors for wood cricket presence within woodland fragments. The logistic regression model for a longhorn beetle living on oak trees developed by Buse et al. (2007) included similar variables as were found for wood cricket. This model also included nearest occupied neighbour distance and variables related to sunlight availability, indicating the potential importance of these factors for woodland invertebrates more generally. In the case of longhorn beetle (Buse et al. 2007), however, specific habitat factors related to life-cycle requirements were also influential, whereas for wood cricket these variables (i.e. leaf litter availability) did not add to the overall performance of the model. Overall, the model for predicting wood cricket presence performed relatively well, explaining 57% of the variation in the data. These results are comparable with model performance values found for invertebrates living in grasslands and brown fields (Strauss and Biedermann 2005). Furthermore, the logistic regression model for a longhorn beetle living on oak trees (Buse et al. 2007) performed slightly less well than the models presented here. For a semi-aquatic woodland carabid beetle, a substantially better model performance was found (Matern et al. 2007). However, compared to the current study, these authors were less rigorous in excluding non-significant response variables from the total model. Still, the best-fit model for wood cricket revealed a substantial proportion of unaccounted variation when using the set of predictor variables described in this study. Including more precise measures of, for example, humidity, light availability at ground level and wind exposure might improve the model performance. The fit could also potentially be improved by adopting a different sampling method. Measurements were taken over a relatively small spatial area (1 m²) at one moment in time. However, it has been shown that wood cricket displays a daily rhythm of movement between more open and closed vegetation at different times of the day (Beugnon 1980). The sampling method therefore might have resulted in over- and/or underestimations of presence locations, that negatively influenced the discriminative power of the individual variables used within the model.

The results suggest that the dispersal ability of the species is limited (see also Brouwers et al. submitted). The analyses indicated that the measurement locations where wood cricket was present were aggregated around occupied permanent edges that were recognised as source locations. The locations where wood cricket was not found were on average 54 m away from a source population. In such locations, either wood cricket was not present because of the lack of suitable habitat or because of their limited dispersal ability, or possibly

because of the presence of internal barriers to dispersal within the woodlands. Another indication of the limited dispersal ability of the species was absence of the species at apparently suitable locations at certain moments in time (Proess and Baden 2000; Brouwers pers obs). In some locations, wood cricket was observed to colonise areas of suitable habitat such as new clearings or coppice coups over a period of 1-3 years, presumably from nearby source populations (Brouwers pers obs). This suggests that because of their dispersal limitations, the species demonstrates a time lag in occupying suitable habitat and their dispersal ability therefore seems to be an important factor in determining the species dynamics within woodlands. Altogether, the dispersal ability of this species is a factor that needs to be considered in order to predict their presence with more accuracy than based on habitat suitability alone. This further highlights the need to obtain species-specific parameters relating to dispersal ability in order to improve and inform future modelling approaches.

Where regular natural disturbances are generally lacking, suitable open woodland habitat conditions for wood cricket are often only present in woodland areas that are under some sort of management regime, such as those in the woodlands that were surveyed. Presence of permanent open edge habitat within fragments was found to be a strong indicator for wood cricket presence (Brouwers and Newton 2008), and generally occurs in locations that are actively managed. Locally very large populations have been recorded at permanent edges along railway lines and wide rides (Gabbutt 1959; Brouwers pers obs), indicating the importance of this particular habitat for wood cricket. Maintenance of these permanent 'source' locations therefore might be critical to secure a viable wood cricket population within individual woodland fragments. To prevent the natural overgrowing of these sites, these locations need to be actively managed through regular removal of the ground vegetation. Furthermore, established management regimes such as coppice rotation are likely to favour the persistence of the species within woodlands, by providing new areas with open woodland habitat with particularly low levels of ground vegetation and high leaf litter volumes at regular time intervals. Woodland restoration efforts (Defra 2005; Forestry Commission 2006) and thinning of woodland stands, which involve opening up the canopy, could also have a temporary positive effect on wood cricket populations by increasing habitat availability. However, when clearings are created, these should preferably be adjacent to already inhabited locations (e.g. permanent open ride edges) in order to increase the potential of dispersal of the species into these newly created habitat areas. Ride edges and open areas (e.g. coppice coups) have been found to be generally important for woodland invertebrate diversity (Warren and Key 1991; Greatorex-Davies et al. 1994), for instance for butterfly species dependant on flowering plants as a nectar source. Management activities

promoting the continuity of these habitats will therefore promote and maintain viable wood cricket populations as well as other woodland species (Bratton and Andrews 1991). Management practices that focus on providing a diversity of woodland habitats through annual interventions such as coppice rotation and yearly mowing of ride and track edges will be highly favourable for wood cricket and similar species.

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Table 1: Variables that were computed from the field measurements and found to influence wood cricket presence/absence within woodland habitat.

Variable group	Description
Habitat variables	
Ground vegetation cover	The total area covered by all ground vegetation (in %)
Cumulative ground vegetation cover	The sum of % area covered for each individual species of ground vegetation
Ground vegetation height	Mean ground vegetation height (in cm)
East orientated canopy closure	Densiometer measurement of overhead canopy in Eastern direction (in %)
South orientated canopy closure	Densiometer measurement in Southern direction (in %)
West orientated canopy closure	Densiometer measurement in Western direction (in %)
East/South orientated canopy closure	Mean of East and South densiometer measurements (in %)
Canopy closure	Mean of North, East, South and West measurements (in %)
Total vegetation cover	Ground vegetation cover + Canopy closure (in %)
Leaf litter depth	Mean of four measurements made in the quadrat (in cm)
Leaf litter volume	Leaf litter depth x quadrat area x % leaf litter cover (in cm ³)
Distance measures	
Euclidean distance to nearest permanent edge	Linear distance (in m) from quadrat location to: The perimeter of a woodland or an open ride edge (as observed in the field)
Euclidean distance to nearest occupied permanent edge	The perimeter of a woodland or an open ride edge occupied by wood cricket
Euclidean distance to nearest occupied woodland edge	The perimeter of a woodland occupied by wood cricket

Table 2: Mann-Whitney U test for the relationship between wood cricket presence/absence and fourteen habitat variables analysed through separate tests. $n = 402$; wood cricket present $n_1 = 201$ and absent $n_2 = 201$; Med Abs/Pres = median value for locations where wood cricket was absent or present, 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 between two groups; P = probability or significance level; r = effect size.

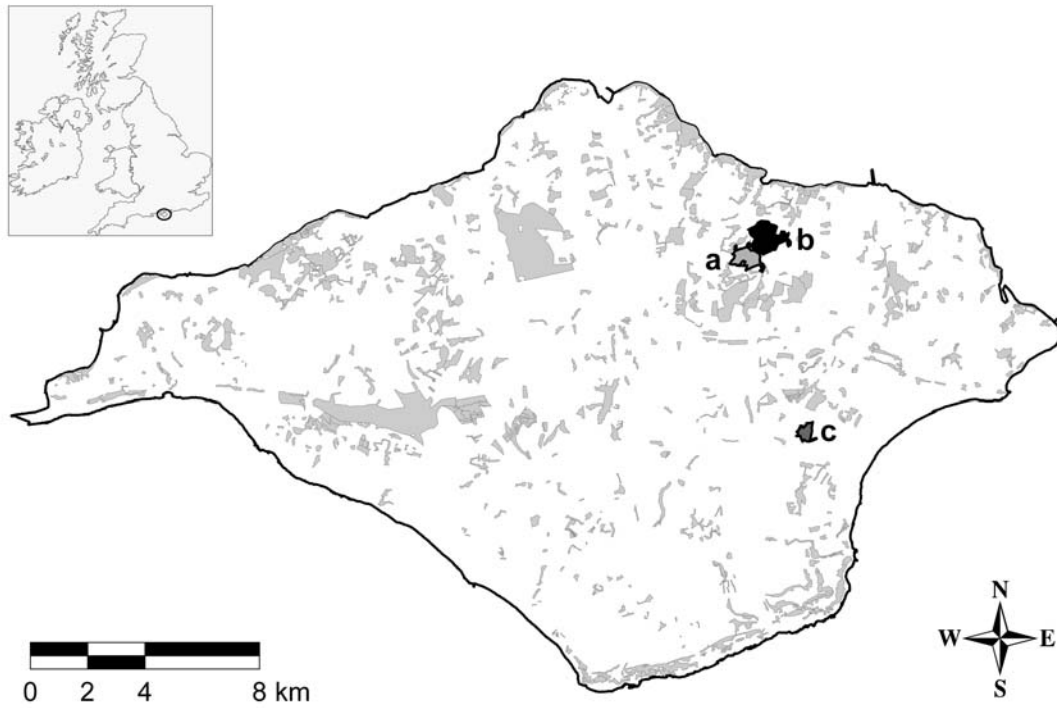
Mann-Whitney U test	Med Abs	Med Pres	U	z	P	r
Euclidean distance to nearest occupied permanent edge	54m	3m	6779	-11.5	<0.001	0.57
South orientated canopy closure	95%	75%	12567	-6.56	<0.001	0.33
Ground vegetation height	41cm	25cm	12946	-6.24	<0.001	0.31
Ground vegetation cover	90%	55%	12989	-6.22	<0.001	0.31
East/South orientated canopy closure	94%	79%	13920	-5.39	<0.001	0.27
Cumulative ground vegetation cover	100%	60%	14042	-5.29	<0.001	0.26
Total vegetation cover	147%	133%	14774	-4.66	<0.001	0.23
Euclidean distance to nearest permanent edge	19m	3m	14840	-4.60	<0.001	0.23
Leaf litter depth	3.00cm	4.25cm	14883	-4.57	<0.001	0.23
Leaf litter volume	27500cm ³	38400cm ³	15030	-4.44	<0.001	0.22
Canopy closure	93%	82%	15835	-3.75	<0.001	0.19
East orientated canopy closure	94%	87%	16430	-3.24	0.001	0.16
Euclidean distance to nearest occupied woodland edge	142m	137m	16650	-3.05	0.002	0.15
West orientated canopy closure	94%	85%	17846	-2.02	0.043	0.10

Table 3: Spearman rank correlation between the individual habitat variables. $n = 402$, r = correlation coefficient, P = significance or probability value. Bold figures indicate correlation coefficients (r) values > 0.50 .

Spearman rank correlation		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Ground vegetation cover	r	.												
		P	.												
2	Cumulative ground vegetation cover	r	0.94	.											
		P	<0.001	.											
3	Ground vegetation height	r	0.68	0.64	.										
		P	<0.001	<0.001	.										
4	East orientated canopy closure	r	-0.38	-0.34	-0.32	.									
		P	<0.001	<0.001	<0.001	.									
5	South orientated canopy closure	r	-0.35	-0.34	-0.33	0.74	.								
		P	<0.001	<0.001	<0.001	<0.001	.								
6	West orientated canopy closure	r	-0.44	-0.42	-0.30	0.54	0.66	.							
		P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	.						
7	East/South orientated canopy closure	r	-0.40	-0.37	-0.35	0.91	0.94	0.65	.						
		P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	.					
8	Canopy closure	r	-0.48	-0.46	-0.37	0.87	0.87	0.82	0.94	.					
		P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	.				
9	Total vegetation cover	r	0.68	0.66	0.37	0.21	0.22	0.13	0.22	0.18	.				
		P	<0.001	<0.001	<0.001	<0.001	<0.001	0.011	<0.001	<0.001	<0.001	.			
10	Leaf litter depth	r	-0.39	-0.36	-0.14	0.26	0.21	0.26	0.26	0.32	-0.11	.			
		P	<0.001	<0.001	0.006	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.028	.		
11	Leaf litter volume	r	-0.41	-0.38	-0.15	0.27	0.23	0.29	0.27	0.34	-0.11	0.97	.		
		P	<0.001	<0.001	0.002	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.026	<0.001	.	
12	Euclidean distance to nearest permanent edge	r	-0.09	-0.16	0.00	-0.07	0.00	-0.01	-0.03	0.00	-0.22	-0.04	0.01	.	
		P	0.059	0.001	0.926	0.138	0.933	0.881	0.564	0.992	<0.001	0.447	0.857	.	
13	Euclidean distance to nearest occupied permanent edge	r	0.08	0.04	0.06	0.04	0.15	0.00	0.10	0.03	-0.03	-0.21	-0.19	0.53	.
		P	0.127	0.450	0.215	0.474	0.002	0.956	0.037	0.510	0.541	<0.001	<0.001	<0.001	.
14	Euclidean distance to nearest occupied woodland edge	r	0.01	-0.01	0.07	0.03	0.06	-0.03	0.05	0.02	0.05	-0.03	0.00	0.18	0.21
		P	0.849	0.801	0.184	0.556	0.197	0.558	0.319	0.672	0.298	0.562	0.923	<0.001	<0.001

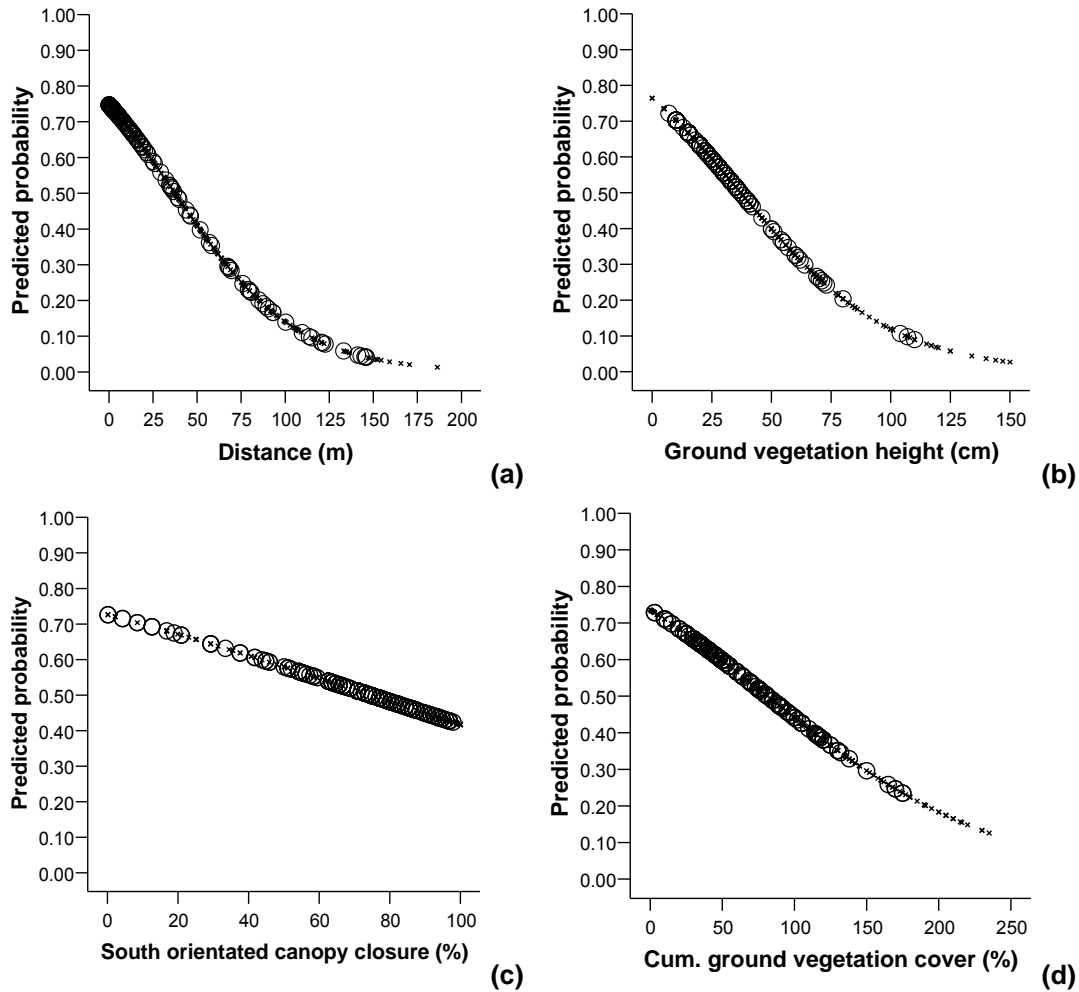
Table 4: Summary of the logistic regression analyses. Model: variables included in the logistic regression model. Model performance: summary of model performance tests. Model fit test: tests if the model fits the data ($P < 0.05$ = good model fit). Hosmer & Lemeshow Model fit test: tests if the model 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 to the model for the individual variables ($P < 0.05$ = significant). B (with Standard Error): indicates the direction of the relationship between the individual variables and wood cricket presence (- indicates a negative and + a positive relationship). Exp. (B) (with 95% Confidence Interval): indicates the odds ratio for wood cricket presence per unit increase of the individual variable (below 1 indicates a decrease above 1 an increase).

Logistic Regression		Model performance										Variables in the equation								
Variables	Model	n	Model fit test			Hos. & Lem. Model fit test			Classification table (%)			Effect size Nagelkerke R^2	Wald test			95% C.I. Exp(B)				
			χ^2	df	P	χ^2	df	P	Absent	Present	Total		z	df	P	B	S.E.	Exp (B)	Lower	Upper
Euclidean distance to nearest occupied permanent edge		402	225.3	4	<0.001	6.608	8	0.579	80	85	82	0.57	64.21	1	<0.001	-0.032	0.004	0.968	0.961	0.976
Ground vegetation height													35.82	1	<0.001	-0.048	0.008	0.954	0.939	0.969
South orientated canopy closure													46.94	1	<0.001	-0.053	0.008	0.949	0.934	0.963
Cumulative ground vegetation cover													15.14	1	<0.001	-0.014	0.004	0.986	0.979	0.993
Constant													78.63	1	<0.001	8.009	0.903	3007		
Euclidean distance to nearest occupied permanent edge		402	101.2	1	<0.001	97.48	8	<0.001	70	82	76	0.30	69.92	1	<0.001	-0.029	0.003	0.971	0.965	0.978
Constant													45.64	1	<0.001	1.085	0.161	2.959		
Ground vegetation height		402	58.50	1	<0.001	29.85	8	<0.001	54	83	68	0.18	42.05	1	<0.001	-0.032	0.005	0.969	0.959	0.978
Constant													34.99	1	<0.001	1.177	0.199	3.245		
Cumulative ground vegetation cover		402	37.83	1	<0.001	55.81	8	<0.001	62	71	66	0.12	33.16	1	<0.001	-0.013	0.002	0.987	0.983	0.992
Constant													25.46	1	<0.001	1.025	0.203	2.788		
South orientated canopy closure		402	10.56	1	0.001	108.2	8	<0.001	70	48	59	0.03	10.07	1	0.002	-0.013	0.004	0.987	0.979	0.995
Constant													8.983	1	0.003	0.977	0.326	2.658		



See attached file: Fig1.tif

Fig. 1 Woodland locations on the Isle of Wight (UK). (a) Briddlesford copse; (b) Firestone copse; (c) Borthwood copse. Derived from digital maps based on the National Inventory of Woodland and Trees (NIWT) (Smith and Gilbert 2003).



See attached files: Fig2a-d.tif (arrange together)#

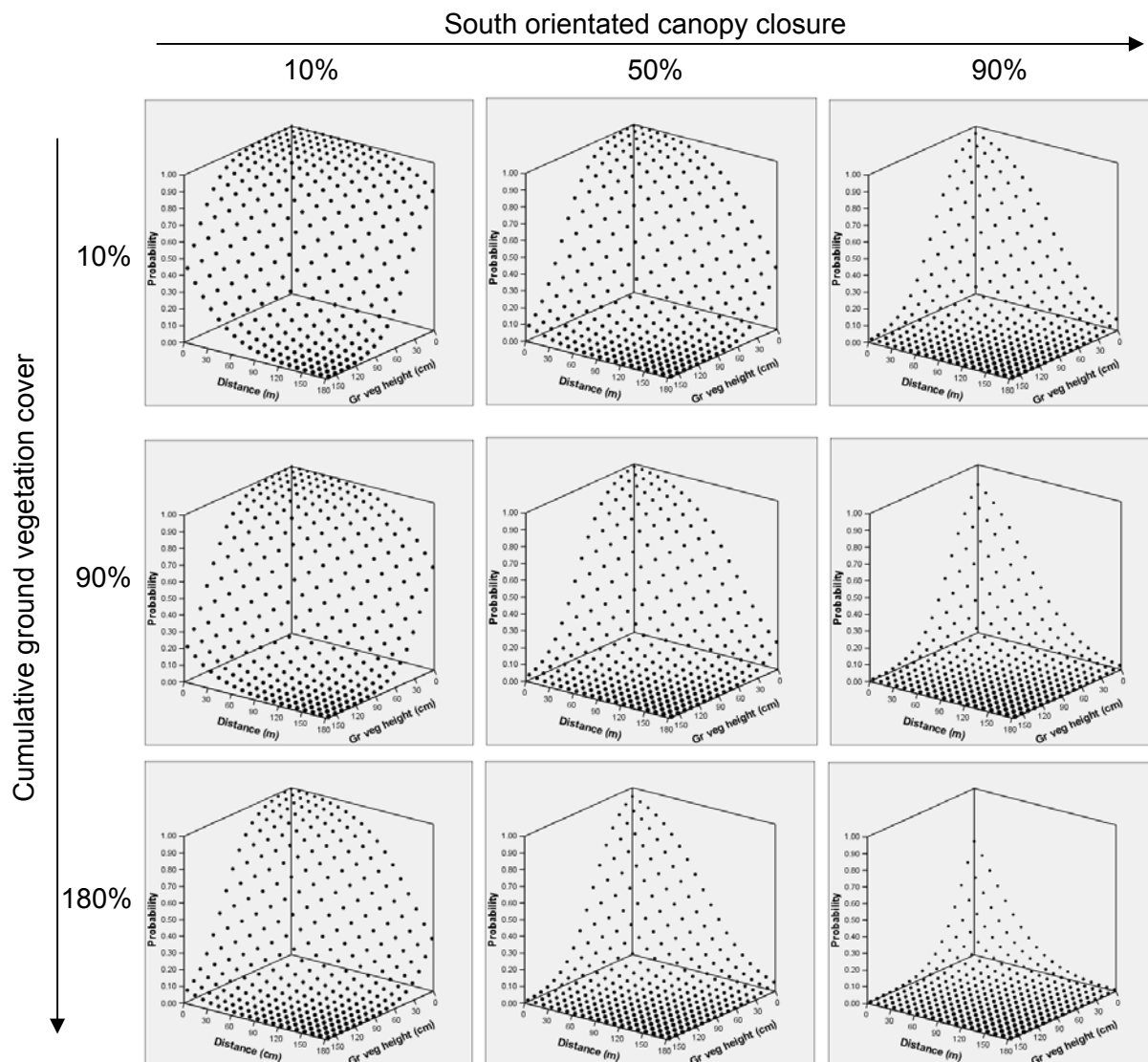
Fig. 2 Predicted probability of wood cricket being present related to the main explanatory variables. O indicates sites where wood cricket was present; x indicates sites where wood cricket was absent. Two outliers (167 cm for vegetation height and 273 m for distance) were omitted from Figure a and b. The curves were calculated with the following probability equations using the B values from Table 4:

$$(a) P(y) = \frac{e^{1.085 + (-0.029)(Distance)}}{1 + e^{1.085 + (-0.029)(Distance)}}$$

$$(b) P(y) = \frac{e^{1.177 + (-0.032)(Ground\ vegetation\ height)}}{1 + e^{1.177 + (-0.032)(Ground\ vegetation\ height)}}$$

$$(c) P(y) = \frac{e^{0.977 + (-0.013)(South\ orientated\ canopy\ closure)}}{1 + e^{0.977 + (-0.013)(South\ orientated\ canopy\ closure)}}$$

$$(d) P(y) = \frac{e^{1.025 + (-0.013)(Cum.\ ground\ vegetation\ cover)}}{1 + e^{1.025 + (-0.013)(Cum.\ ground\ vegetation\ cover)}}$$



See attached file: Fig3.tif

Fig. 3 Predictive probability of the full model represented in 3-D. In each figure probability of wood cricket presence (y-axis) is plotted against occupied nearest neighbour distance (x-axis) and ground vegetation height (z-axis). Columns represent different levels of South orientated canopy cover and rows represent different values of cumulative ground vegetation cover.

$$P(y) = \frac{e^{8.009 + (-0.032)(\text{Distance}) + (-0.048)(\text{Gr vegetation height}) + (-0.053)(\text{S orientated canopy closure}) + (-0.014)(\text{Cum ground vegetation cover})}}{1 + e^{8.009 + (-0.032)(\text{Distance}) + (-0.048)(\text{Gr vegetation height}) + (-0.053)(\text{S orientated canopy closure}) + (-0.014)(\text{Cum ground vegetation cover})}}$$

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