

Mobility, habitat selection and population connectivity of *Lycaena helle* in central Sweden

– Implications for conservation

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Mobility, habitat selection and population connectivity of *Lycaena helle* in central Sweden - implications for conservation

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Abstract

Lycaena helle is an endangered butterfly that is mainly threatened by habitat degradation and fragmentation. For all species with a fragmented distribution, knowledge about mobility, habitat requirements and connectivity is key to developing successful conservation strategies. This study was conducted close to Östersund, in central Sweden, and aimed to investigate the mobility of *L. helle*, identify remote-sensed predictors of *L. helle* occurrence, examine the relationship between *L. helle* density, the abundance of its host plant and vegetation height and to classify local populations according to their importance for the connectivity on a regional level.

A mark-recapture study was performed, which found that *L. helle* is extremely sedentary, faithful to its habitat and appears to be reliant on females for long-distance dispersal. The recorded flight distances were in most cases longer than what has been found in Central Europe. A resource selection function was used to identify important predictors of *L. helle* occurrence among five variables computed from remote-sensed data; vegetation height, variation in vegetation, solar radiation, slope and aspect. Solar radiation and slope can be recommended for inclusion in future models. Probability of occurrence of *L. helle* increased at higher solar radiation, as *L. helle* is dependent on high insolation. Slope had a negative effect and is hypothesized to act as a proxy for wetness, as *L. helle* is strongly linked to wetland habitats and as low-gradient areas gather water whereas steep areas shed water.

Host plant abundance and vegetation height were inventoried and tested for correlations with *L. helle* density. There was a significant but weak positive correlation between the abundance of the host plant and the density of *L. helle*. The weak correlation implies that *L. helle* is either primarily limited by something else than its host plant or that it can only use the host plant when it grows under certain conditions. *L. helle* density was negatively correlated with vegetation height, likely caused by the late succession stage of most habitat patches in the study area, which induces selection for lower vegetation heights.

The connectivity analysis identified so-called stepping stones, i.e. populations that are particularly important from a connectivity perspective and to which conservation efforts should be directed. Retained or improved connectivity is stressed as fundamental for the conservation of the species. Dispersal corridors improve connectivity and are suitable as habitat patches in themselves, meaning that they merit conservation efforts. The timing and frequency of the maintenance of dispersal corridors is crucial and there is a need for better communication with the parties responsible. To improve the long-term viability of the studied metapopulation, it is recommended to make a dispersal corridor to suitable habitats in Tysjöarna nature reserve to increase the extent of the metapopulation. With the onset of climate change, retained connectivity is yet more important since large networks of populations are more viable and have a higher adaptability to new environmental conditions.

Populärvetenskaplig sammanfattning

Violett guldvinge, *Lycaena helle*, är en starkt hotad fjärilsart som i Sverige främst förekommer i Jämtlands län, med traditionellt hävdad jordbruksmark och rikkärr som främsta habitat. Utbredningen har minskat drastiskt i takt med att jordbruket har förändrats och är idag mycket fragmenterad. För fragmenterade arter är det extra viktigt med kunskap om mobilitet, habitatpreferenser och konnektivitet för bevarandearbetet. Denna studie undersöker spridningsförmågan hos violett guldvinge, identifierar fjärranalysbaserade variabler som kan förutsäga dess förekomst, undersöker relationen mellan täthet av fjärilen, förekomsten av dess värdväxt och vegetationshöjd samt klassificerar populationerna i Jämtland utifrån hur viktiga de är för en bibehållen konnektivitet i länet.

En fångst-återfångst-studie genomfördes utanför Östersund och visade att violett guldvinge är extremt stationär, habitattrogen och verkar vara beroende av honor för långdistansspridningar. Spridningsavstånden var i de flesta fall längre än de som har uppmätts i centraleuropeiska studier. Vilka fjärranalysbaserade variabler som kan förutsäga fjärilens förekomst identifierades genom att variablerna inkluderades i modeller och värderades utifrån hur väl modellerna fungerade. De variabler som ingick var solstrålning, lutning, vegetationshöjd, variation i vegetationshöjd och riktning. Solstrålning och lutning var viktigast och kan rekommenderas för inkludering i framtida modeller. Stark solstrålning ökar sannolikheten att fjärilen ska förekomma då den är starkt beroende av solsken. Ökad lutning minskar sannolikheten att fjärilen ska förekomma och kan ha fungerat som ett mått på fuktighet i marken, då violett guldvinge är starkt knuten till fuktiga marker och platta områden samlar mer fukt än områden som lutar.

Förekomst av värdväxt och vegetationshöjd inventerades i fält och testades för korrelationer med täthet av violett guldvinge. Värdväxten och fjärilen var svagt positivt korrelerade, vilket innebär att fjärilen påverkas positivt av förekomsten av dess värdväxt men att den antingen begränsas av något annat än sin värdväxt eller att den bara kan nyttja värdväxten när den växer under vissa förhållanden. Fjärilen var svagt negativt korrelerad med vegetationshöjd, sannolikt på grund av att majoriteten av habitaterna i studien har hög vegetation och violett guldvinge måste söka sig till områden med lägre vegetation inom habitaterna.

Konnektivitetsanalysen identifierade populationer som är extra viktiga för konnektiviteten i länet och som alltså bör prioriteras i bevarandearbetet. Bibehållen eller förbättrad konnektivitet är väsentlig för artens fortlevnad. Spridningskorridorer både förbättrar konnektiviteten och fungerar som habitat i sig själva, vilket innebär att åtgärder i dessa habitat bör prioriteras. Tidpunkt och frekvens för underhållsarbetet i dessa habitat är av stor vikt och bättre kommunikation med ansvariga aktörer behövs. För att förbättra den långsiktiga livskraften hos de studerade populationerna rekommenderas etablerandet av en spridningskorridor till lämpliga habitat i Tysjöarnas naturreservat. Ett klimat i förändring innebär att bevarandet av nätverk av populationer är fundamentalt för artens överlevnad, då de är mer livskraftiga och har högre potential att anpassa sig till nya förhållanden.

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1 Introduction

Loss of biodiversity is a worldwide concern that is driven mainly by habitat degradation and fragmentation (Saunders *et al.*, 1991; Debinski & Holt, 2000; Tilman *et al.*, 2001). Butterflies are some of the organisms that suffer most, as their dispersal abilities are limited and as they often show a high degree of habitat specialisation (Thomas & Hanski, 1997; Swaay & Warren, 1999; Bergman *et al.*, 2004). This sensitivity makes them a useful model group for studies on the effects of habitat loss and fragmentation on species persistence (WallisDeVries *et al.*, 2002).

For all species with a fragmented distribution, knowledge about the determinants behind patch occupancy and local population densities is key to developing successful conservation strategies (Nabielec & Nowicki, 2015). These determinants are in general divided into two main groups, of which the primary relates to habitat quality and the secondary relates to the spatial structure of the habitat patches. In the primary group, factors such as resource abundance and vegetation structure are included (Thomas *et al.*, 2001; Fleishman *et al.*, 2002). To investigate which factors best predict a species' spatial use of a habitat, resource selection functions (RSFs) can be used. RSFs aim to measure non-random relationships between an animal's geographic position and environmental conditions (Morris *et al.*, 2016). This is done by assessing the probability of the species using certain resources compared with the availability of those resources in the environment (Boyce *et al.*, 2002). To compute an RSF, data on the presence locations of the species and of the resource availability across the study area are needed (Manly *et al.*, 2007). RSFs are commonly used within conservation and management (Boyce *et al.*, 2002).

The secondary group of determinants includes patch area and connectivity (Thomas *et al.*, 2001; Fleishman *et al.*, 2002). According to metapopulation theory, patch area and connectivity are crucial predictors of species occurrence and major factors in the long-term survival of populations (Hanski, 1998; Fischer *et al.*, 1999). Fragmentation caused by habitat deterioration leads to an increased risk of extinction due to the collapse of metapopulation-level processes such as source-sink dynamics and a decreased probability of recolonisation (Gilpin & Hanski, 1991). To maintain functioning metapopulations, it is crucial to identify populations that are important from a connectivity perspective and to which

conservation efforts should be directed (Heller & Zavaleta, 2009; Krosby *et al.*, 2010). Connectivity models based on network analysis (graph theory) are being increasingly applied for ecological research and conservation planning (Hanski & Ovaskainen, 2000; Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010). With these models, so-called stepping stones can be identified. Saura *et al.* (2014) define a stepping stone as a habitat patch that facilitates movement between at least two other patches, resulting in a higher probability of dispersal between these two patches than if the stepping stone did not exist. Stepping stones are crucial for species long-distance dispersal and range expansion and can contribute to species persistence across wide temporal and spatial scales (Saura *et al.*, 2014).

In this study, the focal species is the threatened butterfly *Lycaena helle*, or violet copper, which in Fennoscandia occurs as the subspecies *L. helle lapponica*. The nominal form of *L. helle* occurs in Central Europe (Eliasson, 2012), where it is considered one of the most threatened butterfly species (Eliasson *et al.*, 2005). In Sweden, *L. helle* has decreased with 35% (20-45%) during the past ten years and is classified as endangered (Eliasson, 2012). The Swedish population size of *L. helle* has been estimated to 3500-10500 individuals distributed in about 70 populations according to Lindeborg (2014), while Eliasson (2012) estimates that as few as 2750-5000 reproductive individuals remain, spread over 30-100 populations. With a highly fragmented distribution, many of these populations are isolated and not considered viable in the long term (Lindeborg, 2014). The decrease is mainly caused by habitat degradation and fragmentation as a consequence of altered agricultural practices (Eliasson, 2012).

The Fennoscandian populations of *L. helle* are severely understudied. Differences in the ecology between the Central European populations and the Fennoscandian populations make it inadvisable to apply knowledge about the nominal form directly on the Fennoscandian subspecies. The two subspecies differ among others in the choice of host plant, and whereas the Central European populations occur in two generations per summer, the Fennoscandian occur in only one (Lindeborg, 2014). This study aims to fill some of the gaps, focusing on the knowledge about determinants of patch occupancy and local population densities in a metapopulation in Jämtland County. Factors relating to both habitat quality and spatial structures will be addressed. These components provide important pieces for the conservation of metapopulation structures of *L. helle* (Lindeborg, 2014).

Knowledge about dispersal ability is fundamental when investigating connectivity, but the dispersal ability of the Fennoscandian populations has not been studied (Lindeborg, 2014). Studies on the Central European populations show that *L. helle* is extremely sedentary, faithful to its habitat and a poor colonizer (Fischer *et al.*, 1999; Craioveanu *et al.*, 2014; Turlure *et al.*, 2014). The nominal form is mainly dependent on adult females for dispersal (Lindeborg, 2014), who disperse in search of oviposition sites (Fischer *et al.*, 1999). A German study made by Bauerfeind *et al.* (2009) has shown that the main driving factors behind colonisation of new sites are the size of the present site, the connectivity with other sites and the abundance of the host plant *Bistorta vivipara*. The quality of the site itself is less

important (Bauerfeind *et al.*, 2009). Wind-mediated dispersal may occur across open fields, but for active dispersal, *L. helle* is likely to prefer wind-sheltered stands. If barriers are present, *L. helle* has a rather poor individual ability to move between neighbouring habitats. Open areas and spruce forests are examples of likely barriers (Fischer *et al.*, 1999).

The knowledge about the habitat preferences of the Fennoscandian populations of *L. helle* derives from field observations or is inferred from studies on the Central European populations, but has not been tested specifically. In Central Europe, the habitat of *L. helle* has among others been linked to high solar radiation, the presence of its host plant *B. vivipara* (Ryrholm, 2014) and a variable vegetation cover that provides wind shelter (Sawchik *et al.*, 2003). An early succession stage leads to a positive relationship between vegetation height and *L. helle* densities, whereas succession at later stages is detrimental to the species (Skórka *et al.*, 2007). In this study, the habitat preferences will be tested both with an RSF using presence/absence locations and remote-sensed data as well as with correlations between *L. helle* density and inventory-based data on the abundance of the host plant and vegetation height.

Lindeborg (2014) and Eliasson (2012) stress that the conservation of metapopulations is fundamental for the long-term viability of *L. helle*. Fragmentation of habitats and isolation are suggested by Lindeborg (2014) as possible explanations as to why *L. helle* has disappeared from a number of sites where the habitat appears favourable. This is supported by Sawchik *et al.* (2003), who showed that *L. helle* exists in lower numbers in populations with a higher degree of isolation, independent of the quality of the habitat. Out of five studied butterfly species, *L. helle* was one of two species that showed highest sensitivity to isolation (Sawchik *et al.*, 2003). Additionally, smaller populations of *L. helle* that are connected to one another have less inbreeding than large isolated populations, even if the large population occupies the same area as all small populations together (Finger *et al.*, 2009). This means that conserving large but isolated populations is likely not enough for the long-term viability of the population, even if the habitat quality is superior to that of the smaller populations. The efforts should instead be focused on conserving populations with high importance from a connectivity perspective, such as the previously mentioned stepping stones (Lindeborg, 2014). Being able to identify suitable habitat patches and assess their importance for the overall connectivity is key to maximizing the benefits of conservation efforts.

This study has three main aims. The first aim is to investigate the dispersal abilities of *L. helle*, so that these can be used in a connectivity analysis. The second is to identify predictors of *L. helle* patch occupancy among remote-sensed variables relating to habitat quality and to examine the correlations between *L. helle* densities and the abundance of its host plant and vegetation height. The third aim is to make a regional connectivity analysis to identify the populations in Jämtland County that are most important from a stepping-stone perspective and to which conservation efforts should be directed. In the end follows a discussion about the implications for conservation.

The following hypotheses are tested:

- H₁: *L. helle* is a sedentary species with high habitat fidelity.
- H₂: Female butterflies are more mobile than males, and therefore especially important for dispersal and gene flow between populations.
- H₃: Remote-sensed variables relating to solar radiation, vegetation height, variation in vegetation height, slope and aspect can estimate habitat quality for *L. helle*.
- H₄: Population density of *L. helle* is positively correlated with the abundance of the larval host plant *Bistorta vivipara* and is highest at an intermediate vegetation height.

2 Materials and methods

2.1 Study species

The primary habitats of *L. helle* are flower-rich moist meadows and pastures where a traditional land use is applied through moderate grazing or mowing (Lindeborg 2014). Today, Sweden's densest distribution of *L. helle* is in Jämtland County (figure 1). This can partly be explained by the county's large number of wetland areas influenced by limestone ground (Eliasson, 2012), which are described as the original habitat of *L. helle* in Fennoscandia. With the decrease and fragmentation of their agricultural habitats, *L. helle* has become increasingly dependent on the original wetland habitat types again. *L. helle* occurs also between the wetland sites along roadsides, in power-line corridors and on military training fields, where the vegetation is kept low (Ryrholm, 2014). In precipitation-rich areas, *L. helle* can occur in drier habitats (Eliasson *et al.*, 2005), but in general, good access to moving groundwater is important (Eliasson, 2012).

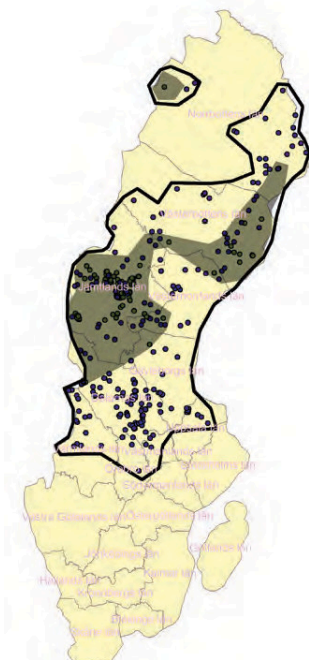


Figure 1. The distribution of *Lycaena helle* in Sweden, where the black lines define the estimated maximal distribution, the dots are all actual observations and the grey area represents the presumed occurrence in 2013. The compilation was made by Mats Lindeborg and modified and used by Nils Ryrholm in the article “The violet copper *Lycaena helle* at its northern distribution range” (2014). Used with permission from both.

L. helle needs the presence of low vegetation for two reasons. Firstly, for the larval development requires much insolation to reach the lower parts of the vegetation, where the eggs have been deposited. Secondly, the larval host plant *Bistorta vivipara* is sensitive to the encroachment of other taller plants (Lindeborg, 2014). As the onset of agriculture caused humans to create more areas with low vegetation, *L. helle* expanded together with *B. vivipara* from the original wetland habitats to agricultural habitats such as pastures and meadows. In the beginning of the 1950s, *L. helle* was a widespread butterfly species in the central and northern parts of Fennoscandia. The estimated past and present distribution can be seen in figure 1 (Ryrholm, 2014). In the decades after 1950, the traditional agricultural practices changed dramatically as small-scale and low-

yield sites were either abandoned or transformed into intensively used units by the introduction of artificial fertilisation and ensilage production. This caused a rapid reduction of suitable habitats for *L. helle* and *B. vivipara* (Ryrholm, 2014).

2.2 Study area

The field study was conducted in a 27 ha large area at about 5 km from central Östersund, Jämtland County in central Sweden. The area was selected because observations on Artportalen indicated that it contains an extant metapopulation of *L. helle*. Part of the study area belongs to the nature reserve Tysjöarna, which has one of the largest calcareous wetlands in the world (Jämtland County Administrative Board, 2014). Another part of the study area is located within a military training field (figure 2a). The study area consists of roadsides (44.3%), power-line corridors (39.6%), abandoned meadows (7.5%), rich fens (4.5%) and forest paths (4.1%) (figure 2b).

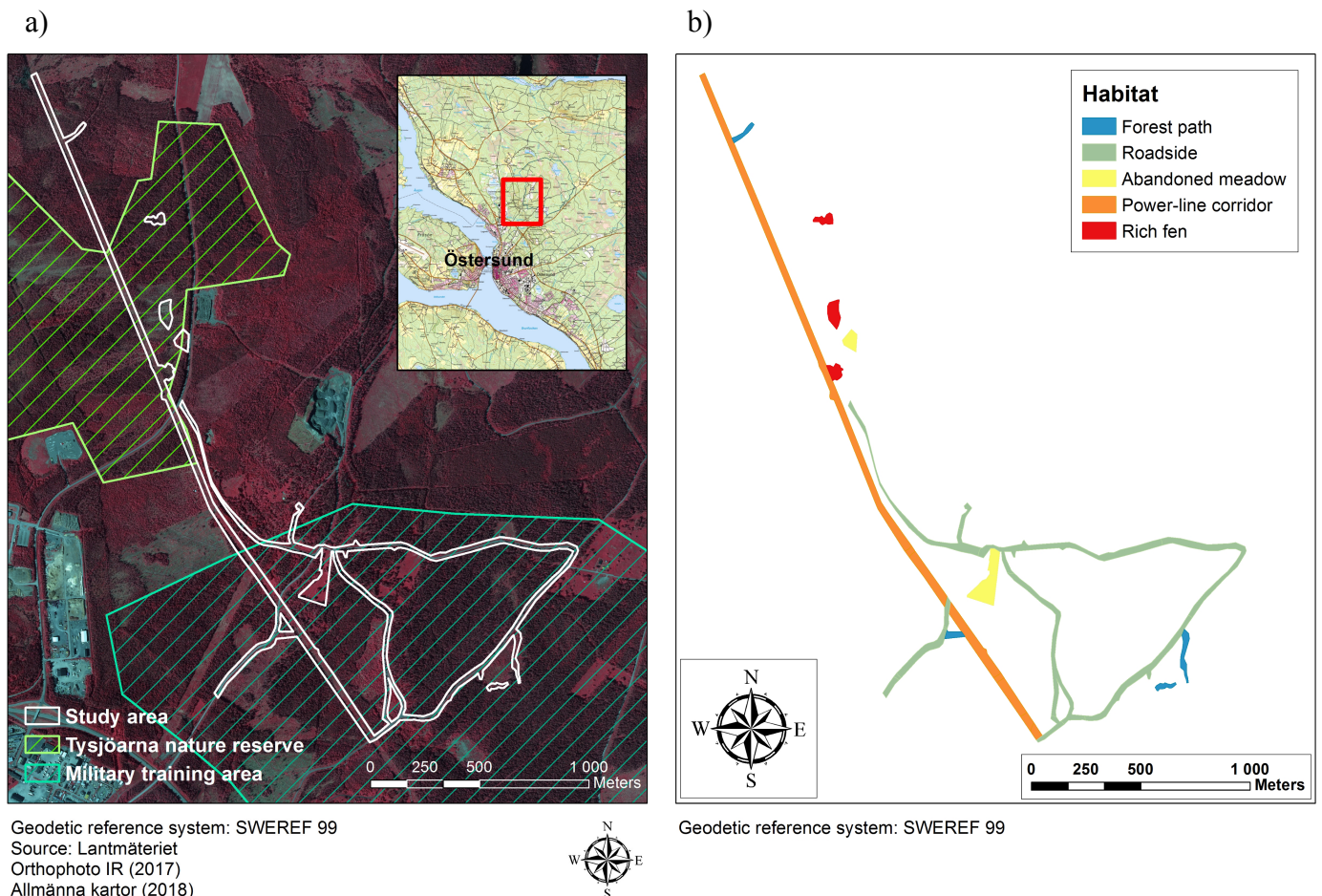


Figure 2. The study area is located about 5 km northeast of central Östersund, in northwest Sweden (figure 2a). Most habitat in the area consists of roadsides, followed by powerline corridors, abandoned meadows, rich fens and forest paths (figure 2b).

2.3 Mark recapture and mobility

To estimate the mobility of *L. helle* in Jämtland County, a mark recapture study was performed. During 23 days with favourable weather conditions between the 23rd of May and the 7th of July 2017, individuals of *L. helle* were captured, marked with a unique ID, released and recaptured (figure 3). Favourable weather conditions means sunny or warm weather with little to moderate wind. GPS locations were taken at the points of capture and recapture. Individuals were always captured, marked and released at the same spot. The study started in a smaller part of the study area and expanded as more of the distribution of the metapopulation became clear, to eventually cover the area marked in figure 1. Depending on the weather conditions, it was sometimes possible to cover the whole area in one day. Care was taken to vary the time of day that was spent at the different locations. The search effort was the same in the whole area.



Figure 3. A captured and marked individual of *Lycaena helle*.

In the data analysis, the shortest distance between capture and recapture was used. This does not reflect the real flight pattern of the butterflies but it roughly indicates dispersal ability and site fidelity. When individuals were recaptured more than once, only the last recapture was used to avoid autocorrelation. At least one night had to pass between capture and recapture. The correlation between number of nights between captures and distance was examined but yielded no significant result.

2.4 Habitat selection

I analysed habitat selection by identifying remote-sensed variables that can predict the local distribution of *L. helle*. The capture locations from the mark recapture study were used as presence points, but, to avoid autocorrelation, the recapture locations were not used. The absence points were randomly distributed in the parts of the study area where no *L. helle* had been found, in spite of frequent visits. The number of absence points was set to equal the number of presence points and were distributed at least 5 m away from each other, outside a fixed radius around the presence locations. The radius was set to equal the median dispersal distance that was found in the mark recapture study. As this study aims to find the habitat preferences of *L. helle* within seemingly suitable habitat, absence points were only distributed in sites where conditions for *L. helle* appeared favourable. Drawing on information provided by Lindeborg (2014), the sites had to meet the following conditions:

- Occurrence of *B. vivipara*
- Presence of wind-sheltered stands

- Solar radiation reaching the ground in some places
- Good access to nectar sources
- Within dispersal distance from presence sites

Five habitat characteristics were included in the RSF to assess their relative importance. All five characteristics are easily extractable from readily available remote-sensed data and include vegetation height, Topographic Position Index (Jenness 2002), slope, solar radiation and aspect. All were computed in ArcMap 10.5.1 (ESRI 2017) and stem from LiDAR data, which were downloaded from Lantmäteriet and created by laser scanning from airplanes (Nordkvist & Olsson, 2013). Laser scanning provides elevation data with the highest resolution available for this area. The laser beams can separate bedrock/ground from vegetation/buildings, making it possible to transform the LiDAR data to a high-resolution digital elevation map (DEM) and digital surface map (DSM). The DEM covers the elevation at ground level, whereas the DSM covers the elevation at the height of the canopy cover. In the area around Östersund, one measurement per 2 m² has been made. Vegetation height was computed by subtracting the DEM from the DSM, resulting in a raster with one value per 2 m² for vegetation height (figure 4b).

The Topographic Position Index (TPI, figure 4c) compares the elevation of each cell in a raster to the mean elevation of a specified neighbourhood area around that cell, thereby identifying its relative position. Normally, DEMs are used as input data, but in this study the DSM was used instead to include the effects of vegetation. When based on the DSM, the TPI provides a measure of the heterogeneity of vegetation height, while still taking into account important terrain features such as ditches. A mean, maximum and minimum DSM were produced by using the tool Focal statistics in ArcMap, with the neighbourhood area set to 3x3 cells. Following the instructions by Cooley (2016b), who has adapted the initial descriptions by Jenness (2006), the TPI map was produced using the following formula in Raster calculator:

$$\frac{\text{Mean DSM} - \text{Minimum DSM}}{\text{Maximum DSM} - \text{Minimum DSM}}$$

The solar radiation raster (figure 4d) was produced using the tool Area solar radiation in ArcMap. The time period was specified to 23rd of May – 7th of July and the interval was set to weekly. As the penetration of sunlight depends on both terrain and vegetation, especially during the growing season, the DSM was used as input data. The slope (figure 4e) and aspect (figure 4f) rasters were computed using the ArcMap tools with the same names, with the DEM as input data. Slope and aspect were included as they can reflect conditions related to water access, wind exposure and solar radiation.

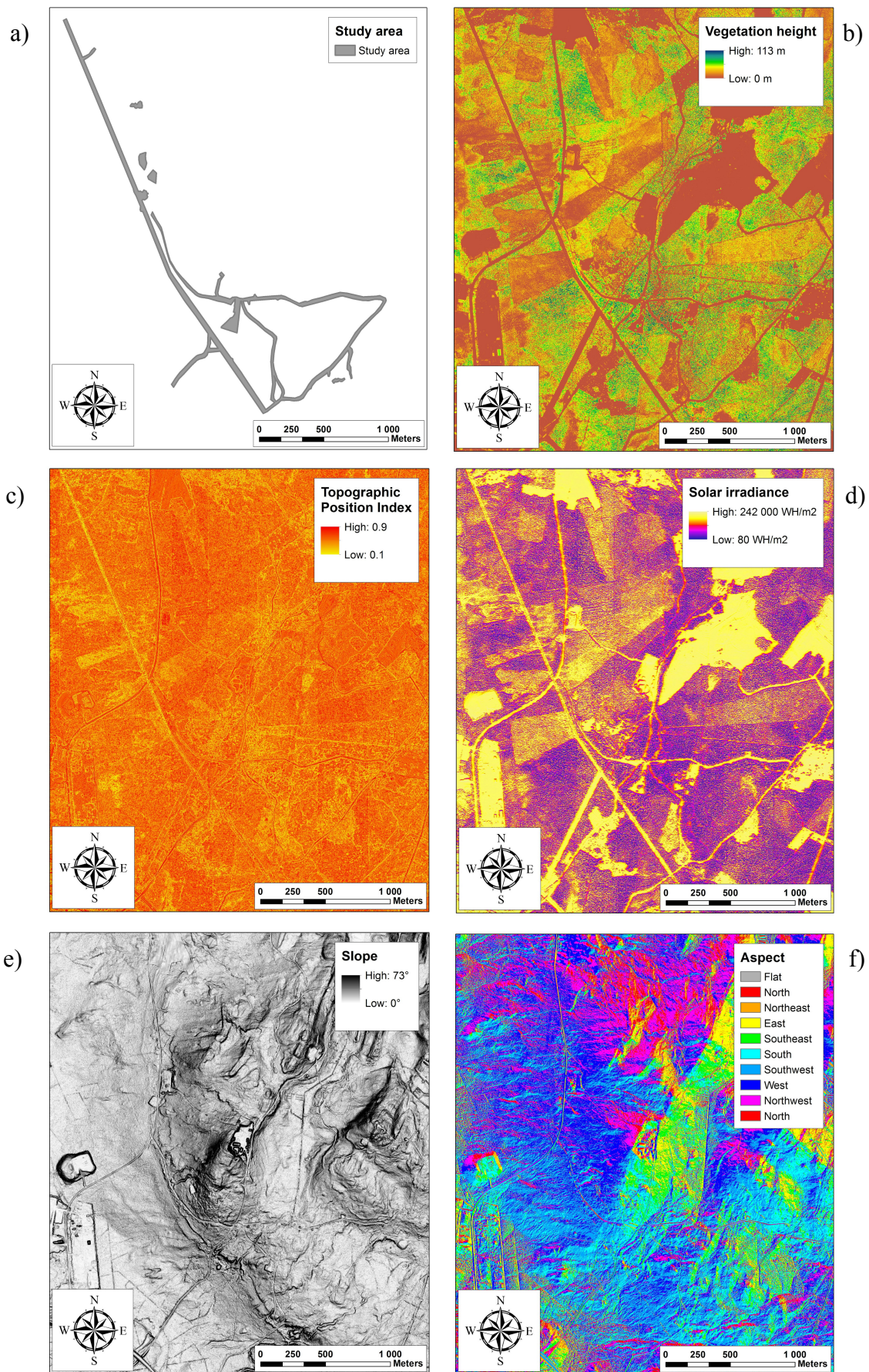


Figure 4. Figure 4a shows the extent of the study area. Figure 4b-f show the raster layers that were used in the habitat selection analysis. In map 4a, the extent of the study area can be seen. Map 4b shows vegetation height, which is a result of subtracting a digital elevation model from a digital surface model. The Topographic Position Index (Jenness 2006, figure 4c) shows the relative height of one cell compared to the surrounding cells. In this study, the index is based on a digital surface map to include the effects of vegetation. The solar radiation raster (figure 4d) was produced using the tool Area solar radiation in ArcMap. Maps 4e and 4f show slope and aspect, which were produced using the tools with the same names in ArcMap. Geodetic reference system: SWEREF 99. The maps were produced using LiDAR data, which was downloaded from Lantmateriet 2017.

The cell values from the habitat characteristics rasters were extracted to the presence/absence points. This resulted in a table with one column for presence/absence and five columns with the corresponding cell values for the different rasters. The aspect data was transformed to instead represent northness or eastness to avoid its inherent circularity, by multiplying aspect with cosines for northness and with sinus for eastness. A cap of 2 m was set on the vegetation height values, as vegetation higher than 2 m was not considered to influence *L. helle* any differently than vegetation of 2 m and higher heights would be related to laser points hitting the canopy cover. Retaining the higher values could create an artificially strong relationship between *L. helle* occurrence and vegetation height. All habitat characteristics data were scaled and the presence/absence data was in a binomial format.

The habitat characteristics were tested for intercorrelations using Spearman's rank-order correlation, the nonparametric version of the Pearson product-moment correlation. Significant correlations were found between solar radiation and TPI, solar radiation and vegetation height, slope and TPI as well as slope and vegetation height. No correlation coefficient (ρ) was particularly strong and the maximum deviation from zero was -0.241 (solar radiation and vegetation height). As a result of the low correlation coefficients, all variables were included in the habitat selection analysis in spite of the four significant correlations.

The data was statistically analysed in R 3.4.1 (R Development Core Team 2017) using the package Glmulti (Calcagno & de Mazancourt, 2010). Glmulti provides automated model selection and model averaging based on a specified Information Criterion (AIC, AICc or BIC). To correct for the small sample size, AICc was used in this study. Glmulti works as a wrapper for generalized linear models, in this study used with a binomial family and logit link function. The models were selected by a genetic algorithm that can be used when large candidate sets make exhaustive screening unfeasible. 64 models were run in the first screening, which included only main effects and no interactions. In the three subsequent screenings, the best-performing model from the first screening was extracted and one pairwise interaction per screening was appended to the best-performing model. The interactions that were hypothesized to be of interest were slope*northness, slope*eastness and vegetation height*TPI. A null model with only intercept was created to compare the other models against.

To evaluate the best model, a receiver operating characteristic (ROC) curve was computed. ROC curves are a dominant tool in evaluating the accuracy of models predicting distributions of species (Peterson, 2008). To compensate for possibly “overfitting” the data by running such a large number of models, focus is successively redirected to the model-averaged estimates of the predictors and their overall importance values. The automated model selection is considered part of a multimodel inference approach.

2.5 Correlations between *Lycaena helle* density, abundance of *Bistorta vivipara* and vegetation height

To investigate the correlations between *L. helle* density, the abundance of *B. vivipara* and fine-scaled vegetation height, field inventories of *B. vivipara* and vegetation height < 1 m were done within the scope of this study (figure 5). 171 quadrats of 1x1 m were inventoried throughout the study area. For each quadrat, the total number of *B. vivipara* was counted and five evenly dispersed measurements of vegetation height were made and then averaged. Vegetation height was only measured up to 1 m, to account for more small-scale differences than in the vegetation raster based on the LiDAR data. Care was taken to distribute the quadrats relatively evenly both along the width and length of the area but as the study area expanded continuously and some inventories were made at the start of the study, the quadrats were more widely dispersed in some parts than in others. The inventories were only made in the areas where the butterflies were found and could therefore not be included in the habitat selection analysis. The counts of *B. vivipara* and the average vegetation height were interpolated using the technique IDW (Inverse distance weighted) in ArcMap, with a fixed radius of 100 m, to create a raster with extractable values.

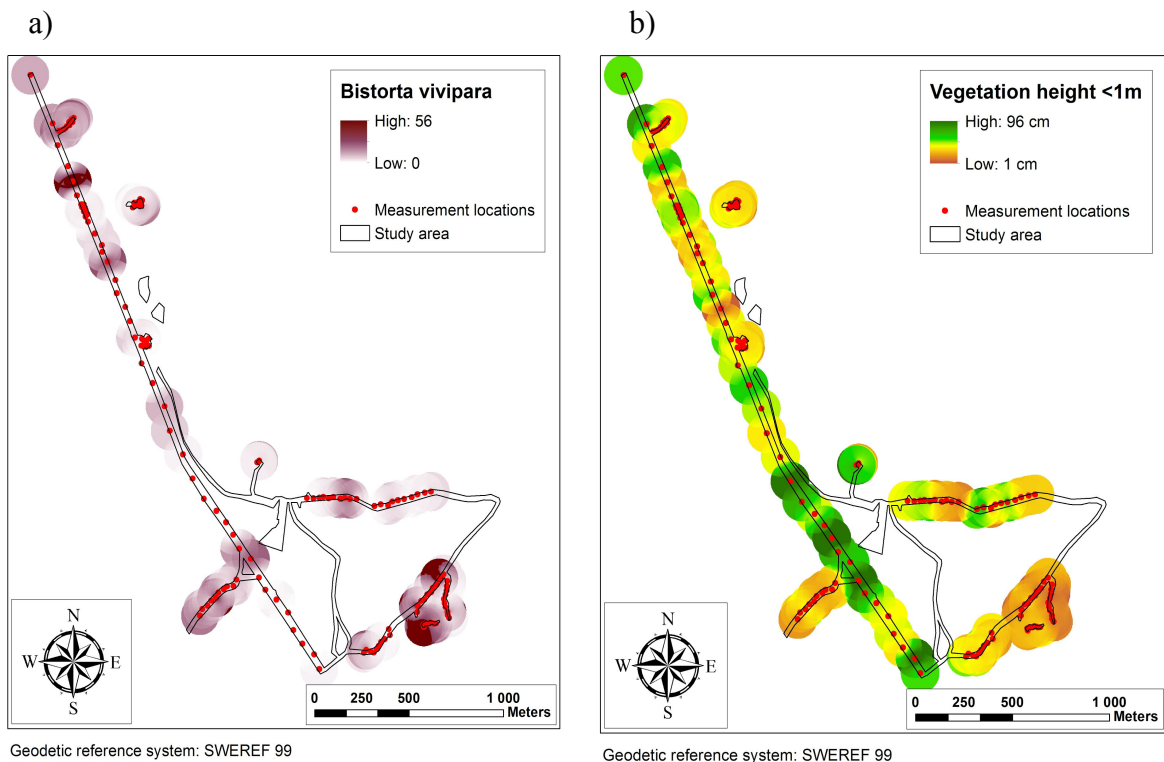


Figure 5. Interpolated field inventories of *Bistorta vivipara* (figure 5a) and vegetation height of less than 1 m (figure 5b). 171 quadrats of 1x1 m were inventoried within the study area. In each quadrat, the number of *B. vivipara* was counted and five evenly dispersed measurements of vegetation height < 1 m were made and then averaged.

A density raster of *L. helle* individuals was calculated from the capture and recapture locations using the Kernel density tool in ArcMap. The search radius was set to equal the median flight distance from the mark recapture study and a geodesic distance method was used. For the density raster, both

capture and recapture locations were used to include effects such as source-sink dynamics. The values from the two interpolation rasters and from the density raster were then extracted to the presence points, i.e. the captured individuals. The recaptures were not included in this step to avoid autocorrelation. Four presence points had to be removed, as there was no data on *B. vivipara* or vegetation height at these locations. Pearson's product-moment correlations were run in R to test how well abundance of *B. vivipara* and vegetation height < 1 m correlate with *L. helle* density. Vegetation height was tested both for a negative quadratic correlation and a linear correlation.

2.6 Regional connectivity

To analyse the connectivity of *L. helle* at county level in Jämtland, all observations of *L. helle* from within the county were downloaded from www.artportalen.se. The observations were included in the analysis if they after consultation with experienced personnel at Jämtland's county administrative board (Carlsson, 2017) were still considered relevant. Relevant observations were those where the probability that the population still exists is seen as reasonably high. For rich fens, which generally constitute a stable habitat over long time, observations from the past 15 years, i.e. the years 2002-2016, were included. For the remaining habitats, observations from the past 10 years, i.e. the years 2007-2016, were included.

In some locations, several observations had been made from the same population. A manual effort was made to delete observations that were within the median flight distance from another observation and that could therefore be considered to belong to the same population. Also observations that were further than the maximum flight distance from all other observations were deleted from the connectivity analysis, as they would not be relevant from a connectivity perspective. The median and maximum flight distances from the mark-recapture study were used. After the selection processes, 156 observations remained and were used in the analysis in this study. In order to not skew the results in favour of the populations within the mark-recapture study area, no observations that were made within the scope of this study have been included.

The connectivity analysis was performed in ArcMap and in the program Conefor 2.6 (Saura & Torné, 2012). In Conefor, the recommended probabilistic index called probability of connectivity (PC) was used (Saura & Pascual-Hortal, 2007). PC is a graph-based habitat availability metric that quantifies functional connectivity (Saura & Pascual-Hortal, 2007; Saura 2008). The index characterises the connections between different populations through a probability of direct dispersal. By using the connection probabilities, the PC index can rank the populations according to their importance for the overall connectivity. The PC index consists of three separate fractions, which quantify the different ways in which individual

landscape elements such as populations or patches can contribute to the overall habitat connectivity in the landscape.

$$\Delta PC_k = \Delta PC_{intra_k} + \Delta PC_{flux_k} + \Delta PC_{connector_k}$$

PC intra represents the contribution of patch k in terms of intrapatch connectivity, i.e. through population size or other relevant patch attribute. *PC flux* corresponds to the weighted dispersal flux through the connections of patch k to or from all of the other patches in the landscape, with k as either the starting or ending patch. *PC flux* depends both on the patch attribute of patch k and on its position within the landscape network. *PC connector* is the contribution of patch k to the connectivity between other habitat patches, as a connecting element or stepping stone between them. This fraction depends only on the topological position of a patch or link in the landscape network (Saura & Rubio, 2010). In this study, focus is on the *PC connector* fraction of the PC index.

To be able to run the PC index, the likelihood of the different connections had to be calculated. For this purpose, a decreasing exponential function was fit to the proportional frequency distribution of flight distances found in the mark recapture study, using automated model selection in the software program Eureka version 0.98 beta (Schmidt & Lipson, 2014). The exponential function was then multiplied with the length of the different connections, yielding the probability for each connection to be used by an individual from any of the connected populations. The maximum distance at which two populations could be considered connected was set to the maximum flight distance found in the mark recapture study. All connections consisted of the shortest straight between the observations. The patch attribute was fixed to 50 for all patches, as no attributes were known for all populations and no influence from varying patch attributes was desired. All PC connector values were joined to their respective populations and the accuracy and performance of the method was evaluated visually in ArcMap.

3 Results

3.1 Mobility

In total, 229 individuals were marked during the mark-recapture study. The total number of encounters was 279, of which 229 were first-time encounters, 40 final encounters and 10 intermediate encounters. The overall recatchability was 17.9%, if both final and intermediate encounters are included. The 10 intermediate encounters were not used in the mobility study to avoid autocorrelation. The marked individuals were recaptured after 1-26 nights, with a mean of 10 nights and a median of 9 nights passing between first and last encounter. 55% of the final recaptures took place within 10 nights since marking. As can be seen in table 1, considerably less females than males were recaptured. Females dispersed more than twice as far as males, both when regarding the median and maximum distances. The mean distance was more than three times larger for females than for males.

Table 1. Distances (m) between first and last capture.

	Mean	Median	Minimum	Maximum	N
Female	256.5 ± 83.0 SE	172.2	5.1	599.7	8
Male	78.0 ± 11.7 SE	77.7	1.2	297.6	32
All	113.7 ± 21.6 SE	81.9	1.2	599.7	40

Figure 6 shows the frequency distribution of the direct distances between the first and last capture. Males flew predominantly short distances, with a clear negative trend as the distances increase. 78% of the males flew less than 50 m and no recaptured male flew more than 300 meters. Female flight distances were in general more evenly distributed, although no recaptured females had flight distances in the span of 250-450 meters. Three females were evenly distributed in the interval of 450-600 meters. Although males had a four times larger sample size than the females, their variation in flight distances was considerably smaller (figure 5b).

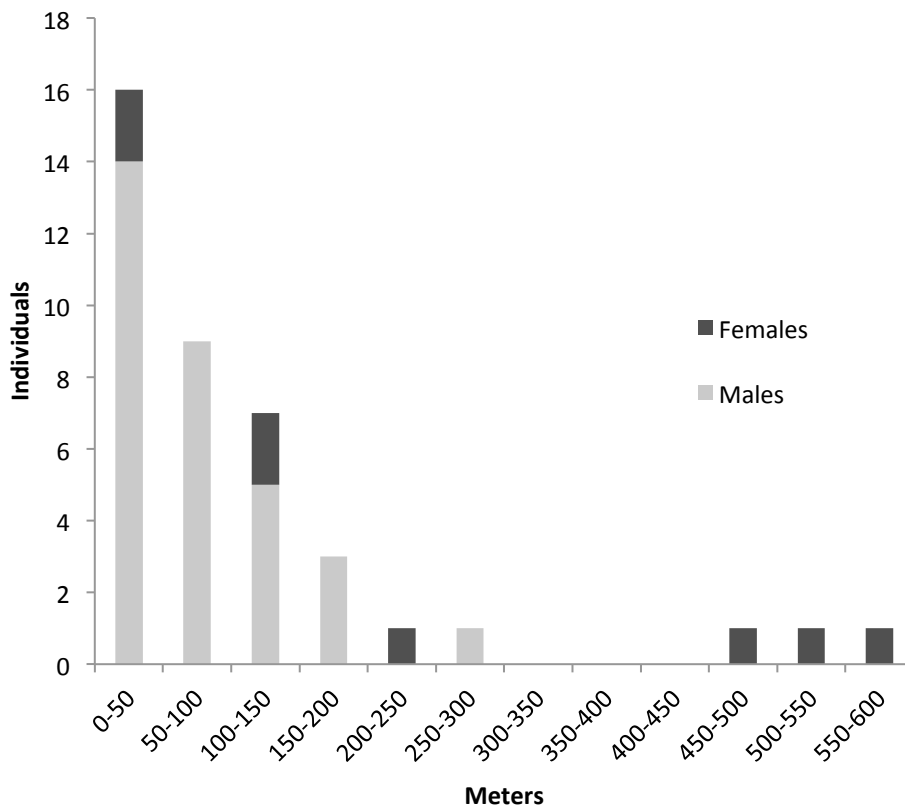
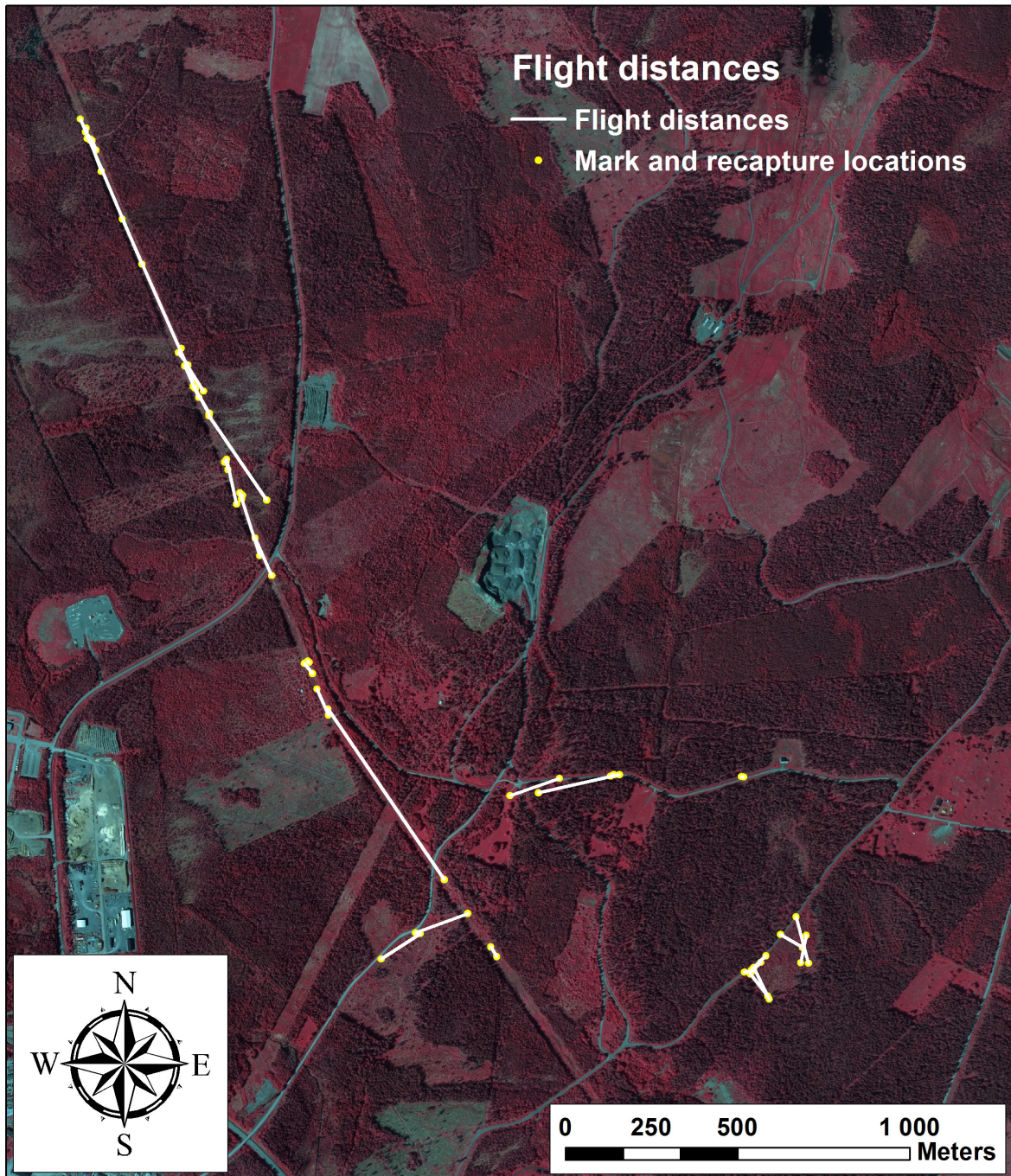


Figure 6. Frequency distribution of distance between first and last capture.

Six individuals (15%) were recaptured in a different habitat patch than where they had been marked. One individual had flown from a gravel road to an overgrown pasture, one from a rich fen to the power-line corridor and four from a forest path to a gravel road. These flights can be discerned in figure 7, where all flight distances used in the mobility study and the mark and recapture locations are mapped. For very short distances, only the mark and recapture locations can be seen as they obscure the line representing the flight distance. None of the habitat-changing individuals had to pass any barriers to get to the other habitat. Overall, only one individual crossed what had been considered a potential barrier (Öckinger, 2017), in form of a stretch with high and dense vegetation along the power-line corridor.

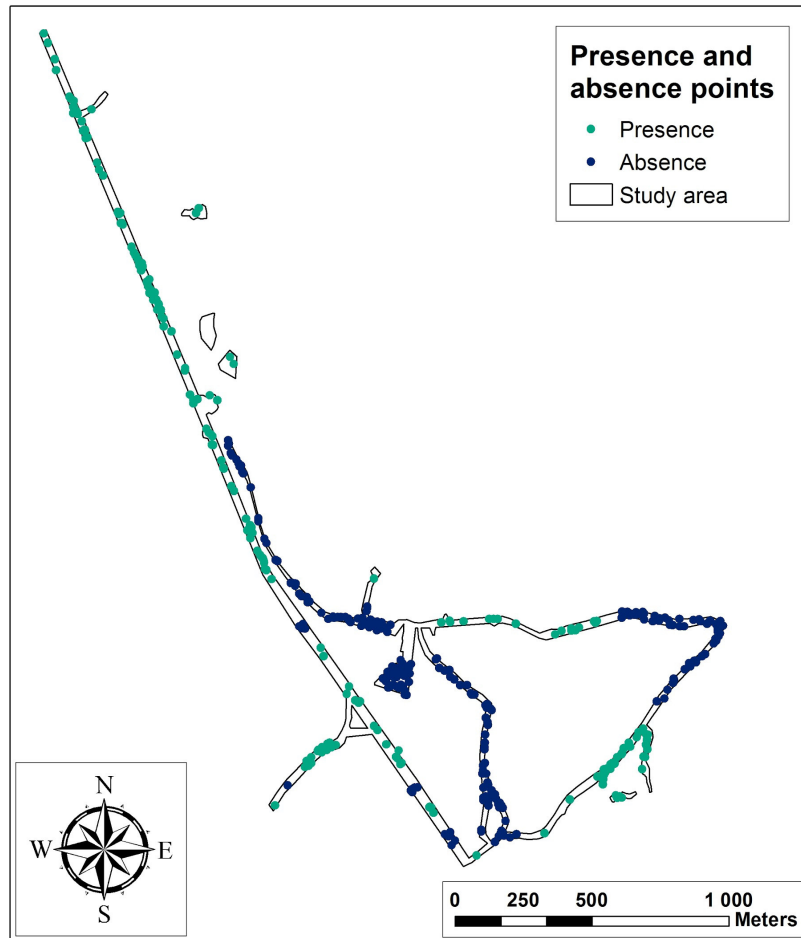


Geodetic reference system: SWEREF 99
 Source: Lantmäteriet, Orthophoto (2017)

Figure 7. The straight distances between mark and recapture locations.

3.2 Habitat selection

Figure 8 depicts the presence and absence points used in the habitat selection study. All absence points are outside a radius of 81.9 m, i.e. the median flight distance, from all encounter locations. The presence points only consist of the first-time encounters. For this reason, there are some gaps in the study area where neither presence nor absence points are located.



Geodetic reference system: SWEREF 99

Figure 8. The presence points consist of the 229 first-time encounters, whereas the absence points are made up by 229 random points distributed where no encounters were made.

The presence and absence points were distributed unevenly in the different habitat types (figure 9). Whereas the majority of the presence points (58.1%) occur in the power-line corridor, only 7.0% of the absence points were distributed in the same habitat type. Instead, the vast majority of absence points (79.0%) occur along roadsides. No absence points are distributed in any of the forest paths or rich fens.

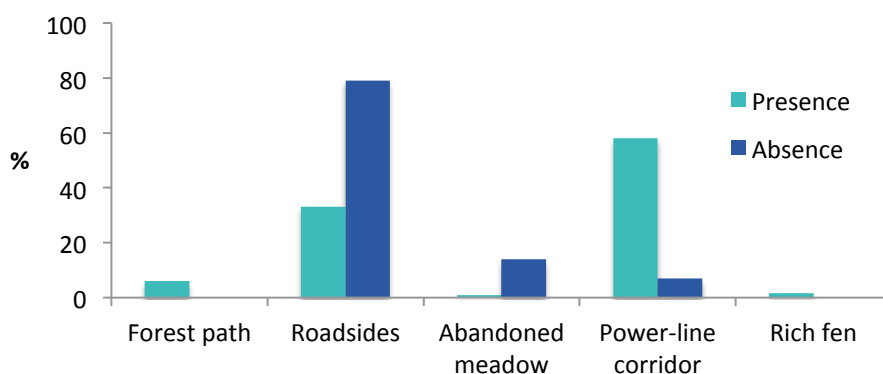


Figure 9. The distribution of presence and absence points in the different habitats.

The model selection screening with only main effects resulted in 64 models with AICc values ranging from 579.29 for the best model to 640.72 for the worst. This can be compared to the null model, i.e. a model with intercept only, which has an AICc of 636.93 and thus performs considerably worse than the best model but slightly better than the worst model. The genetic screening converged after 100 generations. In table 2, the eleven best-performing models, i.e. the models with 95% of the evidence weight, are presented. There is a steep drop from the best to the second-best model, making the best model considerably more likely than the second-best. Two models are within two IC units. Solar radiation and slope were included in all ten models. All models also include an intercept.

Table 2. The AICc and model weights of the eleven best-performing models, which hold 95% of total evidence weight.

Ranking	Independent variables (+ intercept)	AICc	Model weight
1	Solar radiation, slope, TPI, vegetation height	579.29	0.362
2	Solar radiation, slope, TPI, vegetation height, northness	581.22	0.137
3	Solar radiation, slope, TPI, vegetation height, eastness	581.34	0.130
4	Solar radiation, slope, TPI	582.26	0.082
5	Solar radiation, slope, vegetation height	582.95	0.058
6	Solar radiation, slope, TPI, vegetation height, northness, eastness	583.29	0.049
7	Solar radiation, slope, TPI, northness	584.07	0.033
8	Solar radiation, slope, TPI, eastness	584.28	0.030
9	Solar radiation, slope, vegetation height, northness	584.82	0.023
10	Solar radiation, slope, vegetation height, eastness	584.93	0.022
11	Solar radiation, TPI, vegetation height	585.51	0.016

Table 3 provides a closer examination of the best-performing model. The best-performing model includes an intercept and the variables solar radiation, slope, TPI and vegetation height. As all predictors have been scaled prior to model selection, the parameter estimates are relative to one another. All variables in the model were significant predictors, with solar radiation having the lowest p-value ($\ll 0.001$). The parameter estimate of solar radiation was estimated to be as high as 0.696, which means that it had a considerable effect on whether the result will be tipped over to a 1 or a 0 in the binomial output of the model (i.e. presence or absence). Its effect was

positive, with a higher probability of occurrence of *L. helle* where there is high solar radiation. Slope had a parameter estimate that is nearly half as strong as solar radiation, but with a negative effect and a considerably lower significance. As the ground became steeper, the probability of occurrence of *L. helle* decreased slightly. TPI had a slightly weaker parameter estimate and significance than slope, showing a negative relationship with *L. helle* occurrence. A more variable vegetation height led to lower probability of *L. helle* occurrence. Vegetation height had nearly the same parameter estimate as slope, but with a slightly weaker significance. Also here, the relationship was negative and lower vegetation height led to a higher probability of *L. helle*.

Table 3. A closer examination of the best-performing model.

Independent variables	Estimate	Standard error	z value	p-value
(Intercept)	-0.053	0.102	-0.521	0.603
Solar radiation	0.713	0.133	5.357	<<0.001
Slope	-0.297	0.105	-2.827	0.005
TPI	-0.252	0.105	-2.366	0.018
Vegetation height	-0.247	0.114	-2.209	0.027

To evaluate the best model, a Receiver Operating Characteristic (ROC) curve was computed (figure 10a). The true positive rate (sensitivity) was plotted as a function of the false positive rate (100-specificity) at different cut-off points. Each point on the ROC curve represents a sensitivity/specificity pair corresponding to a particular decision threshold. A test with perfect discrimination (no overlap between the two distributions) has a ROC curve that passes through the upper left corner (100% sensitivity, 100% specificity). This means that the closer the ROC curve is to the upper left corner, the higher the overall accuracy of the test (Zweig & Campbell, 1993). The curve in figure 10a is far from the upper left corner, which means that the overall accuracy of the model was rather low. The area under the curve (AUROC) was 0.685. According to a rough guide by Tape (n/a), 0.6-0.7 represents a poor result whereas 0.7-0.8 represents a fair result. This means that the best model in this study is on the border between the general categories “poor” and “fair”. The ROC curve of the best-performing model can be compared to the ROC curve of the null model, which had no curvature at all toward the upper left corner (figure 10b). The AUROC for the null model was 0.5, thereby qualifying as “fail” according to Tape (n/a).

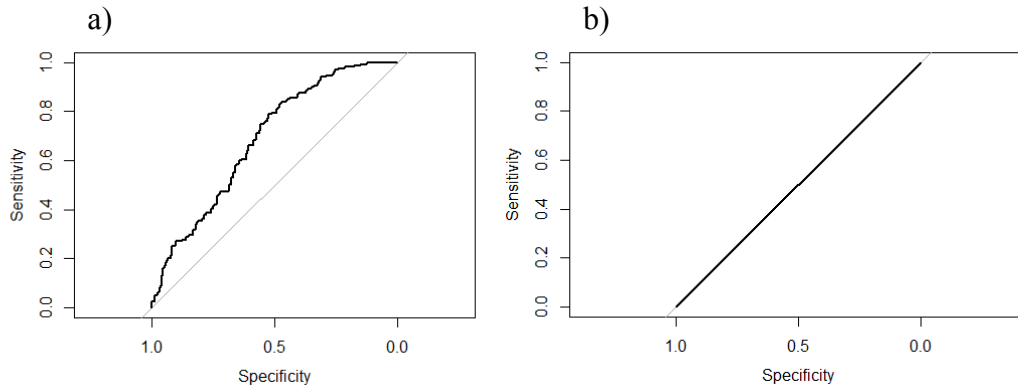


Figure 10. An ROC curve was produced to evaluate the overall accuracy of the best-performing model (figure 10a). The curve is far from the upper left corner, which means that the accuracy of the best-performing model is rather low. The ROC curve of the null model completely lacks curvature toward the upper left corner and falls within the category “fail” (figure 10b).

To be able to make inferences about the various predictors, it is necessary to widen the perspective from the best-performing model and instead look at all possible models and the relative importance of the predictors (table 4). The importance value for a particular predictor is equal to the sum of the weights for the models in which the variable appears. A variable that is included in many models with large weights receives a high importance value. These values can be regarded as the overall support for each variable across all models in the candidate set. A cut-off is generally made at an importance level of 0.8, to differentiate between important and less important variables. Solar radiation, slope, TPI and vegetation height all had importance values above 0.8, although vegetation height was close to the cut-off at 0.821. With importance levels of 1 and 0.966, solar radiation and slope were by far the two most important variables. TPI had an importance value of 0.867 and was thus closer to vegetation height. Northness and eastness were both well below 0.8, making the separation rather distinct. The unconditional estimates are weighted averages of the parameter estimates across all 64 models. They had the same directions and similar strengths as the parameter estimates in the best-performing model, meaning that the same general relationships apply as described for the best-performing model.

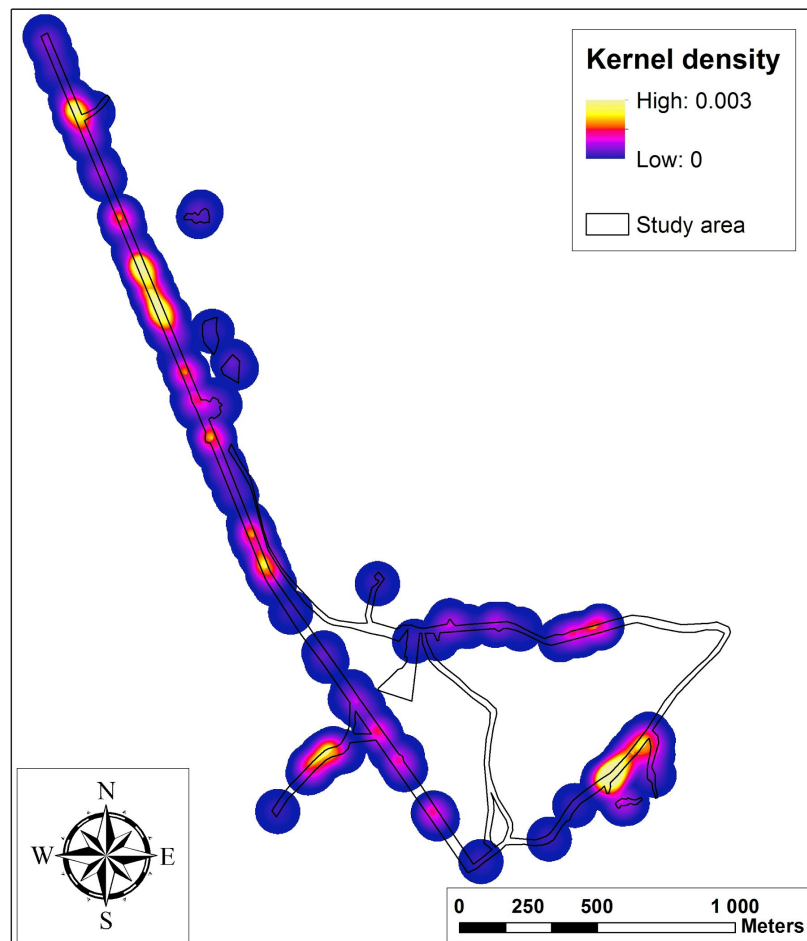
Table 4. The model-averaged predictor statistics, with unconditional estimates, variance and importance of each variable.

Independent variables	Unconditional estimate	Unconditional variance	# of models found	Importance	+/- (alpha=0.05)
(Intercept)	-0.051	0.010	64	1.000	0.200
Solar radiation	0.715	0.019	32	1.000	0.269
Slope	-0.296	0.013	32	0.966	0.222
TPI	-0.216	0.015	32	0.867	0.244
Vegetation height	-0.209	0.019	32	0.821	0.272
Northness	-0.010	0.001	32	0.278	0.071
Eastness	0.003	0.001	32	0.265	0.057

The addition of certain pairwise interactions did not improve the best-performing model. While the best-performing model scored an AICc of 578.08, the addition of slope*northness gave an AICc of 581.25, slope*eastness gave an AICc of 581.30 and vegetation height*TPI gave an AICc of 581.07.

3.3 Correlations between *Lycaena helle* density, abundance of *Bistorta vivipara* and vegetation height

Correlations were made between the kernel density of *L. helle* and the interpolated abundance of *B. vivipara* and vegetation height < 1 m, both inventoried in the field. The kernel density layer was based on all 279 encounters with *L. helle* individuals (figure 11).



Geodetic reference system: SWEREF 99

Figure 11. The kernel density of all 279 encounters with *Lycaena helle*.

There was a statistically significant (p -value < 0.001) but relatively weak positive correlation (correlation coefficient = 0.233) between kernel density of *L. helle* and the abundance of *B. vivipara* (figure 12). With an R^2 of 0.054, the correlation offered a poor explanation of the data.

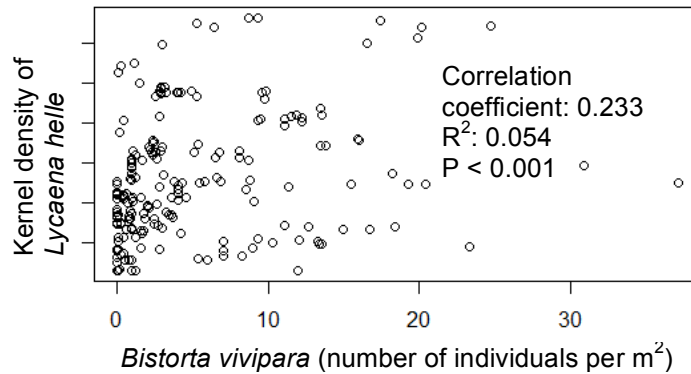


Figure 12. Linear correlation between *Bistorta vivipara* and kernel density of *Lycaena helle*.

No significant negative quadratic correlation was found between vegetation height and *L. helle* density (p -value = 0.534, figure 13). Also a linear correlation was tested, yielding a statistically significant result (p -value $\ll 0.001$). The correlation coefficient was negative and relatively weak, at -0.315. Also here, the R^2 was low (0.099).

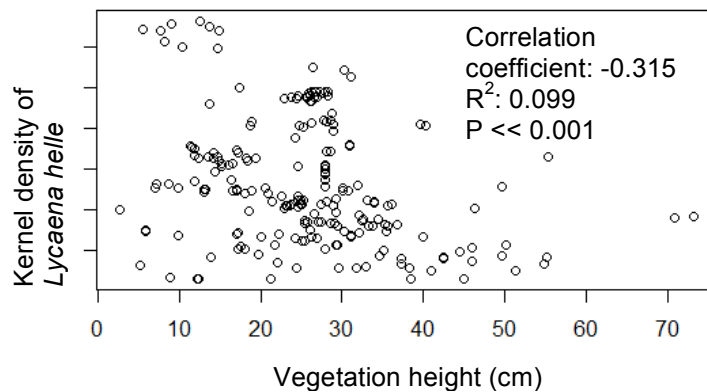


Figure 13. Linear correlation between vegetation height and kernel density of *Lycaena helle*.

3.4 Regional connectivity

Among the 156 populations that were included in the connectivity analysis, 28 were found to be of importance from a stepping-stone perspective (ΔPC connector > 0). The populations can get a ΔPC connector value > 0 only if they are part of the best (maximum product probability) path for dispersal between two other patches. The white markers in figure 14 and 15 show some of the 128 populations that were not part of the best path for dispersal between any other two patches, thus rendering them with a ΔPC connector value of 0. Figure 14 provides some zoomed-in examples of how the populations were classified according to their position within the network. Populations with values > 0 were found in clusters of at least three populations in total, as they need to act as the connector between at least two other patches. A large or small part of the overall connectivity may be lost when a certain population is removed from the landscape, depending on the alternative paths between the remnant populations that are available after the loss. If a large part of the connectivity is lost in case the population disappears, the concerned population gets a high ΔPC connector value.

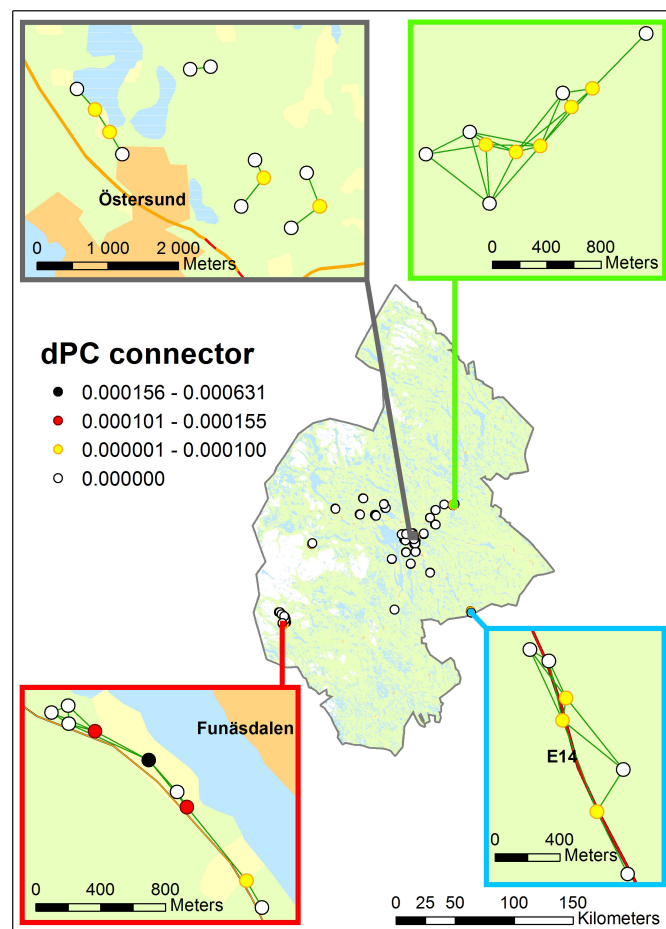


Figure 14. An overview of the results from the connectivity analysis, with four zoomed-in examples. In the figure, ΔPC is denoted dPC. High dPC means that the population was of high importance from a stepping-stone perspective.

Southeast of Flon in Härjedalen, the Artportalen observations indicate a metapopulation of considerable extent. Figure 15 shows the links between the different populations and how the populations' importance for connectivity depends on whether there are any alternative stepping stones between the populations that they are connecting. Most observations occur along the road, with more observations along some parts of the road than others. In table 5 in appendix 1, the coordinates of all populations with a ΔPC connector value > 0 can be found.

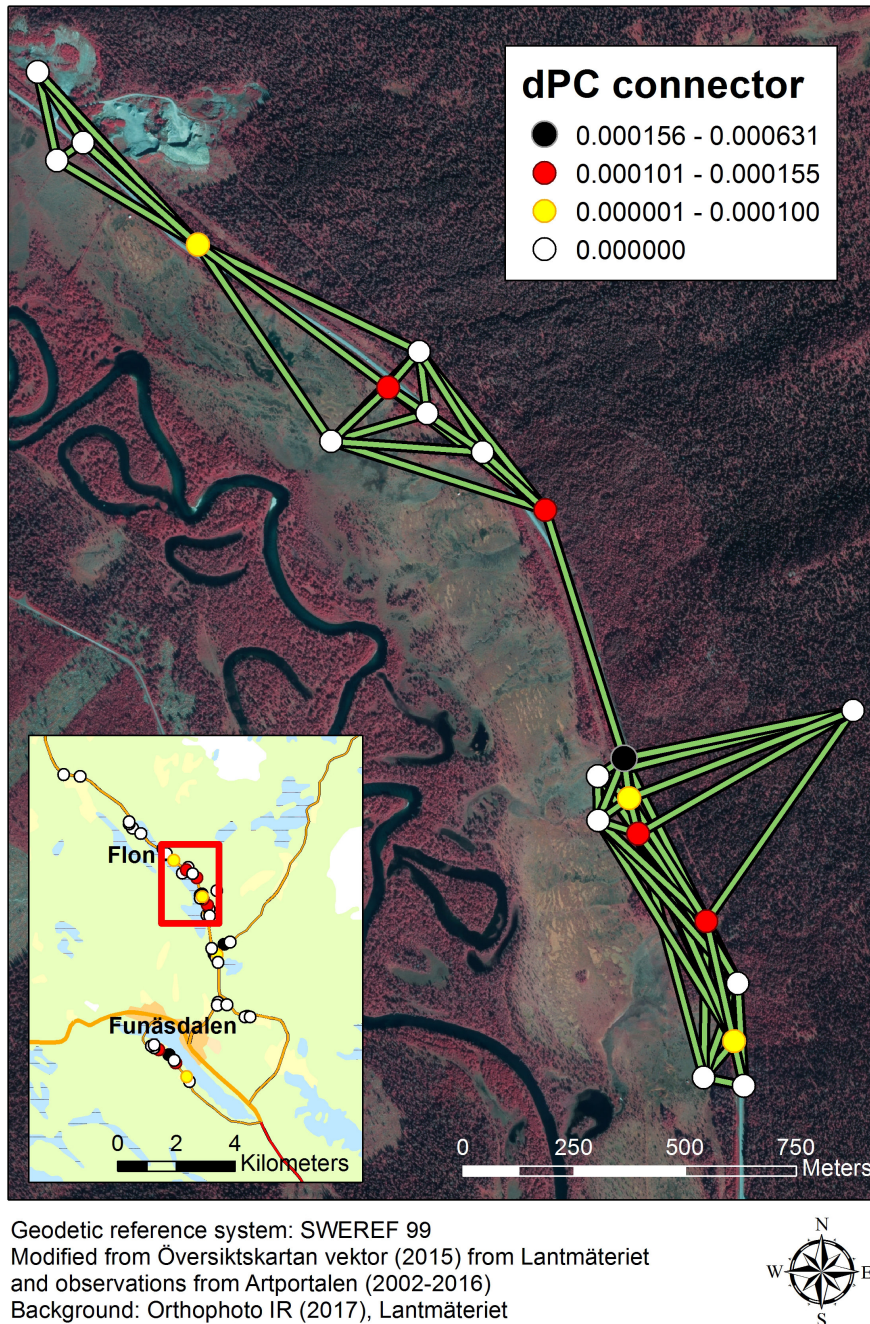


Figure 15. A zoomed-in example of connected populations in Flon, Härjedalen. The populations where there are no alternative routes have the highest ΔPC values. In the figure, ΔPC is denoted dPC.

4 Discussion

4.1 Mobility

This study has found a longer average female flight distance and longer maximum flight distance than ever recorded before for this species. Previously, four other studies have been performed on the mobility of *L. helle* in Germany, Mongolia, Romania and Belgium (Fischer *et al.*, 1999; Gantigmaa *et al.*, 2008; Craioveanu *et al.*, 2014; Turlure *et al.*, 2014). The German study found the shortest overall flight distances, with an average distance of 61 m for females and 37 m for males (Fischer *et al.*, 1999), followed by the Mongolian study which found average flight distance at 107 m for females and at 44 m for males (Gantigmaa *et al.*, 2008). The Romanian study stands out, as it found longer flight distances for males than for females, with an average of 135 and 111 m respectively. The Belgian study averaged the flight distances only among the individuals that emigrated or travelled between two zones and found an average of 108 m for both sexes. In this study, the average female flight distance of 257 m was the longest that has ever been recorded and the average male flight distance of 78 m was only surpassed by the males in the Romanian study. The average female flight distance in this study was 146 m longer than the second longest flight distance, which was found in the Romanian study. The average male flight distance was longer than in the German and Mongolian studies but shorter than in the Romanian study. No comparisons can be made with the Belgian study, as it pooled the results for both females and males. The four earlier studies found maximum flight distances of 560, 386, 590 and 522 m in Germany, Mongolia, Romania and Belgium respectively, compared to a maximum flight distance of 599 m measured in this study.

Although the maximum flight distance and average female flight distance in this study are longer than what has been recorded before, they are not longer than the flight distances of other territorial Lycaenidae species that are also considered to be extremely sedentary (Scott, 1973; Marschalek & Klein, 2010; Turlure *et al.*, 2010). With this in mind, the hypothesis that *L. helle* is extremely sedentary must be supported in spite of the new longer flight distances. Only 15% of the individuals were recaptured in a different habitat than where they had been marked, and none of them had crossed any barriers to get to the new habitat. This supports the second half of the first hypothesis, which states that *L. helle* has high habitat fidelity. Female flight

distances were considerably longer than male flight distances, but the difference could not be tested statistically due to the small female sample size ($n = 8$). The data appears to support the second hypothesis, i.e. that females are more mobile than males, but cannot be claimed to do so with certainty.

The variation in recorded flight distances between the studies merits some extra attention. Schneider (2003) has shown that the observed distances in mark recapture may be more related to the size of the study area than to the species' actual dispersal ability. In the German study, the size of the study area was not specified, but in the Mongolian, Romanian and Belgian studies the size was 10, 64 and 14 ha respectively (Gantigmaa *et al.*, 2008; Craioveanu *et al.*, 2014; Turlure *et al.*, 2014). This study was conducted in an area of 27 ha. Compared with the three studies that provide their study area in the text, this study has the second largest study area and has the longest flight distances except for average male flight distance, where the study with the largest area also measured the longest distance.

Other than being affected by the size of study area, dispersal has also been shown to correlate with the degree of fragmentation. For the butterfly species *Proclossiana eunomia*, dispersal propensity was lower in more fragmented landscapes. This was suggested to be caused by a reluctance of individuals to cross habitat patch boundaries as fragmentation increases (Schtickzelle *et al.*, 2006). The German study area has been described as having a high degree of fragmentation, as it consists of suitable grassland patches isolated within an old-growth spruce afforestation (Fischer *et al.*, 1999). Craioveanu *et al.* (2014) hypothesized that the short flight distances in the German study are related to its high degree of fragmentation. In the Mongolian study, where the populations occurred in an open habitat complex, longer distances than in the German study but shorter distances than in the Romanian study were found (Gantigmaa *et al.*, 2008). The open areas likely acted as less efficient barriers than the spruce forests and the habitat patches were thus less isolated than in the German study. In the Romanian study, the suitable habitat stretched over large interconnected areas inside a natural oak forest (Craioveanu *et al.*, 2014). The lack of efficient barriers and low degree of fragmentation can, according to Craioveanu *et al.* (2014), explain why these dispersal distances were longest. In the same way, the interconnectedness of the study area in this study has contributed to a low degree of fragmentation and thus long dispersal distances.

The occurrence of corridors is important for dispersal, as they lower the degree of fragmentation. According to Fischer *et al.* (1999), linear structures like forest edges appear to be favoured during flight movements, and corridors may be used by *L. helle* to travel considerable distances between adjacent habitats. I hypothesize that also the long-stretched shape of the corridors influences the results of mark recapture studies. In this study, the majority of the habitat patches are corridor-shaped. Power-line corridors, roadsides and forest paths are all long-stretched by nature and have in this study been surrounded by barriers in the form of dense coniferous forest in the majority of the study area. By effectively allowing movement only in

two directions, the individuals have been forced to take paths that maximize the straight distances from the starting point to the end point and thus also maximize the distance observed in a mark-recapture study.

Wind-mediated movement mean that also the direction of the corridors relative to the wind important. When the corridors are aligned in the same direction as the prevailing wind, they can likely further increase the flight distances of *L. helle*. In this study, several observations were made where strong tail wind caused *L. helle* to travel long distances in short time, especially in the power-line corridor. The power-line corridor is almost perfectly aligned with the prevailing wind in Östersund, which comes from west-northwest during the summer (Gyllenhammar, 2012; Windfinder, 2018).

Mark-recapture studies always underestimate total mobility (Shreeve, 1992), but to varying degrees (Hanski & Kuussaari, 1995). Most likely, an intricate interplay between size, direction and shape of study area as well as fragmentation decides to what degree the flight distances are underestimated. The amount of influence from the various factors cannot be specified and may also be related to differences in ecology between the Fennoscandian and Central European populations. In this study, there may be a relatively low degree of underestimation of flight distance, as it was performed in a study area where the large size, high occurrence of corridors and low degree of fragmentation should contribute to maximizing the recordable flight distances.

According to Fischer *et al.* (1999), the Central European populations of *L. helle* have likely been subjected to a strong selection against dispersal. With their original wetland habitat being rare and often isolated, the probability of reaching a suitable and free habitat would be low for those individuals that ventured from their site. Site fidelity likely paid off in the form of increased survival since wetland habitats are generally relatively constant over time. Today, when nearly all wetland in Central Europe has been destroyed or deteriorated, the Central European populations of *L. helle* colonize almost exclusively ephemeral anthropogenic habitats such as abandoned moist meadows. This causes a great conservation issue, as the biology of *L. helle* is not adapted to a high turn-over rate of habitats. Colonisation of new habitats is likely to only happen at a strongly restricted spatial scale (Fischer *et al.*, 1999).

4.2 Habitat selection

The best resource selection function (RSF) model had a performance on the border between the categories “poor” and “fair”, meaning that using the model to predict the occurrence of *L. helle* is not advisable. The third hypothesis, that remote-sensed variables relating to solar radiation, vegetation height, variation in vegetation height, slope and aspect can estimate habitat quality for *L. helle*, is thus not supported. This study can however be considered a first step in the process of identifying significant

predictors of *L. helle* occurrence. The most important predictors, i.e. solar radiation, slope, TPI and vegetation height in due order, can be the starting point in future model selection where other predictors are successively added and tested. With there being a considerable drop in importance from solar radiation and slope to TPI and vegetation height, it is debatable whether the two latter merit the inclusion in future models, but they will still be discussed in the following paragraphs.

Meyer and Helminger (1994) have made a study that supports the strong positive relationship between solar radiation and *L. helle*. This relationship is given several reasons in the literature. The larval development of *L. helle* is dependent on strong solar radiation reaching the lower leaves of *B. vivipara*, where the eggs are laid, to guarantee a high body temperature of the developing larvae. Especially in Fennoscandia, where the season is short and the climate is harsh and cool, the species needs high solar radiation to produce warm microclimatic conditions (Ryrholm, 2014). Sun basking is a common activity of adults (Goffart *et al.*, 2014), who, according to Lindeborg (2014), only fly in sunshine. As most habitat patches in this study are long-stretched, the influence from surrounding vegetation is high. The surrounding vegetation mainly consists of high and dense coniferous forests, which effectively blocks the sunlight from different parts of the habitat patches during different times of the day. Some patches are instead bordered by rich fens, moist meadows or other lower vegetation, which lets through more incoming solar radiation. The selection for these areas appears to be strong. The ecology of *L. helle* together with the shape of the habitat patches and the climate in Jämtland make solar radiation an important predictor of the studied metapopulation.

Slope is negatively related to *L. helle*, with a higher occurrence of *L. helle* at lower inclinations. As can be seen in the model-averaged predictor statistics (table 4), the relationship is a little less than half as strong as the relationship between solar radiation and the occurrence of *L. helle*. No support of the negative relationship between slope and *L. helle* has been found in the literature, but the explanation may lie in slope acting as a proxy for wetness. In general, low-gradient areas gather water, whereas steep areas shed water (Cooley, 2016a). *L. helle* is strongly linked to wetland habitats, with calcareous wetlands being its presumed original habitat in Fennoscandia and with the species now becoming increasingly dependent on its original wetland habitat types again as the agricultural habitats decrease. Also the host plant *B. vivipara* is strongly linked to wetland habitats, as its original habitat is believed to be sites with high water levels or moving groundwater, which prevented the establishment of taller plants (Ryrholm, 2014). In future studies, an attempt can be made to exchange slope for a wetness index to investigate whether the results improve.

The relationship between *L. helle* and TPI is of considerably lower importance than the relationship with solar radiation and slope (table 4). The negative relationship between TPI and *L. helle* that was found in this study contradicts the results of other studies. A Belgian study found that a Central European population of *L. helle* has a high preference for proximity to shrubs and trees as they provide wind shelter, whereas the species is

deterred by large, open and wind-exposed areas (Sawchik *et al.*, 2003). Other studies have found a higher abundance of trees and shrubs in occupied patches than in vacant patches (Fischer *et al.*, 1999; Bauerfeind *et al.*, 2009). In the mentioned studies, *L. helle* appears to favour habitats with heterogeneous vegetation heights, i.e. habitats that would have high TPI values. In this study, the opposite relationship has been found. This may be caused by a methodological weakness, as the narrowness of the roadsides means that their TPI values are inflated by the surrounding tall coniferous forest to a higher extent than the other habitats in this study. Most absence points are located along the gravel roads, giving a strong bias for absence at high TPI values. In the map depicting the TPI index (figure 4c), it can clearly be seen that the roadsides have higher TPI values than the power-line corridor, although the opposite should be true.

The relationship between LiDAR-derived vegetation height and *L. helle* is negative and slightly less important than the relationship between TPI and *L. helle*. Higher vegetation is linked to lower occurrence of *L. helle*, but the effect is rather weak. Some studies have investigated how Central European populations of *L. helle* are affected by vegetation height. Nabielec and Nowicki (2015) found a positive relationship between vegetation height and *L. helle* densities in recently abandoned meadows. They hypothesize that the positive relationship is caused by higher turf providing better shelter (Nabielec & Nowicki, 2015). Skórka *et al.* (2007) showed the same positive relationship in habitats at an early succession stage, with the addition that succession at later stages is detrimental to the species. In this study area, regular maintenance is performed on the roadsides and in the power-line corridors. According to Svenska kraftnät (2017), major clearings in power-line corridors are done once every four to eight years and only tall-growing trees and shrubs are removed. Low-growing species like junipers are left (Svenska kraftnät, 2017). The roadsides in this area are in general mown once every year in August (Gullberg, 2018). The remaining habitat types in this study, i.e. the abandoned meadows, the rich fens and the forest paths, are not maintained. All habitats but the roadsides are at a late succession stage, with high vegetation and the encroachment of taller and wooded plants. At this stage, *B. vivipara* can be outcompeted and there may be too little ground-reaching light for the larval development (Ryrholm, 2014), explaining the negative relationship between vegetation height and *L. helle*. Selection for stretches with lower vegetation should be high in these habitats, both for *L. helle* and its host plant.

The LiDAR data is of high resolution compared to other remote-sensed data, but the differentiation between the DSM and DEM data appears to have a considerably lower accuracy. In many occasions, a vegetation height of 0 m was erroneously reported. This has caused the vegetation height predictor in the RSF to be severely zero-inflated and has decreased the performance statistically as well as making it a less accurate representation of reality. The variable was however still included as the extracted relationship was similar to the relationship between the inventory-based vegetation height and *L. helle* and it was therefore deemed to be a fair representation of reality.

Another weakness in this RSF relates to the uneven representation of the different habitats among the presence and absence points. While the vast majority of the presence points are within the power-line corridors, most absence points were distributed on roadsides. This has skewed the results and limits the possibility of drawing general conclusions about the habitat selection of *L. helle*.

The RSF in this study includes only predictors that are related to habitat quality, meaning that all predictors belong to the primary group of determinants of patch occupancy and local population densities. Of these, only one predictor directly affects the species' physiology, i.e. solar radiation, whereas the remaining predictors have no direct physiological significance for the species. Predictors that directly affect the species' physiology are called direct gradients, whereas those that do not are called indirect gradients (Austin, 1987; Guisan & Zimmermann, 2000). Although being cost-effective and easy to upscale, this model's high reliance on indirect gradients reduces the model transferability. To improve model generality and applicability over larger areas, more direct gradients could be included and measures of consumable resources could be added (Murphy & Lovett-Doust, 2007; Randin *et al.*). This would however demand considerably more resources.

Including predictors related to the secondary group of determinants of patch occupancy and local population densities, i.e. patch area and connectivity, could improve the model considerably. In a study by Bauerfeind *et al.* (2009), patch area and connectivity were found to be the most important determinants of patch occupancy. The importance of connectivity has been stressed earlier in this study, as fragmentation has been described as the most likely limiting factors of *L. helle* in Fennoscandia today (Lindeborg, 2014). In Central European populations, studies have shown that *L. helle* is highly sensitive to isolation and exists in higher numbers at a low degree of isolation (Sawchik *et al.*, 2003). Including connectivity and patch area as predictors in this study was planned but not possible, as nearly all habitat patches were interconnected.

4.3 Correlations between *Lycaena helle* density, abundance of *Bistorta vivipara* and vegetation height

The fourth hypothesis includes two parts. The first part, that population density of *L. helle* is positively correlated with the abundance of *B. vivipara*, was only weakly supported by the data in this study. The correlation, although significant, was relatively weak and explained only a low proportion of the variance. As *L. helle* is monofagous on *B. vivipara* during its larval stage and the eggs are laid on the leaves of *B. vivipara* (Ryrholm, 2014), *L. helle* is naturally dependent on the occurrence of *B. vivipara*. The results of this study do however suggest that abundance of *B. vivipara* is not a particularly strong predictor of *L. helle* density and that *L. helle* is primarily limited by something else than its host plant or only able to use *B. vivipara* when it grows under certain circumstances. *L. helle* being limited

by something else than its host plant is suggested by Lindeborg (2014) as an explanation of why *L. helle* has disappeared from many areas where *B. vivipara* still persists. Although *B. vivipara* has decreased considerably due to the changes in land use, it is still quite common within its range and is not considered threatened (Ryrholm, 2014). In the study area, *B. vivipara* was common both in areas with low and high density of *L. helle*.

The second part of the hypothesis, that the density of *L. helle* is highest at an intermediate vegetation height, is not supported by the data in this study. A negative quadratic correlation between vegetation height < 1 m and *L. helle* density was tested but yielded no significant result. Instead, a significant linear correlation was found, which had a relatively weak negative correlation coefficient and a low R^2 . As previously mentioned, earlier studies have found highest *L. helle* densities at intermediate succession stages (Skórka *et al.*, 2007). The inventoried field data shows the same relationship as the remote-sensed vegetation height data in the RSF, where higher vegetation was linked to a lower probability of occurrence of *L. helle*. As has been argued for the RSF-related vegetation height data, the negative correlation between vegetation height and *L. helle* may be due to the late succession stage of the majority of the habitat patches in the study. A selection pressure would then have acted on *L. helle* to find stretches with sufficiently low vegetation where enough solar radiation reaches the oviposition sites. Just as vegetation height was a predictor of low importance in the RSF, the inventory-based vegetation height < 1 m has a relatively weak correlation with *L. helle* density, meaning that the selection for lower vegetation is rather weak.

4.4 Regional connectivity

In the connectivity analysis, the aim was to identify populations in Jämtland County that are important from a stepping-stone perspective and to which conservation efforts should be directed. A visual evaluation of figure 14 and 15 indicates that the method has been successful in identifying so-called stepping stones. The points that appear to act as important facilitators of movement between surrounding points have consistently scored the highest ΔPC connector values.

The connections consist of straight lines and no consideration has been taken to the presence of barriers, corridors or other landscape features affecting the movement of *L. helle*. This represents an oversimplification of the movement pattern of *L. helle* and is an inherent weakness of the analysis, possibly overestimating the connectedness of some nearby populations or assuming connectedness where there is none. According to Fischer *et al.* (1999), the arrangement and structure of barriers between the occupied habitats is the most important factor for the connectivity between adjacent populations. At the same time, basing the connectivity analysis on mark-recapture data also leads to a likely underestimation of connectivity. Recent intensive and large-scale studies on butterflies have revealed that long-distance dispersal exists in species that are regarded as sedentary

(Zimmermann *et al.*, 2011). Observed colonisation events and genetic analyses suggest that adults of *L. helle* can actually move larger distances than estimated in mark-recapture studies (Bachelard & Descimon, 1999; Finger *et al.*, 2009; Turlure *et al.*, 2014). Although simplified and with over- or underestimated dispersal, the connectivity analysis may provide a much-needed indication of which populations that are most important from a connectivity perspective.

Many clusters of observations occur along roads, power-line corridors or other long-stretched habitat patches. The large amount of observations in corridors highlights the importance of dispersal corridors for the connectivity and long-term viability of metapopulations of *L. helle*. When doing this inference, it should however be remembered that many of these habitats have a high number of people passing through, which contributes to high observation numbers.

In the connectivity analysis, observations of *L. helle* from as far back as 2002 were included, which means that some of the populations are most likely not extant today. The majority of the observations have not been quality checked, as only some photos were available. The reported positions were used in the connectivity analysis, although some have an error range of several hundred meters.

4.5 Other observations

During the first weeks of the study, *L. helle* was observed in close proximity to species belonging to the genus *Salix*, i.e. willow species. Willows are an important source of nectar, especially at the beginning of the flying period when no or few herbaceous plants have started to flower. The branches of *Juniperus communis*, i.e. the common juniper, were common roosting sites for males throughout the season. With its dense structure and relatively dark colour, *J. communis* provides good shelter from the wind and heats up fast, thus radiating heat that *L. helle* can benefit from.

According to Lindeborg (2014), *L. helle* only flies in sunshine. During the unfavourable season in the summer of 2017, *L. helle* was frequently observed on cloudy and windy days. When having access to wind shelter in the form of shrubs and sparse forest patches, it appears as though *L. helle* has a higher tolerance for bad weather than has previously been assumed. Individuals were commonly seen flying in and out of the surrounding vegetation and were active as long as the vegetation could provide suitable microclimatic conditions. Especially medium-height vegetation, e.g. *J. communis*, seems to fill this need.

4.6 Implications for conservation

An action plan for the preservation of *L. helle* in Sweden has been compiled by the Swedish Environmental Protection Agency (SEPA). The suggested habitat-related measures mainly include the use of traditional agricultural methods such as mowing and moderate grazing on moist meadows and pastures where *L. helle* exists. The aims are in general to keep the vegetation at a suitable length and decrease the nutrient load to lessen the competitive pressure on *B. vivipara*, at the same time as ensuring the presence of a mosaic-like landscape with vegetation at different heights where *L. helle* can find shelter from the wind. Currently, the biggest threats to *L. helle* habitats in Sweden are described as the cessation of mowing and grazing, fertilisation and too intense grazing and trampling (Lindeborg, 2014).

With this study, a few additional suggestions for the conservation of *L. helle* can be made. A first step could be to further inventory the extent of the metapopulation in this study, as its distribution most likely continues outside the study area. With a number of rich fens distributed along the power-line corridor and with a wide-stretched network of corridors, the metapopulation in this study may represent some of the densest and widest distributions of *L. helle* in the county.

Part of the metapopulation in this study is located within Tysjöarna nature reserve (figure 2a). The nature reserve has one of the largest calcareous wetlands in the world and spans over 455 ha (Länsstyrelsen Jämtlands län, 2013). It includes several potentially suitable habitats for *L. helle*, in the form of calcareous wetlands, pastures, moist meadows, power-line corridors and forest paths. *L. helle* has previously been sighted regularly in the western parts of the reserve, but after large-scale wetland restorations commenced in 2013 (Landin, 2013), only two observations have been made and there is a risk that the elevated water levels drowned the overwintering pupae nearby. Directing resources to a reestablishment of *L. helle* in the reserve would be in line with one of the aims of the reserve, which is to benefit species that are tied to calcareous grounds. Improving the connectedness between the metapopulation and suitable habitats within the western parts of the nature reserve by creating a dispersal corridor would be an efficient way of improving the long-term viability of the metapopulation at the same time as adding value to the nature reserve. A dispersal corridor would also benefit other species with similar habitat requirements and low dispersal ability. It has been stressed many times that network structures are fundamental for the conservation of *L. helle*, and Tysjöarna nature reserve represents an ideal area for this type of conservation efforts as the County Administrative Board has high influence over the management in the area.

To maintain the suitability of the habitat patches in the study area, some measures should be taken. In 2017, the roadsides in the study area were mown on the 13th of June, which is well outside the recommended time period for the mowing of roadsides where *L. helle* occurs. The recommended time period is set to the 10th of July to the 15th of August and *L. helle* is considered most vulnerable to disturbances between the 20th of

May and 31st of July, from the beginning of the flight period to the end of the larval stage (Lindeborg, 2014). In several places, the mowing removed all vegetation, including rich abundances of *B. vivipara*, leaving only bare soil. As the roadsides are in a military training area, the Swedish Fortifications Agency (SFA) does all maintenance. According to Gullberg (2018) at SFA, the mowing is usually done once a year in the end of August, which explains how *L. helle* has been able to persist in the area. The mowing that occurred in the middle of June 2017 was, according to Gullberg (2018), an exception. As the Swedish Transport Administration (STA) does not maintain these roadsides, they cannot become part of the project Artrika vägkanter (Species-rich roadsides). A dialogue about timing and method of mowing between the County Administrative Board in Jämtland County and SFA is necessary to ensure maintained habitat quality of the roadsides in the military training area.

Conservation measures should also be discussed with Svenska kraftnät, the Swedish authority that maintains power-line corridors. Most *B. vivipara* grow along the path under the power line, where there is sufficiently low vegetation for *B. vivipara* to persist since the vegetation is maintained by Svenska kraftnät every four years. When major clearings are made every eight years, forest machines are normally used. These forest machines may be beneficial as they disturb the current vegetation and create areas with low vegetation where *B. vivipara* can establish, but this has not been studied. The impact of the forest machines should preferably be monitored, and it can then be discussed whether chainsaws should be used instead or if care should be taken to avoid the current establishments of *B. vivipara* with the forest machines. The maintenance performed by Svenska kraftnät does in general appear to be beneficial for *L. helle*, as low-growing species such as *J. communis* and various willow species are left, and as more areas with low vegetation are created.

The negative relationship between both remote-sensed and inventory-based vegetation height and *L. helle* implies that the species would benefit from lower vegetation heights in the power-line corridor, which could be achieved by regular mowing and clearing of unwanted vegetation (Svensson *et al.*, 2017). Today, there is a lack of funding for conservation-oriented maintenance of power-line corridors although studies have shown their importance for many red-listed species. According to Svensson *et al.* (2017), conservation efforts directed to broad, moist and flower-rich power-line corridors could benefit a large number of butterfly species.

Although this study has shown a negative relationship between *L. helle*, vegetation height and variation in vegetation height, the reliance on shrubs and trees for wind shelter appears clear when drawing on other relevant literature (Fischer *et al.*, 1999; Sawchik *et al.*, 2003; Bauerfeind *et al.*, 2009) and from observations made in this study. When restoring rich fens or other habitats it is therefore important to leave some higher vegetation that can provide wind shelter. This is especially true in the area around Östersund, where the winds more often come from the north than in the rest of the country. Winds from the north are generally colder, which means that *L. helle* has a strong need for protection from the wind (Gyllenhammar, 2012).

Lately, efforts have been made to maintain and restore wetland habitats in Jämtland County, (Länsstyrelsen Jämtlands län, n/a) among them the rich fens where *L. helle* occurs (Länsstyrelsen Jämtlands län, 2013). When comparing restored rich fens with unrestored rich fens in the surroundings of the study area, the latter appear more suitable for *L. helle* as nearly all taller vegetation except for pine trees had been removed in the restored wetlands. For future restorations, it is important to remember that *L. helle* is deterred by open, wind-exposed areas, which act as a barrier to dispersal (Sawchik *et al.*, 2003).

This study strengthens the notion that corridors are important both as mediators of dispersal and as habitats in themselves. Corridors can offer high-quality habitats, much as an effect of the high exposure to edges. Turlure *et al.* (2014) hypothesize that the presence of edges may be beneficial and even necessary for several reasons. Firstly, many tree and bush species are used as nectar resources in the beginning of the flying period when no or few herbaceous plant species are flowering. Secondly, edges can provide suitable microclimatic conditions by providing wind shelter and a beneficial thermal profile. Finally, the sunny edges are used as encounter sites, where males perch and defend territories (Turlure *et al.*, 2014). Power-line corridors and roadsides may appear to be less ideal than the primary agricultural and the original wetland habitats, but have other features that make them crucial for the conservation of *L. helle*.

The regional connectivity analysis in this study can help identifying stretches with lower habitat quality. In figure 15, the long distance from the black point to the red point may be caused by lower or insufficient habitat quality in-between the two points. If the adjacent habitat quality is allowed to degrade, the stretch with insufficient habitat quality may become longer than the maximum flight length of *L. helle*, effectively splitting the metapopulation in two. This would have negative effects on the genetic status of the metapopulation and could undermine its long-term viability.

The low dispersal ability of *L. helle* makes it vulnerable to climate change. Climate change has been theorized to lead to further fragmentation by forcing populations of *L. helle* to move to higher altitudes and thereby making them more isolated (Lindeborg, 2014). In Central Europe, this process has been shown to lower the genetic variation, as gene flow between populations decreases (Habel *et al.*, 2011). Additionally, the increased precipitation that is expected may lead to less sunlight and thereby cause longer periods of inactivity in *L. helle* (Lindeborg, 2014). As climate change can act as an additional driver of fragmentation, retaining or improving connectivity is vital for the long-term viability of the species. Conservation efforts should be directed to the preservation of metapopulations, since large networks of populations have a considerably higher viability and potential of adapting to new environmental conditions (Sawchik *et al.*, 2003). According to Eliasson (2012), *L. helle* has extreme fluctuations in the number of adults from year to year. As a species with extreme fluctuations due to current environmental and demographic stochasticity, *L. helle* has a great need for metapopulation processes such as rescue effects to buffer against the future additional fluctuations caused by climate change.

5 Conclusions

The studied population of *L. helle* is extremely sedentary, but the recorded flight distances are in most cases longer than what has been found in Central Europe. The reasons for this are unknown, but may be connected to factors such as the size of the study area, degree of fragmentation and shape and direction of the habitat patches, or to differences in ecology between the two subspecies. As only few individuals switched from one habitat to another, the studied population can be regarded as having high habitat fidelity. Females generally flew further than males, but due to the small female sample size the differences could not be tested statistically.

The best-performing RSF model has low accuracy, but the model-averaged predictor statistics still provide useful information. Solar radiation and slope had highest importance values and are recommended for inclusion in future models. TPI and vegetation height had considerably lower importance, but still above the threshold at which a variable can be considered important. Whereas the relationship with solar radiance is positive and strong, the remaining predictors have negative and considerably weaker parameter estimates. The strong selection for areas with high solar radiation is linked to the dependence of both *L. helle* and *B. vivipara* on high insolation. Slope is hypothesized to act as a proxy for wetness, as *L. helle* is strongly linked to wetland habitats and low-gradient areas gather water whereas steep areas shed water. The negative relationship with TPI is likely caused by a model weakness, as the roadsides have erroneously high values. Vegetation height also has a negative parameter estimate, which might be a consequence of the late succession stage in the majority of the habitat patches. This causes both *L. helle* and *B. vivipara* to select for areas with low vegetation. To improve the model accuracy, predictors that relate to direct effects on the physiology of *L. helle*, consumable resources, patch area and/or connectivity can be included.

A weak but significant correlation was found between *L. helle* density and the abundance of its host plant *B. vivipara*. The results suggest that the presence of *B. vivipara* is not a particularly strong predictor of *L. helle* density and that *L. helle* is either primarily limited by something other than the presence of its host plant or that *L. helle* can only use *B. vivipara* that grows under certain circumstances. No significant negative quadratic correlation was found between *L. helle* density and vegetation height, but a weak negative linear correlation was found. Just as for the vegetation height

in the RSF model, this relationship may be caused by the late succession stage of the majority of the habitat patches in the study area. The connectivity analysis identified so-called stepping stones. Many of the identified networks occur along roads or other long-stretched habitat patches, which highlights the importance of dispersal corridors for the connectivity and long-term viability of metapopulations of *L. helle*.

L. helle was frequently observed in close proximity to *Salix* species during the first weeks of the flying period, as trees in the genus are an important nectar source early in the season. *J. communis* was favoured for roosting and wind shelter. *L. helle* appears to be less weather sensitive than previously thought, as long as the surrounding vegetation can provide suitable microclimatic conditions.

A number of suggestions are made for the continued conservation of the species. The importance of metapopulation structures and retained or improved connectivity is stressed. The studied population may be one of the densest and most extensive in the county and it would be beneficial to inventory its full distribution. To improve the long-term viability of the studied population, it is recommended to make a dispersal corridor to suitable habitats in Tysjöarna nature reserve. The timing and frequency of maintenance is crucial and there is a need to communicate this to the parties responsible for the management. Corridors have a value both as mediators of dispersal and as habitat patches in themselves, and are thus of high importance for conservation. The connectivity analysis helps identify populations that are of extra importance for metapopulation structures of *L. helle* and to which extra conservation efforts should be directed. With the onset of climate change, the preservation of extant metapopulations is yet more important as large networks of populations are more viable and have a higher potential of adapting to new environmental conditions.

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Appendix 1

In table 5, the coordinates of all populations with a ΔPC connector value > 0 can be found. Also their overall ΔPC value is included.

Table 5. The coordinates (SWEREF 99), ΔPC and ΔPC connector values of the populations with ΔPC values > 0 . The table is sorted after ΔPC connector value, with highest first.

East	North	ΔPC	ΔPC connector
375101	6940251	0.61	0.000631
374350	6941961	1.21	0.000542
373227	6936501	0.59	0.000376
374382	6941792	1.2	0.000155
372896	6936678	0.71	0.000151
373463	6936212	0.72	0.000142
484588	7004220	0.66	0.000124
373820	6942795	1.02	0.000118
374535	6941594	0.77	0.000117
374173	6942519	0.64	0.000108
517938	7037085	0.65	0.000100
373391	6943116	0.57	0.000091
532331	6946051	0.57	0.000086
374598	6941325	1.07	0.000085
517151	7036671	0.71	0.000084
481501	7010856	0.56	0.000074
374361	6941871	1.45	0.000067
532119	6946612	0.68	0.000065
481297	7011173	0.56	0.000062
373830	6935758	0.61	0.000061
374875	6939903	0.98	0.000047
483681	7010209	0.57	0.000043
517375	7036618	0.68	0.000032
397692	7003905	0.57	0.000027
517783	7036946	0.76	0.000020
532141	6946751	0.71	0.000014
517554	7036661	0.64	0.000005
484474	7009806	0.55	0.000004