Importance of habitat quality and landscape factors for a monophagous shield bug on a rare host plant

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Abstract

Understanding the factors affecting species distribution and at what scale a species respond to these factors is a major challenge in conservation biology. I studied the distribution and abundance of a monophagous shield bug Canthophorus impressus at three spatial scales: host plants, patches and circular landscapes (area ca. 3 km²), to determine the relative importance of the different spatial scales and how habitat quality, amount and spatial configuration affect the distribution of C. impressus. Influence of habitat characteristics on occurrence and abundance of the bug was analysed with separate generalised linear mixed models. The data show that effects of habitat quality and amount dominate over configuration in determining the distribution of C. impressus. The bug prefers large host plants in warm conditions on a plant scale and abundant host plants in a landscape scale, whereas patch scale was not important for the distribution of the bug. Management should aim to preserve sites with abundant host plants and promote large host plants with low to moderate grazing. To secure sufficient number of host plants in the landscape, high densities of suitable habitat such as semi-natural grasslands should be preserved. This study suggests that analyses of multiple spatial scales are crucial for identifying appropriate actions for successful conservation of species living in fragmented habitats.

Keywords: Canthophorus impressus, conservation, habitat quality, landscape, spatial scale, Thesium alpinum
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1 Abstract
Understanding the factors affecting species distribution and at what scale a species respond to these factors is a major challenge in conservation biology. I studied the distribution and abundance of a monophagous shield bug *Canthophorus impressus* at three spatial scales: host plants, patches and circular landscapes (area ca. 3 km²), to determine the relative importance of the different spatial scales and how habitat quality, amount and spatial configuration affect the distribution of *C. impressus*. Influence of habitat characteristics on occurrence and abundance of the bug was analysed with separate generalised linear mixed models. The data show that effects of habitat quality and amount dominate over configuration in determining the distribution of *C. impressus*. The bug prefers large host plants in warm conditions on a plant scale and abundant host plants in a landscape scale, whereas patch scale was not important for the distribution of the bug. Management should aim to preserve sites with abundant host plants and promote large host plants with low to moderate grazing. To secure sufficient number of host plants in the landscape, high densities of suitable habitat such as semi-natural grasslands should be preserved. This study suggests that analyses of multiple spatial scales are crucial for identifying appropriate actions for successful conservation of species living in fragmented habitats.

Keywords: *Canthophorus impressus*, conservation, habitat quality, landscape, spatial scale, *Thesium alpinum*

2 Introduction
Fragmentation and loss of natural habitat continues to be major threats to global biodiversity (Hilton-Taylor et al. 2009). In fragmented landscapes, the persistence of a species might be dependent on metapopulation dynamics (Hanski et al. 1996). A metapopulation consists of discrete local populations connected through migration (Hanski 1997). In the classical view, the long-term existence of a metapopulation of a species is dependent on an equilibrium between extinction and colonisation of habitat patches (Hanski 1997). Initially, area and isolation effects have been in focus of metapopulation studies (Hanski 1999), although more recent work suggests that also variation in habitat quality can be at least as important as area and isolation of patches for predicting metapopulation dynamics (Dennis & Eales 1999, Thomas et al. 2001, Fleishman et al. 2002). Most current studies on metapopulations include variation in habitat quality, although its importance compared to that of area and isolation remains under debate (Moilanen & Hanski 1998, Dennis & Eales 1999, Thomas et al. 2001, Fleishman et al. 2002, Rabasa et al. 2008, Vögeli et al. 2010).
The relative importance of habitat quality for species occurrence might be a matter of spatial scaling, since habitat quality operates at a more local level than the spatial parameters of area and isolation (Thomas et al. 2001, Thomas & Hanski 2004). Moreover, the relative importance of patch size and isolation for distribution patterns of a species may also change across spatial scales (Rukke & Midtggaard 1998, Menéndez & Thomas 2000). Depending on the spatial scale examined, the spatial structure of a species population may differ (Hecnar & M‘Closkey 1997, Rukke & Midtggaard 1998, Menéndez & Thomas 2000). Consequently, taking only a single spatial scale into account might lead to erroneous conclusions about the dynamics of a species. Furthermore, assessing multiple spatial scales simultaneously may be a way to identify processes that take place on different temporal scales. In this context, large-scale patterns are assumed to reflect more long-term dynamics (Menéndez & Thomas 2000). So far, few studies on species distributions have covered a broad range of spatial scales (Procheş et al. 2010).

Semi-natural grassland is a habitat often containing a remarkably high small-scale density of plant species (Eriksson & Eriksson 1997, Austrheim et al. 1999). Semi-natural grasslands are defined as grasslands with a long tradition of management like mowing or grazing, and without signs of fertilization to improve forage production (Eriksson et al. 2002). In Sweden, semi-natural grasslands have been subjects to substantial area reduction during the last century (Ekstam & Forshed 2000), mainly due to changes in farming practise (Eriksson et al. 2002). As a result, species abundance and diversity has been reduced (Maes & Van Dyck 2001, Luoto et al. 2003). Although semi-natural grasslands have gained a lot of attention in ecological studies, few studies have explicitly assessed species distributions across multiple spatial scales in this habitat (but see Steffan-Dewenter et al. 2002 for an example).

One species connected to semi-natural grasslands is the shield bug Canthophorus impressus Horváth (Hemiptera, Cydnidae). Not much is known about the habitat preferences of C. impressus apart from the requirements of its host plant and the bug is the subject of a recent species action plan from the Swedish Environmental Protection Agency (2011). In Sweden, it has only been recorded on the perennial plant Thesium alpinum L. (Santalaceae; Karlsson et al. 2007). The host plant grows mainly on nutrient-poor, sandy open grasslands but has also been found on other types of land, such as road verges (Karlsson et al. 2007). It depends on soil disturbance for its regeneration and the distribution of T. alpinum in Sweden is fragmented. Given the fragmented distribution of its host plant, metapopulation dynamics might be important for the long-term persistence of C. impressus, but as far as I am aware, there are no such studies.
The aim of the present study was to investigate how the distribution of a monophagous insect is affected by the amount and distribution of its host plant. A multiscale approach was employed to examine the distribution and abundance of *C. impressus* at a hierarchy of three spatial scales: plants, patches with plants and circular landscapes (area ca. 3 km²) with patches. The relative importance of the different spatial scales and how habitat quality, amount and spatial configuration affect the distribution of *C. impressus* was assessed.

3 Materials and methods

3.1 Study species

*Canthophorus impressus* is a shield bug distributed from the British Isles through Europe to Siberia (Karlsson et al. 2007). In Sweden it is restricted to the south-eastern parts, mainly the provinces of Småland and Östergötland, following the distribution of its host plant *Thesium alpinum* (Karlsson et al. 2007). The imagines of *C. impressus* overwinter as clusters in the leaf litter near the host plants (Southwood & Leston 2005). Mating occurs in May and eggs are probably laid in or on the ground beneath a host plant, similarly to other related species (Filippi et al. 2009). The nymphs appear in June and are completely developed in July-August (Karlsson et al. 2007).

3.2 Study area

This study was conducted throughout most of the distribution range of *T. alpinum* in Sweden, in the south-eastern provinces of Östergötland and Småland (56°59’-58°23’N, 14°19’-16°11’E; Figure 1). The area is dominated by coniferous forest, and around 2% of it is semi-natural grassland.

The occurrence of *T. alpinum* and *C. impressus* was assessed in 30 landscape circles with 1 km radii, each centred on a known population of *T. alpinum*, from 12 June to 11 August 2011. The central populations of *T. alpinum* were chosen in such a way that variation in both number of known sites and densities of the plant within circles were maximised, keeping as large geographical distribution as possible. The selection was based on previous data on the two species taken from the Swedish ‘Species Gateway’. This website is open for anyone to report their sightings (Swedish Species Information Centre 2011) and contained on 23 March 2011 when data was collected 1411 Swedish records of *T. alpinum* and 149 of *C. impressus*. 
3.3 Field methods and plant level variables
In each landscape circle, I searched for *T. alpinum* in all potential habitats, starting with the previously known sites. The potential habitat areas were delimited by using aerial photographs and detailed maps. Potential habitat included grasslands, road verges and other open areas such as old gravel pits. All *T. alpinum* plants were mapped individually with a handheld GPS navigator (GPSMAP 60CSx, Garmin, Olathe, Kansas). Each plant was checked for *C. impressus* and the number of imagines and nymphs were counted. The inventory was only carried out on days when weather conditions were favourable for *C. impressus* activity, i.e. a temperature above 15 degrees Celsius without rain. If there were short rainfalls during the day, the survey was interrupted and then continued when the rain stopped.

As a measure of individual plant quality, a set of habitat parameters were recorded (Table 1). Vegetation height was measured with a drop disc method: a metal disc with diameter 50 cm and weight 430 g was dropped down a vertical ruler and the height where the disc settled was recorded in centimetres. Sun exposure was recorded by looking at the sky and estimating the percentage of the sun’s path (average path 6 weeks ± summer solstice) that the plant would be exposed to light. If the plant was standing in a slope, inclination was measured with an inclinometer (PM-5, SUUNTO, Helsinki), and the aspect of the slope noted.

3.4 Patch and landscape level variables
Point pattern analysis was used to make an objective delimitation of patches of *T. alpinum*. Ripley’s *K* function was used to assess the degree of
spatial dependence based on distances between all points in the area of interest (Wiegand & Moloney 2004). To facilitate visual interpretation, a square-root transformed version of the $K$ function, the $L$ function was used (Wiegand & Moloney 2004). The $L$-statistic was plotted against distance for all 30 landscape circles separately using the software Programita (Wiegand & Moloney 2004) and the first peak was noted, as this is the distance where the smallest scale clustering appears. The median value of the first peaks for all circles was 55 m and this distance was used as an approximation of the smallest scale clustering for the whole study area. Patches were then delimited using buffers with radii of half the value of the small-scale clustering distance, i.e. 27.5 m, around each plant in ArcGIS 9.3 (ESRI 2008). The total area covered by overlapping buffers, or by just one single buffer, was defined as one patch (Figure 2).

![Figure 2](image.png)

*Figure 2. Description of how patches were delimited. Each cross represents a plant and around this a circle with radius 27.5 m was drawn. The total area covered by overlapping circles (a) or by just one single circle (b) was defined as one patch.*

Habitat variables on patch and landscape level (Table 1) were derived from observed data on plant level. The patch level variable was number of plants in patch, which was used as a measure of patch size. On landscape level, number of patches in a circle was included to get a measure on the habitat configuration. Area of grassland was calculated on the basis of data from a national grassland inventory made during 2002-2004 (Swedish Board of Agriculture 2011). This variable was used as a proxy for the amount of suitable habitat available for *T. alpinum*. Calculations were done in ArcGIS 9.3 (ESRI 2008).

### 3.5 Statistical modelling

The influence of habitat characteristics on (i) occurrence and (ii) abundance of *C. impressus* on a *T. alpinum* plant was assessed with a separate generalised linear mixed model for each. To account for the hierarchical design of the study, landscape circle and patch (nested within circle) were
included as random effects. For occurrence, binomial models with a logit link function were fitted. For abundance, negative binomial models (due to Poisson over-dispersion) with a logarithmic link function were fitted.

For the abundance models, a reduced data set was used, including only the plants in patches where *C. impressus* was present. As this reduced the number of landscape circles to 15, only one explanatory variable on landscape level was included in the abundance models to avoid overfitting. Out of the three variables on landscape level (Table 1), number of plants in circle was chosen because it measured the habitat of the bug most accurately.

Two model sets with all possible models including eleven variables for occurrence and nine for abundance were created and Akaike’s Information Criterion (AIC) was used to rank the models. As AIC is on a relative scale, it is more useful to report results as AIC differences,

\[ \Delta_i = AIC_i - \text{minAIC}, \quad (1) \]

where \(i\) denotes the \(i\)th model. Models with \(\Delta_i \leq 2\) can be considered to have substantial support (Burnham & Anderson 2002) and for these I calculated Akaike weights. The Akaike weight of a model provides weight of evidence that the given model is the best model in the set (Burnham & Anderson 2002). Further, to assess the relative importance of each variable, the Akaike weights were summed for all models where a given variable was present. The larger the sum of Akaike weights for a variable is, the more importance it has relative to the other variables in the set (Burnham & Anderson 2002). Parameter estimates for occurrence and abundance respectively, are reported from multimodels which average over all models with substantial support. All explanatory variables were standardised before they were entered into the models to allow comparison of the effect sizes.

A binomial generalised linear model (logit-link) was also fitted, predicting the occurrence of *C. impressus* in a landscape circle by the number of *T. alpinum* plants in the circle.

The modelling was done in R 2.14.0 (R Development Core Team 2011), using the lme4 package version 0.999375-42 (Bates et al. 2011) for the occurrence models and glmmADMB version 0.6.6 (Skaug et al. 2011) for the abundance models. For the model-averaging, the package MuMIn version 1.7.2 (Barton 2012) was used.
Table 1. Description and characteristics of habitat variables at the three levels of spatial scale. Sample sizes were 30 landscape circles, 74 patches and 3105 plants.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Median</th>
<th>Mean ± SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plant level</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant length</td>
<td>Summed length (cm) of all branches on a plant</td>
<td>42</td>
<td>55±43.4</td>
<td>6-420</td>
</tr>
<tr>
<td>Bare ground</td>
<td>Cover of bare ground (%) in a 20 cm radius circle around a plant</td>
<td>0</td>
<td>5±14.7</td>
<td>0-95</td>
</tr>
<tr>
<td>Veg. height</td>
<td>Height of vegetation (cm) surrounding a plant</td>
<td>6</td>
<td>6.3±2.55</td>
<td>0-22</td>
</tr>
<tr>
<td>Sun exposure</td>
<td>A plant’s estimated percentage daily exposure to light</td>
<td>80</td>
<td>75±16.1</td>
<td>25-100</td>
</tr>
<tr>
<td>Inclination</td>
<td>Inclination of slope (degrees)</td>
<td>0</td>
<td>3.8±4.65</td>
<td>0-24</td>
</tr>
<tr>
<td>Aspect</td>
<td>Aspect of slope (categorical: None and 8 categories of aspect starting from N moving clockwise)</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>No. of plants 1 m</td>
<td>Number of plants in 1 m radius circle around a plant</td>
<td>3</td>
<td>4±3.0</td>
<td>1-21</td>
</tr>
<tr>
<td>Patch level*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of plants patch</td>
<td>Number of plants in a patch</td>
<td>16</td>
<td>42±53.1</td>
<td>1-257</td>
</tr>
<tr>
<td>Landscape level*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of plants circle</td>
<td>Number of plants in a landscape circle</td>
<td>74</td>
<td>104±10.2</td>
<td>1-469</td>
</tr>
<tr>
<td>No. of patches circle</td>
<td>Number of patches in a landscape circle</td>
<td>2</td>
<td>2.5±1.53</td>
<td>1-7</td>
</tr>
<tr>
<td>Area grassland circle</td>
<td>Area of grassland (km²) in a landscape circle</td>
<td>0.01</td>
<td>0.15±0.155</td>
<td>0-0.69</td>
</tr>
</tbody>
</table>

*See text for definition of patch and landscape.

4 Results

A total of 3105 Thesium alpinum plants were found, distributed among 74 patches situated in 30 landscape circles. Canthophorus impressus was present in 25 (34%) of the patches and in 15 (50%) of the landscape circles. The occupied circles were distributed throughout the studied area with exception of the western-most part of the study area. In total, 504 bugs were found in the study, distributed on 9.6% of the T. alpinum plants. On a single plant, the maximum number of C. impressus specimens recorded was 27 (1.7 ± 2.0, mean ± SD, calculated for plants with presence of bugs, n = 299).

Characteristics of the habitat variables included in the study are listed in Table 1. The plants were distributed in the 9 categories of aspect as follows: 50% of the plants were standing on flat terrain (aspect = “none”), 1.6% in north-east slopes, 6.2% in east slopes, 4.2% in south-east slopes, 17% in south slopes, 9.3% in south-west slopes and 11% in west slopes.

4.1 Habitat characteristics and occurrence

Twenty-four models for occurrence had substantial support (Δi ≤ 2). Based on summed Akaike weights most of the higher ranked variables were on plant level, but number of plants in a landscape circle was also among the top ranked variables (Table 2).
The occurrence of the bug increased with increasing length of the plant (Figure 3, Table 2). This explanatory variable was ranked along with aspect of slope as the most important variable in the set of model-averaged variables (Table 2). Based on the averaged model with all other variables held constant at their means and with the aspect category “flat terrain”, the probability of occurrence for the bug was 73% on a 420 cm long plant (the maximum length recorded in the study; Figure 3). Regarding aspect of slope, there were more bug occurrences in slopes facing south-east, south and south-west compared to plants standing on a flat surface. North-east, east and west facing slopes had fewer occurrences of the bug compared to flat terrain. South-east facing slopes had the highest proportion, 17.6%, of plants with bug occurrence (Figure 4). The second highest proportion occurred on plants standing on flat terrain, with 13.8% occurrence of bugs.

![Graph](image_url)

*Figure 3. Probability of occurrence of Canthophorus impressus on a Thesium alpinum plant in relation to summed length of branches on the plant. The prediction is based on the averaged model, all other variables kept at their means and with “flat terrain” as the aspect category. Solid line shows the prediction and dotted lines 95% confidence interval.*
Figure 4. Proportion of occurrences of Canthophorus impressus on a Thesium alpinum plant standing in slopes in relation to aspect of slope.

Increasing number of plants in a landscape circle increased the probability of occurrence of the bug on a plant. Based on the averaged model, the predicted probability of occurrence on an individual plant was 36% on a plant surrounded by 469 other plants (the highest number recorded in the study) within a radius of 1 km. Moreover, based on the landscape scale model, 84 plants were required for 50% probability of occurrence in a landscape circle (logit probability of occurrence = -1.875 + 0.0223*Plants in landscape circle, $\chi^2 = 11.998, p = 0.0005$; Figure 5).

Figure 5. Probability of occurrence of Canthophorus impressus in a landscape circle with radius 1 km in relation to number of Thesium alpinum plants in the circle. Solid line shows the prediction and dotted lines 95% confidence interval.
The occurrence of *C. impressus* on a host plant increased with both higher amount of sun exposure and larger proportion of bare ground, although the effect sizes were lower than for the higher ranked variables (Table 2). The probability of occurrence on a plant with 100% sun exposure was 2%, all other variables kept at their averaged values. The corresponding probability for a plant with 95% bare ground was 4%.

### 4.2 Habitat characteristics and abundance

Eleven models explaining abundance of *C. impressus* on a plant had substantial support ($\Delta_i \leq 2$). Only variables measured at plant level were important for explaining abundance (Table 2), i.e. variables at patch and landscape level could not explain abundance.

Similarly to occurrence, abundance was best explained by plant length (highest absolute value of the regression coefficient), although bare ground and sun exposure also had the same support as measured by the relative importance of the variables (Table 2). The abundance of the bug on a plant increased with increasing plant length (Figure 6, Table 2). In the averaged model with all other variables kept constant at their means, the predicted abundance on a plant of 420 cm was 5.6 bugs. The other variables had considerably smaller effect on abundance, resulting in that a medium sized plant would have essentially no bugs even if other circumstances were optimal.

The observed abundances were highest on plants with 51-75% bare ground beneath them (Figure 6). However, there were only a few plants with a higher proportion of bare ground than 50%. The predicted abundance on a plant with 90% bare ground (the maximum in the abundance data set) was 0.42 bugs. Furthermore, there was a tendency in the observed abundances for an optimal sun exposure of 61-70% (Figure 6). This pattern was not tested though, as no second order terms were evaluated in the models. A plant with 100% sun exposure had 0.15 bugs based on the averaged model. There were also more bugs on plants with increasing number of plants in the surrounding 1 m (Figure 6). This variable had a similar effect size as sun exposure in the averaged model. The abundance was 0.16 bugs on a plant with 15 surrounding plants in 1 m.
Table 2. Generalised linear mixed models explaining occurrence and abundance, respectively, of Canthophorus impressus on a Thesium alpinum plant. Averaged models based on models with $\Delta_i \leq 2$, which were 24 and 11 models for occurrence and abundance respectively.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
<th>$\sum w_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Occurrence model</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-4.04</td>
<td>-5.002</td>
<td>-3.081</td>
<td>-</td>
</tr>
<tr>
<td>Plant length</td>
<td>0.60</td>
<td>0.445</td>
<td>0.746</td>
<td>1.00</td>
</tr>
<tr>
<td>Aspect*</td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
</tr>
<tr>
<td>North-east</td>
<td>-15.55</td>
<td>-2713.4</td>
<td>2682.3</td>
<td>-</td>
</tr>
<tr>
<td>East</td>
<td>-2.02</td>
<td>-5.014</td>
<td>0.981</td>
<td>-</td>
</tr>
<tr>
<td>South-east</td>
<td>1.51</td>
<td>-0.437</td>
<td>3.464</td>
<td>-</td>
</tr>
<tr>
<td>South</td>
<td>1.13</td>
<td>-0.120</td>
<td>2.372</td>
<td>-</td>
</tr>
<tr>
<td>South-west</td>
<td>1.54</td>
<td>-0.567</td>
<td>3.638</td>
<td>-</td>
</tr>
<tr>
<td>West</td>
<td>-1.13</td>
<td>-3.025</td>
<td>0.757</td>
<td>-</td>
</tr>
<tr>
<td>No of plants circle</td>
<td>1.04</td>
<td>0.126</td>
<td>1.958</td>
<td>0.97</td>
</tr>
<tr>
<td>Sun exposure</td>
<td>0.23</td>
<td>-0.007</td>
<td>0.462</td>
<td>0.91</td>
</tr>
<tr>
<td>Bare ground</td>
<td>0.15</td>
<td>-0.027</td>
<td>0.324</td>
<td>0.75</td>
</tr>
<tr>
<td>Area grassland circle</td>
<td>0.41</td>
<td>-0.243</td>
<td>1.060</td>
<td>0.33</td>
</tr>
<tr>
<td>Inclination</td>
<td>-0.34</td>
<td>-0.873</td>
<td>0.203</td>
<td>0.32</td>
</tr>
<tr>
<td>No. of patches circle</td>
<td>-0.51</td>
<td>-1.293</td>
<td>0.282</td>
<td>0.29</td>
</tr>
<tr>
<td>No. of plants patch</td>
<td>0.54</td>
<td>-0.432</td>
<td>1.505</td>
<td>0.18</td>
</tr>
<tr>
<td>No. of plants 1 m</td>
<td>0.07</td>
<td>-0.119</td>
<td>0.264</td>
<td>0.07</td>
</tr>
<tr>
<td>Veg. height</td>
<td>0.03</td>
<td>-0.147</td>
<td>0.209</td>
<td>0.03</td>
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<tr>
<td><strong>Abundance model</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>Intercept</td>
<td>-2.29</td>
<td>-2.893</td>
<td>-1.697</td>
<td>-</td>
</tr>
<tr>
<td>Plant length</td>
<td>0.43</td>
<td>0.323</td>
<td>0.539</td>
<td>1.00</td>
</tr>
<tr>
<td>Bare ground</td>
<td>0.17</td>
<td>0.076</td>
<td>0.271</td>
<td>1.00</td>
</tr>
<tr>
<td>Sun exposure</td>
<td>0.28</td>
<td>0.077</td>
<td>0.475</td>
<td>1.00</td>
</tr>
<tr>
<td>No. of plants 1 m</td>
<td>0.11</td>
<td>-0.021</td>
<td>0.245</td>
<td>0.72</td>
</tr>
<tr>
<td>Inclination</td>
<td>0.21</td>
<td>-0.111</td>
<td>0.534</td>
<td>0.43</td>
</tr>
<tr>
<td>No. of plants patch</td>
<td>-0.30</td>
<td>-0.845</td>
<td>0.254</td>
<td>0.29</td>
</tr>
<tr>
<td>Veg. height</td>
<td>0.05</td>
<td>-0.080</td>
<td>0.177</td>
<td>0.14</td>
</tr>
<tr>
<td>No of plants circle</td>
<td>0.20</td>
<td>-0.476</td>
<td>0.882</td>
<td>0.10</td>
</tr>
</tbody>
</table>

Estimates are standardized on 1 SD. Relative importance ($\sum w_i$) of each parameter was calculated by summing Akaike weights for the top ranked models ($\Delta_i \leq 2$) where the predictor was included.

*Aspect was a categorical variable, with the estimates referring to difference from the reference category of flat terrain.
5 Discussion

*Canthophorus impressus* was affected by habitat variables at plant and landscape level, but not at patch level. Occurrence of the bug was affected by factors on landscape level, whereas abundance was not, which is in line with what is predicted from metapopulation theory where local populations have independent dynamics and thus are not affected by factors on landscape level (Hanski & Simberloff 1997). Habitat quality as well as habitat amount were important factors for the distribution pattern of the bug, while habitat configuration (size and number of patches) had no impact.

This study showed that the local habitat preferences of *C. impressus* can be described as large host plants standing in southward facing slopes or flat terrain with a high proportion of bare ground and sun exposure. Larger host
plants affect host-specific insects positively in other studies as well (Gutiérrez et al. 1999, Menéndez & Thomas 2000, Anthes et al. 2003, Bulman et al. 2007). A reason for this finding is that large plants could be more easily discovered than smaller ones. Alternatively, large host plants could be actively selected by the bugs because of for example higher resource quantity, as large plant individuals presumably have a higher number of available fruits for the bugs to feed on. By laying eggs beneath host plants with enough resources, females of *C. impressus* ensure that the nymphs have a better chance to survive until adulthood because they avoid risks like exposure to predators connected with moving to another plant. Moreover, it might also be possible that larger host plants are older than smaller ones, as *T. alpinum* is a perennial plant. Then it might be the age of the plant that is important for the bug, rather than the size per se. However, a possible relationship between size and age of the plant remains untested but could be an interesting subject for further studies. In the present study, really large *T. alpinum* individuals (above 200 cm when summing all branches) were uncommon, suggesting that a high number of plants is required to increase the probability to find some exceptionally large. Furthermore, the habitat needs to be preferable for the plants to grow large. *Thesium alpinum* is favoured by grazing (Ekstam & Forshed 1992), although too intensive management is probably not desirable. In the present study, vegetation height per se was unimportant for occurrence and abundance of the bug, but grazing might be preferable to other management such as mowing or to lack of management because trampling of grazing animals creates spots of bare ground, which was found to be important for the bug. Bare ground might be required for effective oviposition as females of *C. impressus* probably lay the eggs on or in the ground similarly to other related species (Filippi et al. 2009). The observed preference for bare ground could also reflect the bug’s need for a warm microclimate, as the preference for high sun exposure and for host plants in southward slopes is likely to do. Many invertebrate species at the northern margins of their ranges, such as *C. impressus* in Sweden, are restricted to parts of their habitat with warmer microclimate to compensate for the cooler macroclimate (Thomas et al. 1999, Bourn & Thomas 2002).

The results further suggest that the distribution of *C. impressus* cannot solely be explained by factors on plant level, but that the bug also requires abundant host plants on a landscape level. In contrast, the patch level was not important for the distribution of the bug. Moreover, occurrence of *C. impressus* was affected by factors on landscape level, whereas abundance was not. This is consistent with patterns predicted by metapopulation theory (e.g. Hanski & Simberloff 1997, Hanski 1999). Dispersal ability limits the presence of a species at landscape scale, while the growth of
local populations is not affected by landscape factors. As the host plant of the bug lives in successional habitats the long-term regional persistence of the bug is probably dependent on metapopulation dynamics due to deterministic successional changes in habitat quality that leads to local extinctions (Harrison 1991). This notion is further supported by data from the ‘Species Gateway’, a website for collecting sightings of species in Sweden (Swedish Species Information Centre 2011), collected by amateur botanists monitoring threatened vascular plants (the so-called flora guardians; Aronsson 2007). The observations indicate highly dynamic plant populations with occasional large local interannual variation in number of plants. Sites in the province of Östergötland visited regularly specifically to count number of plants had an average coefficient of variation of 0.79 (data from years 1996-2011). Hence, turnover (appearance and disappearance) of T. alpinum patches might occur frequently and the bug’s dynamics reflects the population dynamics of its host.

However, the spatial scale at which metapopulation processes could be important for a given species depends on the dispersal ability of that species (Menéndez & Thomas 2000, Krawchuk & Taylor 2003). For C. impressus no information on dispersal distances is available, but that the intermediate patch scale was not important for the distribution of the bug in the present study could suggest that its dispersal ability is either relatively good or relatively poor with metapopulation dynamics operating at a larger or a finer spatial scale respectively. A species with high dispersal ability in relation to spacing of its habitat will be able to disperse freely among habitat patches connecting them into might be called a patchy population (Harrison 1991). Depending on the distribution of habitat in a region, it might be possible that metapopulation processes act at an even larger spatial scale, joining a set of patchy populations through occasional longer dispersals. Conversely, if the dispersal ability of a species is low, an individual host plant might be perceived as a patch in the metapopulation sense. For C. impressus, the positive effect of large host plants could be consistent with single plants as patches in a metapopulation as extinction risks of local populations decrease with increasing patch area (Hanski 1997). However, further examination of dispersal ability of the shield bug is required.

Habitat quality affected C. impressus at the plant scale, whereas habitat amount was important at the landscape scale. Several spatial scales might be important for a species because processes on different time scales and hence on different spatial scales act simultaneously. Variables at local scale reflect individual processes such as foraging behaviour or egg laying, while variables at landscape scale reflect processes connected to population dynamics (Krawchuk & Taylor 2003). To address both short-term and
long-term processes, multiscale approaches are necessary (Heenar & M'Clokey 1997, Menéndez & Thomas 2000, Krawchuk & Taylor 2003). Furthermore, a conservation strategy focused on optimizing local habitat quality might increase population sizes at the sites in focus and thus decrease extinction probability locally. However, such a strategy will not be successful in preserving the species regionally or nationally in the long-term unless it also incorporates habitat amount on a landscape scale. Anthes and colleagues (2003) came to similar conclusions for the butterfly *Euphydryas aurinia* in Germany.

To conclude, this study showed that *C. impressus* prefers large host plants in warm conditions on a plant scale and abundant host plants in a landscape scale. Patch scale was not important for the distribution of the bug. For successful conservation of *C. impressus*, management should aim to preserve sites with abundant *T. alpinum* plants and promote large host plants with low to moderate grazing or other management when grazing is not feasible (such as in road verges). Management should also be carried out to keep the sites open and sunny. The bug needs sufficient number of host plants in the landscape, which can be best achieved by ensuring that a large amount of suitable habitat for *T. alpinum* is present, i.e. a high density of mainly semi-natural grasslands should be preserved. These management advices for *C. impressus* follow the recommendations for a range of other (threatened) species, with higher species richness and density in extensively rather than intensively managed grasslands (Di Giulio et al. 2001, Söderström et al. 2001, Krueß & Tscharntke 2002). Furthermore, previous studies on semi-natural grasslands have also highlighted the importance of landscape composition in addition to local habitat quality (Di Giulio et al. 2001, Söderström et al. 2001, Thomas et al. 2001, Eriksson et al. 2002, Öckinger & Smith 2006). The results from the present study further emphasise that approaches accounting for multiple spatial scales are crucial for successful conservation of species living in fragmented habitats.

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