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How do low dispersal species establish large range sizes? The case of the water beetle *Graphoderus bilineatus*

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Species' dispersal abilities have been considered a major driving force in establishment and maintenance of large range sizes. However, recent studies question the general validity of this relationship because the relationship between dispersal ability and range size might in some cases be less important than species phylogeny or local spatial attributes. In this study we used the water beetle *Graphoderus bilineatus* a philopatric species of conservation concern in Europe as a model to explain large range size and to support effective conservation measures for such species that also have limited dispersal. We recorded the presence/absence of *G. bilineatus* and measured 14 habitat and 20 landscape variables at 228 localities in Estonia, Poland and Sweden within the core range of the species. Using information theory and average multivariate logistic regression models we determined that presence of *G. bilineatus* depended on landscape connectivity, distance to a possible source habitat, and stability of the site; however, specificity of habitat characteristics was not vital for the species. We reason that the large range of *G. bilineatus* is best explained by the historical combination of lakes, river systems and wetlands which used to be highly connected throughout the central plains of Europe. Our data suggest that a broad habitat niche can prevent landscape elements from becoming barriers for species like *G. bilineatus*. Therefore, we question the usefulness of site protection as conservation measures for *G. bilineatus* and similar philopatric species. Instead, conservation actions should be focused at the landscape level to ensure a long-term viability of such species across their range.

At the frontiers of ecology, biogeography, and interest in climate-driven species extinction, there is considerable interest in the distributions and range sizes of species (Brown et al. 1996, Gaston 2006, Hof et al. 2011). For a broad range of taxa, dispersal ability appears to be a major driving force in establishment of large range sizes (Brown et al. 1996, Gaston 1996, Gutierrez and Menendez 1997, Mora and Robertson 2005, Lowry and Lester 2006). However, in a recent review, Lester et al. (2007) questioned the general validity of this relationship. In addition, recent studies have shown that the positive relationship between dispersal ability and range size may, in some cases, be an artifact of phylogenetic bias or local spatial attributes (Gove et al. 2009, Garcia-Barros and Benito 2010, Mora et al. 2011). Thus dispersal ability should be regarded as only one of several factors that may shape range size of a species (Lester et al. 2007). Dennis et al. (2005), for example, have suggested that species ranges are fundamentally a result of interaction between niche-breadth and dispersal ability and niche-breadth itself is often regarded as an important characteristic for establishing large range sizes (Gaston 2006). Nonetheless, few studies have empirically addressed the basis of species range sizes. In particular, little is known about

how species with low dispersive power attain large range sizes and what processes drive the persistence of such large ranges.

Habitat and landscape features, which affect the local distribution of species, are generally regarded as decisive for the viability of populations at the local scale and, thus, the distribution of species at the global scale (Joly et al. 2001, Bakker et al. 2002, Lowe and Bolger 2002, Armstrong 2005). In this study we explored the paradoxical distribution pattern of a philopatric but widespread aquatic insect species, the aquatic water beetle *Graphoderus bilineatus*, and attempted to understand its range size in relation to the factors that limit local persistence. We examined the habitat and landscape dependencies of this species across three different landscapes in northern and eastern Europe. *Graphoderus bilineatus* uses a well-defined habitat (lakes, ponds and other stagnant waters), and has a large European range size despite low dispersal capacity and is thus an ideal candidate for the purposes of this study.

Graphoderus bilineatus is considered a threatened species throughout its western distribution range where its occurrence is rare and patchy (Nilsson and Holmen 1995, Foster 1996, Hendrich and Balke 2000). It is strictly protected within the EU-countries (Council of the European

Union 1992) and is thereby among the few invertebrates worldwide receiving substantial attention in terms of active conservation measures. Hence, empirically clarifying habitat–landscape relationships for this species will contribute to successful protection of the species and its habitats within the framework of the EU Habitat Directive and the NATURA 2000 network.

Material and methods

Study species

Graphoderus bilineatus is a medium size, predacious water beetle (body length 14–16 mm) from the family *Dytiscidae*. It has a univoltine life cycle with oviposition in spring–early summer, followed by aquatic larvae stages and a terrestrial pupa stage (Nilsson and Holmen 1995, Foster 1996). Although some adults of *G. bilineatus* fly (Nilsson and Holmen 1995, Hendrich and Balke 2000) and these beetles have normally developed flight muscles, only a fraction of specimens in a population seems to do so (Iversen unpubl.). Flight studies in areas where *G. bilineatus* occur have not documented any flight activity for the species (Lundkvist et al. 2002). Overall, the descriptions of the flight ability of *G. bilineatus* are rare or anecdotal and the species is regarded as having low dispersal power (Kehl and Dettner 2007). Nonetheless, the species has a wide distribution, ranging west-east from France to western Siberia, and north-south from central Finland to northern Italy (Nilsson and Holmen 1995, Foster 1996).

Several authors have described *G. bilineatus* as a highly stenoeious species with a distribution restricted to a specific combination of habitat characteristics (Holmen

1993, Hendrich and Balke 2000, Cuppen et al. 2006). However, reports on specific habitat requirements of the species are contradictory and differ across the species range. Habitats assumed to be essential for the species can be divided into two general categories: 1) clear and mesotrophic or oligotrophic larger lakes or canals with sparse vegetation (Galewski 1971, Nilsson and Persson 1989, Cuppen et al. 2006), or 2) lakes with sun-exposed shallow zones and dense marginal vegetation (Holmen 1993, Nilsson and Holmen 1995, Hendrich and Balke 2000).

Study areas

The study was carried out in three areas located in the core of the European distribution of *G. bilineatus*: the floodplain valley of the Narew River in eastern Poland; three national parks (Haanja, Karula and Emajõe-Suursoo) in southeastern Estonia and the forest landscape of north-eastern Scania in Sweden (Fig. 1). These three areas were chosen based on differences in landscape shaping processes, and results gained across these areas form a general pattern of the environmental variables determining the presence of the species. They may be characterized as follows. The river valley in Poland is a dynamic landscape with large floodplains dominated by grassland and cultivated rural areas. Beavers are active both in the floodplains and in the cultivated areas. The aquatic habitats are small to medium-sized natural ponds and oxbow lakes and artificial man-made ponds used for watering cattle and breeding fish. The sites in Estonia are situated in a moraine landscape with hilly areas and larger wetlands. The landscape is a mosaic of extensively used agricultural land and mixed or coniferous forests. Both large and medium-sized lakes are present in the

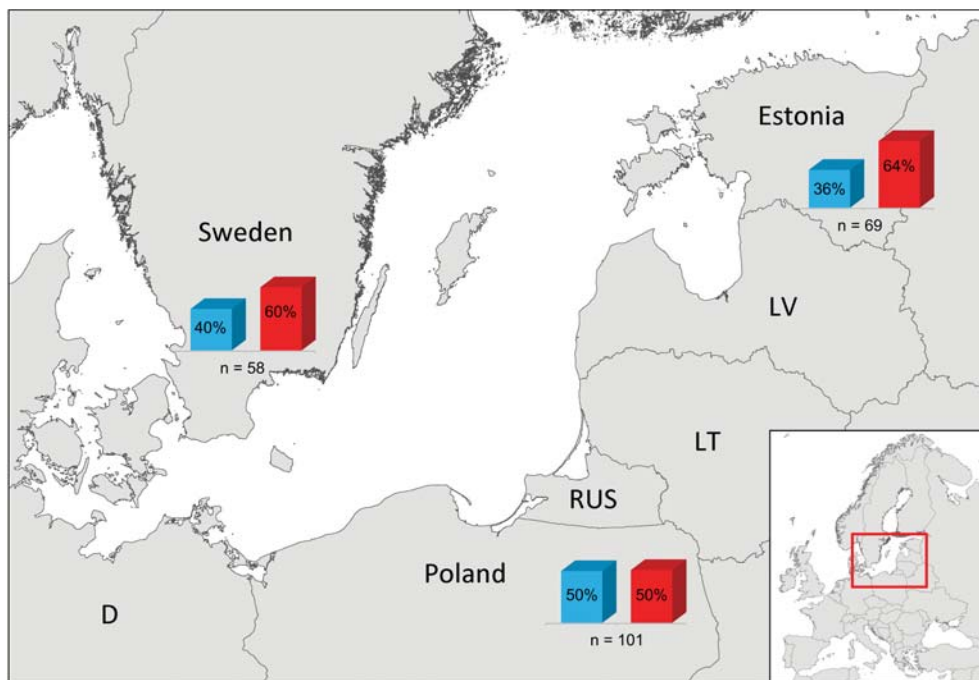


Figure 1. The geographic location of the 3 study areas. The bar graphs illustrates the percentage occurrence of *G. bilineatus* at numerous sites (n) within each study area (blue = present, red = absent).

landscape and flooding because of beaver activity is common in depressions and along streams. Small artificial ponds are scattered throughout the landscape, either due to their function as sauna- or fishponds, or due to extensive conservation of small water bodies in this area (Rannap et al. 2009). The Swedish landscape consists of a mixture of conifer-dominated forests and cattle-grazed farmland. The landscape is formed by exposed bedrock, creating a myriad of lakes, mires and bogs. In contrast to the two other areas there are no beavers.

Data collection

A total of 228 localities were investigated in 2010 and 2011 within the breeding period of *G. bilineatus*. A semi-standardized dipnetting method adopted from Nilsson and Svensson (1995) was used. The species was actively sought during 45 min at each site by sweeping a hand dipnet (40 × 40 cm frame) through vegetation and detrital material and based on the search the species was recorded as either present or absent at each site. This survey method has proven to be the most time effective for *G. bilineatus* (Klečka and Boukal 2011), with a coverage as good as or better than other sampling methods (Koesse and Cuppen 2006). To rule out skill-related sampling bias, all fieldwork was carried out by the same person (LLI). We believe that detection of adult specimens serves as a reliable proxy for breeding site status, because *G. bilineatus* has a univoltine lifecycle and therefore it must reproduce every year for a population to persist. Additionally the presence of the species did not show any signs of spatial autocorrelation (Results), which indicate that it is within site reproduction and not yearly migration that is the major determinant of the presence of the species. Prior to the fieldwork sites that were directly interconnected by waterways, only one of them was randomly selected for the study, though 228 localities were still examined. Finally, to assess the reliability of the survey data, 10 Swedish sites were re-sampled in 2011. The surveys generated the same results as those obtained in 2010 (i.e. the same 5 localities had *G. bilineatus* and the same 5 did not).

In total, 14 habitat characteristics and 20 landscape level variables were collected for each site (see Table 1 and 2 for detailed description). Variables assumed to influence presence/absence of *G. bilineatus* were selected based on existing literature and results of preliminary fieldwork conducted on the species. The 20 landscape variables described environmental resistance to dispersal such as connectivity parameters (number of ponds within a given distance and distance to a lake or node in the landscape), land cover types (ranging from open to closed and disturbed to natural land cover classes) and the level of heterogeneity in landscape structure. These habitat variables were derived by GIS (ArcGis 9.3, <www.ESRI.com>) from contemporary land cover maps of each region.

Data analysis

To explore the relationship between the presence of *G. bilineatus* and the environmental variables of interest, an information theoretic approach (Burnham and Anderson

Table 1. Habitat variables measured at each of the 228 sites; significance levels were determined by univariate logistic regression.

Habitat variables	Acronym	p-value
Surface area (m ²)	log(area)	<0.001
Shape: length/width ratio	Shape	<0.01
Maximum shallow zone: 0–30 cm (m)	max.shal	<0.05
Minimum shallow zone: 0–30 cm (m)	min.shal	<0.05
Max depth (>0.5, 0.5, 1 or 1.5 m)	Depth	<0.001
Maximum edge slope: (5, 10, 25, 45 or 90 degrees)	max.slope	<0.01
Minimum edge slope (5, 10, 25, 45 or 90 degrees)	min.slope	<0.001
Water color (clear, muddy, algal-green, brown)	factor(water)	<0.05
Grazing (yes/no)	factor(grazing)	0.12
Shading from surrounding trees (%)	Shadow	<0.001
Vegetation above 1 m in height (%)*	vega1m	0.48
Vegetation below 1 m in height (%)	vegb1m	0.07
Floating vegetation (%)	Fveg	<0.01
Submerged vegetation (%)*	Sveg	0.23

*Variables omitted from multivariate analysis.

2002) was used in a multivariate logistic regression model environment. Information theory relaxes some of the problems induced by stepwise model selection and classic null-hypothesis testing (Johnson and Omland 2004, Whittingham et al. 2006, Stephens et al. 2007). The main effect of the 34 environmental variables was used as explanatory variable. Given that the predictive power of one single model may not be clearly superior, model averaging was performed across a set of candidate models. Estimates of parameters by model averaging are robust in the sense that they reduce model selection bias and account for model selection uncertainty (Johnson and Omland 2004).

Hegyí and Garamszegi (2011) argued that only when a full model containing all initial variables is analyzed, information theory can overcome the errors caused by stepwise model reduction. However, creating an initial model from all 34 variables produces an overly complex model and 2³⁴ potential sub models. Thus, following the recommendation of a prior explorative data search by Grueber et al. (2011), two selection steps were applied in order to create a set of candidate variables.

Firstly, a univariate analysis of each environmental variable was conducted, testing the effect of the variable on the presence of *G. bilineatus* on a log-odds scale. A logistic regression model with the environmental variable as the explanatory variable was performed, assessing the effect of each variable by a χ^2 -test (Table 1 and 2). From the univariate tests all variables with a p-value >0.15 were omitted from further analysis. Prior to the first selection step, lake area was log-transformed to ensure that the probability of *G. bilineatus* presence would be zero when lake area is zero. Additionally, the effect of landscape and latitudinal or longitudinal gradient effects on *G. bilineatus* presence were tested in the same framework as the environmental variables.

Table 2. Landscape variables measured at each of the 228 sites; significance levels were determined by univariate logistic regression.

Landscape variables	Acronym	p-value
No. of ponds < 100 m from site	ponds100m	0.07
No. of ponds between 100 and 200 m from site	ponds200m	< 0.05
No. of ponds between 200 and 800 m from site*	ponds800m	0.30
Distance to lake (m)	dist.lake	< 0.001
Distance to stream, ditch or river (m)	dist.node	< 0.001
Habitat 0–500 m. % Forest of total area*	forest500	0.50
Habitat 0–500 m. % Open land (grassland and field) of total area*	open500	0.31
Habitat 0–500 m. % Urban/farm of total area	urban500	0.14
Habitat 0–500 m. % Bogs/swamps of total area	bog500	0.13
Habitat 500–1000 m. % Forest of total area*	forest1000	0.23
Habitat 500–1000 m. % Open land (grassland and field) of total area	open1000	0.15
Habitat 500–1000 m. % Urban/farm of total area*	urban1000	0.80
Habitat 500–1000 m. % Bogs/swamps of total area*	bog1000	0.56
Habitat 1000–2000 m. % Forest of total area*	forest2000	0.34
Habitat 1000–2000 m. % Open land (grassland and field) of total area*	open2000	0.20
Habitat 1000–2000 m. % Urban/farm of total area*	urban2000	0.33
Habitat 1000–2000 m. % Bogs/swamps of total area*	bog2000	0.88
No. of patches 10 000 ha ⁻¹ (0–500 m)	pd500	< 0.05
No. of patches 10 000 ha ⁻¹ (500–1000 m)	pd1000	0.05
No. of patches 10 000 ha ⁻¹ (1000–2000 m)*	pd2000	0.25

*Variables omitted from multivariate analysis.

Secondly, two initial logistic regression models were created, containing habitat variables and landscape variables respectively (Table 2). These models were used to find the habitat and landscape level variables potentially affecting the presence of *G. bilineatus*. From these initial models second-order Akaike information criterion (AIC_c) values were calculated from all possible submodels. AIC_c was chosen due to the low number of samples in relation to the number of parameters present in the initial model (Symonds and Moussalli 2011). From all the possible submodels the model with the lowest AIC_c value was identified, and a group of candidate models selected, containing all models within two units of this AIC_c value (Burnham and Anderson 2002).

These models were averaged by the use of the MuMIn package in R (Barton 2012), and parameter estimates were calculated from this average model. Before conducting the analysis, all input variables were standardized to a common scale with a mean of 0, and an SD of 0.5, in order to ease the parameter interpretation and allow comparisons of effects. From the average habitat and landscape model, explanatory variables with unidirectional parameter estimations (within the 95% confidence intervals) were selected as variables potentially affecting the presence of *G. bilineatus* (Supplementary material Appendix 1, Table A2).

A final initial model was then formulated based on these two selection steps (Table 3). The final model underwent the same procedure as the habitat and landscape model, and from the 2ΔAIC_c models an average model was created. From this averaged final model parameter estimates and 95% confidence intervals were determined. The relative effect of each explanatory variable was expressed as the sum of Akaike weights (w_i) in the 2ΔAIC_c models, where the variable occurred. The larger the sum of the Akaike weight, the more important the variable is relative to the other variables in the average model.

An increasing amount of literature highlights the presence of spatial auto-correlation in ecological data and

possible overestimation of the degree that habitat variables affect species occurrence (Legendre 1993, Keitt et al. 2002) – a problem which also exists in parameter estimation by information theory (Diniz-Filho et al. 2008). Spatial auto-correlation in the distribution of *G. bilineatus* could occur in the data for the following reasons: the descriptor for species presence may not reflect independent breeding populations, but could be an artifact of temporary emigration from nearby sources. If this was true, auto-correlation should occur within close distance of a site with species presence. Secondly, if long distance movements occur frequently, spatial auto-correlation would be present in the catchment areas of each site. One way to assess the extent of spatial auto-correlation is correlograms of data, a graphical representation of the spatial correlation between locations at a range of a given lag distances. In this study the presence of spatial auto-correlation was assessed after accounting for the level of spatial auto-correlation explained by the explanatory model variables. This was achieved by a spline correlogram produced from the Pearson residuals of the final average model, using the R package ncf (Bjørnstad and Falck 2001). The x-intercept in the spline correlogram is the distance at which an object is no more similar than what is expected by random placement across the region.

Table 3. Variables included in separate habitat and landscape models and a final model combining habitat and landscape variables.

Models	Initial explanatory variables
Habitat model	Grazing, depth, vegb1m, min.shal, max.shal, water, max.slope, min.slope, fveg, shadow, logarea, shape
Landscape model	urban500, field500, bog500, open1000, ponds100m, ponds200m, pd500, pd1000, dist.node, dist.lake
Final model	logarea, depth, max.slope, shadow, fveg, ponds200m, dist.lake, dist.node, bog500, pd1000, open1000

Possible spatial auto-correlation is assessed using 95% point wise bootstrap confidence intervals calculated from 1000 bootstrap samples.

The final model was evaluated for predictive ability against the average habitat model and landscape model using a ROC curve. The ROC curve represents the relationship between true presences and false presences for a range of threshold values classifying the probability of presence based on the predicted probabilities of *G. bilineatus* occurrence in the area (Fielding and Bell 1997). Differences between the predictive abilities of the three models were evaluated based on their AIC-values using a method for paired ROC-curves (DeLong et al. 1988). The ROC-curves and test statistics were created in the qROC package in R (Robin et al. 2011).

All analysis were conducted in R ver. 2.14.2 (<www.r-project.org>).

Results

Graphoderus bilineatus was found in 43% of the 228 localities investigated, and site occupation varied between 36% in Estonia and 50% in Poland (Fig. 1 and Supplementary material Appendix 1, Table A1). The chance of finding the species did not differ significantly ($p = 0.19$) among the three countries, nor did either longitude or latitude influence probability of occupation ($p = 0.79$ and $p = 0.07$ respectively). Thus, the data suggested no evidence of a geographic gradient.

Two habitat variables and 10 landscape characteristics were omitted from further analyses after the univariate analyses (Table 1, 2; see also Methods). From the variables used initially in the habitat and landscape models (Table 3), respectively, six and four models were found to be within $2\Delta AIC_c$ (Supplementary material Appendix 1, Table A3). Model averaging of these top models identified five habitat variables and six landscape variables with unidirectional parameter estimation (Supplementary material Appendix 1, Table A2). These eleven variables were thus included in our final model (Table 3). From different combinations of variables in the final model, five submodels were selected within the $2\Delta AIC_c$ (Supplementary material Appendix 1, Table A3). The results from the model averaging of these five models and the parameter estimates of the standardized variables are shown in Table 4. Three habitat variables (log (surface area), maximum edge slope and the degree of shadow) had constant parameter direction. With a one unit increase in log(area), there was a positive effect on the log-odds of *G. bilineatus* being present (relative change in odds by a factor of 12.21 [4.53–33.12] (mean and 95% CL)). In contrast, increases in maximum slope and the degree of shadowiness at a site negatively affected the log-odds of finding *G. bilineatus* (odds changed by a factor of 0.30 [0.12–0.73] and 0.34 [0.14–0.84] by one unit increase of the two predictor variables, respectively).

Five landscape variables with unidirectional parameter estimations can be referred to the following three groups: 1) distance to a possible immigration source. Both increasing distance to nearest lake and nearest node in the landscape had a negative effect on the presence of *G. bilineatus*

Table 4. Parameter estimates and relative importance of the landscape and habitat variables for the final model. The estimates are derived from an average model of five possible models explaining the presence-absence of *Graphoderus bilineatus*.

Parameter	Estimate	95% confidence intervals	Relative importance
(Intercept)	-0.59	[-0.99, -0.19]	
bog500	1.10	[0.03, 2.17]	1
Depth	0.49	[-0.38, 1.37]	0.32
dist.lake	-1.77	[-2.82, -0.72]	1
dist.node	-1.16	[-2, -0.32]	1
Fveg	-0.87	[-1.81, 0.07]	0.85
Logarea	2.50	[1.51, 3.5]	1
max.slope	-1.21	[-2.1, -0.32]	1
open1000	2.03	[1.05, 3.01]	1
pd1000	-1.55	[-2.42, -0.68]	1
ponds200m	-0.74	[-1.65, 0.16]	0.63
shading	-1.08	[-1.99, -0.18]	1

(with a one unit increase of the two variables odds decreased by factors of 0.17 [0.06–0.49] and 0.31 [0.14–0.73] respectively). 2) Type of land-cover. The amount of wetland within 500 m of each site was positively related to the presence of *G. bilineatus* (the odds changed by a factor of 2.99 [1.03–8.76]). The amount of open landscape between 500 and 1000 m from the study site had a positive effect to the species (odds changed by a factor of 7.64 [2.86–20.29]). 3) Landscape structure. The extent of landscape heterogeneity between 500 and 1000 m from each site affected the presence of *G. bilineatus* negatively (with a one unit increase in patch density, the odds decreased by a factor of 0.21 [0.09–0.51]).

There was no evidence of spatial auto-correlation in the spline correlogram from the Pearson residuals of the final average model (Fig. 2). Thus, spatial auto-correlation is not likely to influence parameter estimates for the average model (Table 4). The combination of habitat and landscape variables in one average model (Fig. 3) provided a better predictive model than habitat variables or landscape variables alone ($Z = 2.44$, $p < 0.02$ and $Z = 3.90$, $p < 0.001$ respectively). These results reflect findings of other studies (Richard and Armstrong 2010), highlighting the importance of integrating both the landscape characteristics and habitat variables in ecological models.

Discussion

Our results explore the factors that potentially determine population viability of *G. bilineatus*, and illuminate the landscape features that may have lead to its current distribution. The weak relationship between species presence and habitat variables suggests a wide habitat niche and contrasts with the widespread perception of the species as being stenotypic. Interestingly, none of the habitat variables, traditionally thought to reflect suitability (e.g. vegetation type, water quality, depth of water, presence of shallow areas) had substantial effect on the presence of *G. bilineatus*, although in the literature they have long been regarded as being crucial (Hendrich and Balke 2000, Cuppen et al. 2006). We point out that these presumptions about the nature of typical habitat are at the root of the EU Habitat

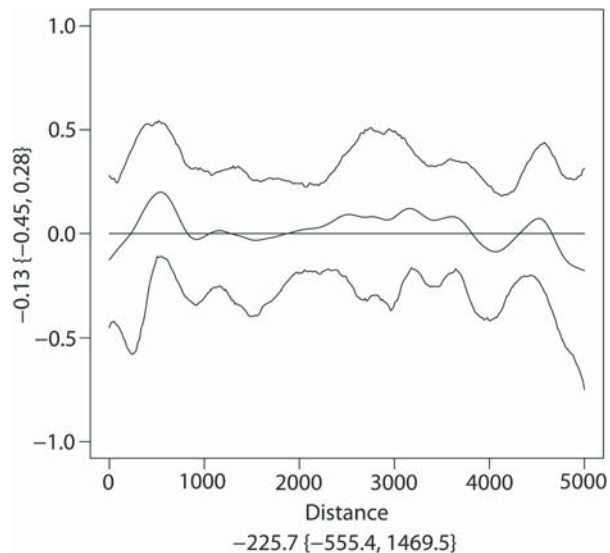


Figure 2. Spline correlogram, with 95% point-wise bootstrap confidence intervals of the Pearson residuals from the final averaged model.

Directive and European NATURA 2000 Nature Conservation Network guidelines for conservation of the species across the majority of its range.

Our analysis did identify some features useful for making predictions about site occupancy. For example, the negative effect of the degree of shadow from surrounding trees on species presence does seem to indicate that either sun-exposed areas or an open flight path are important for *G. bilineatus*. The species was also more commonly found at lakes with natural edges, but not necessarily in lakes with a wide shallow zone. Steep edges were, however, associated with man-made waters such as stone quarries,

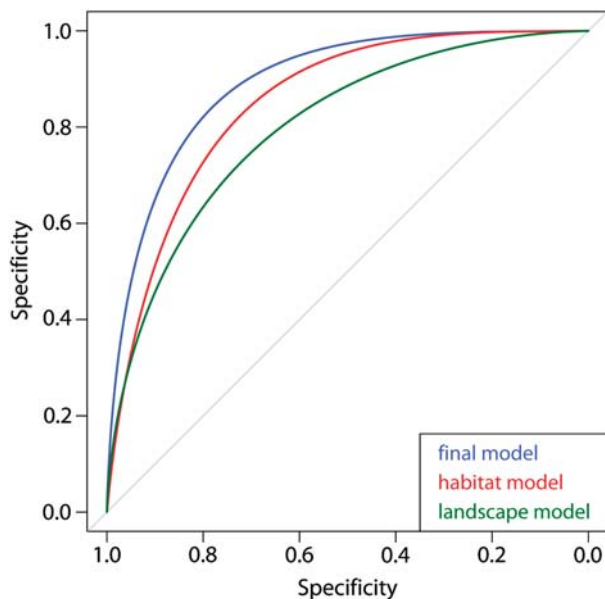


Figure 3. Smoothed ROC-curves describing the final model (AUC=0.89) and the two sub-models containing habitat variables (AUC=0.85) and landscape variables (AUC=0.80) respectively.

sauna ponds and fish ponds. This could imply that the negative effect of steeper maximum slope might be solely related to the unsuitable nature of these human created waters. The positive effect of lake area on presence of *G. bilineatus* reflects two important dependencies of a philopatric species with low mobility: stability and immigration (Gaston 2006). Because filling of lakes to a great extent takes place by in-growth of emergent plants and input of terrestrial material across the periphery, larger lakes have a greater longevity than small lakes of the same mean depth (Wetzel 1983). Greater wind exposure in large lakes will also slow sedimentation rates and enhance gas exchange rates with the atmosphere and, thereby, stabilize oxygen and pH conditions of benefit for water beetles (Sand-Jensen and Staehr 2009, Staehr et al. 2012). Overall, larger lakes are more temporally stable compared to smaller waters, hence the turnover rate is longer and mechanisms of metapopulation dynamics less vital.

The positive relationship between nearby dispersal sources and the presence of *G. bilineatus* is doubtlessly driven by the limited dispersal ability of the species (Taylor et al. 1993, Tischendorf and Fahrig 2000). The odds of a locality being occupied are closely related to the distance to a potential source population. This source effect includes direct sources (distance to a lake) but also dispersal corridors (rivers and ditches). However, the latter features can potentially act as both dispersal corridors and breeding sites (Vermeulen 1994). The fact that rivers, streams, and smaller channels in the landscape are used by *G. bilineatus* was confirmed in all three countries, where the species was found in slow flowing canals or in larger meandering rivers. Positive association of occupied sites with wetlands within a buffer distance of 500 m likely reflects a tendency for short-distance movement in *G. bilineatus*. However, overall, our results suggest a stronger effect of corridors as dispersal routes, as opposed to stepping stones (in this case as number of ponds within a given distance). Thus, it seems that site occupation depends on a dense network of lakes and temporally stable connectivity corridors.

Openness in the landscape up to 1000 m from each site was positively related to the presence of *G. bilineatus*. When flight does occur, it is assumed that localities in an open landscape are more likely to become occupied than localities in closed forest landscapes. Chin and Taylor (2009) documented that an open landscape enhanced long distance movements in a philopatric dragonfly, and this mechanism could also be important for *G. bilineatus*. Thus, the dependence of site occupation on an open landscape at 500–1000 m from each site may reflect an effect on arrival potential of dispersing individuals. This hypothesis is further supported by the negative relationship with landscape heterogeneity between 500 and 1000 m of the site. These ideas about mechanism behind the patterns revealed by our models should be further tested through empirical studies focused on the potential flying capacity and dispersal range of the species.

Clearly, *G. bilineatus* shows high dependence on landscape connectivity, distance to a possible source population and temporal habitat stability in its area of occupancy. Importantly, the results suggest that *G. bilineatus* is something of a habitat generalist, and that landscape features are

the major factors associated with the current distribution of the species. This conclusion is equally evident in all three countries and on the different landscape types investigated.

Given that *G. bilineatus* is philopatric with limited dispersal capacity and that the local distribution is highly dependent on landscape features and structure, our findings can be evaluated in the context of the abundance-distribution range theory. Such theory assumes that abundant species establish large range sizes simply due to their relation to widely distributed habitats (Gaston 2006). For a species with low dispersal ability such as *G. bilineatus*, a large range would then depend on presence of its habitat across the entire range. This pre-condition would in turn be highly influenced by the habitat niche-breadth of the species because stenotypic species are restricted to a smaller number of suitable habitats than are habitat generalists. Hence, the chance of high habitat connectivity is larger for species with a broad niche.

For *G. bilineatus*, establishment and maintenance of a large range is likely due to generality in habitat demands (a broad niche) and landscape connectivity. If the species had been more stenotopic about habitat use, barriers to establishment of populations would have been more probable, thereby restricting the range of the species by environmental resistance to effective colonization. High connectivity between lakes, wetlands, and river systems throughout its range combined with a broad habitat niche, has likely enabled *G. bilineatus* to occupy a variety of habitats over a vast range in Europe. However, today the landscape in the entire western part of the species' distribution range is influenced by strong anthropogenic impacts, leaving a less stable and unfavorable habitat structure for *G. bilineatus*, and this is likely to affect its long-term persistence.

Such information can be integrated into an informed conservation strategy for the species. The Natura 2000 habitat conservation network and the habitat directive (Council of the European Union 1992) provides the current basis for conservation of biodiversity in Europe. This strategy allocates substantial resources to protecting rare habitats which are vital for persistence of rare stenotypic species in the region. However, based on our study, it seems that taking this approach exclusively is not likely to be successful in the long term for species such as *G. bilineatus*. In contrast, our results clearly emphasize the importance of integrating the concepts of landscape structure and stability into conservation strategies and suggest that such approaches are important even for conservation on a local scale. The case of *G. bilineatus* provides a useful example of how neglect of geographical pattern and the associated dispersal processes may be problematic in conservation planning. Such concerns amplify the problem of long-term viability of species, thought to be protected in the Natura 2000 network, in relation to the ongoing concern about climatic changes (Araújo et al. 2011). Incorporating predictions about long term species persistence in the Natura 2000 network will be a daunting task; however, our study suggests that for a species like *G. bilineatus* conservation planning to achieve long-term persistence must be conducted at a landscape level, and not solely through designations of specific protection sites.

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Supplementary material (Appendix ECOG-00001 at <www.oikosoffice.lu.se/appendix>). Appendix 1.