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RESEARCH ARTICLE

How do local habitat management and landscape structure at different spatial scales affect fritillary butterfly distribution on fragmented wetlands?

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Abstract Habitat fragmentation, patch quality and landscape structure are important predictors for species richness. However, conservation strategies targeting single species mainly focus on habitat patches and neglect possible effects of the surrounding landscape. This project assesses the impact of management, habitat fragmentation and landscape structure at different spatial scales on the distribution of three endangered butterfly species, *Boloria selene*, *Boloria titania* and *Brenthis ino*. We selected 36 study sites in the Swiss Alps differing in (1) the proportion of suitable habitat (i.e., wetlands); (2) the proportion of potential dispersal barriers (forest) in the surrounding landscape; (3) altitude; (4) habitat area and (5) management (mowing versus grazing). Three surveys per study site were conducted during the adult flight period to estimate occurrence and density of each species. For the best disperser *B. selene* the probability of occurrence was positively related to increasing proportion of wetland on a large spatial scale (radius: 4,000 m), for the medium disperser *B. ino* on an intermediate spatial scale

(2,000 m) and for the poorest disperser *B. titania* on a small spatial scale (1,000 m). Nearby forest did not negatively affect butterfly species distribution but instead enhanced the probability of occurrence and the population density of *B. titania*. The fen-specialist *B. selene* had a higher probability of occurrence and higher population densities on grazed compared to mown fens. The altitude of the habitat patches affected the occurrence of the three species and increasing habitat area enhanced the probability of occurrence of *B. selene* and *B. ino*. We conclude that, the surrounding landscape is of relevance for species distribution, but management and habitat fragmentation are often more important. We suggest that butterfly conservation should not focus only on a patch scale, but also on a landscape scale, taking into account species-specific dispersal abilities.

Keywords Connectivity · Detectability · Dispersal · Fens · Habitat quality · Landscape context · Metapopulations · Population density · Switzerland

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Introduction

Fragmentation, habitat loss and deterioration of habitat quality are major threats to biodiversity and increase the risk of species extinction (Debinski and Holt 2000). Because many species persist as metapopulations in isolated, well-defined habitat patches (Hanski 1999), the protection of these habitat patches

is a main focus in conservation biology (e.g., Haight et al. 2002). Metapopulation approaches consider the patch matrix uniform and hostile and account only for patch connectivity. But, other spatial effects are neglected (Hanski 1999). However, many ecological processes occur at spatial scales larger than the patch scale (Steffan-Dewenter et al. 2002). Species distribution should therefore not only relate to habitat-specific characteristics such as habitat area and quality but also on the surrounding landscape at different spatial scales.

Species-specific responses at different spatial landscape scales are little understood for insects (but see Roland and Taylor 1997), but landscape effects on insect community responses have been reported (e.g., Weibull et al. 2000; Aauri and de Lucio 2001; Steffan-Dewenter et al. 2002; Krauss et al. 2003; Clough et al. 2005; Thies et al. 2005; Öckinger and Smith 2006). One predictor for single species distribution is the amount of available habitat in the surrounding landscape (e.g., Heikkinen et al. 2004; Binzenhöfer et al. 2005), which is usually correlated with isolation and connectivity measurements used in metapopulation studies (Winfree et al. 2005). Another landscape predictor, important for species distribution is the amount of potential dispersal barriers (van Dyck and Baguette 2005), but studies testing the effects of dispersal barriers in multiple landscapes are lacking. Apart from the surrounding landscape, habitat patch-specific characteristics are important for the colonisation and survival of species (Hanski 1999; Thomas et al. 2001). Habitat area (Connor et al. 2000; Krauss et al. 2004, 2005), habitat quality (Thomas et al. 2001) and altitude (Boggs and Murphy 1997; Wettstein and Schmid 1999) affect the distribution of species. Management strategies can be applied to enhance habitat quality and can be actively controlled and adapted to match particular target species requirements (Pöyry et al. 2005; Johst et al. 2006). Management therefore plays a key role in conservation practice. However, management concepts on landscape scales are only starting to develop and require further landscape-scale field studies (Moilanen et al. 2005).

Wetlands in central Europe harbour a high number of endangered and rare species and are of high importance for species conservation (BUWAL 2002). In recent decades, Switzerland has seen a massive reduction of wetlands to only 10% of their former areas (BUWAL 1990). A Swiss citizens' initiative in

1989 (Rothenurm Initiative) protected the remaining wetlands and prevented further habitat and species loss. Semi-natural fens depend on regular management such as late season mowing or low impact cattle grazing. Conservation strategies involving the broader surrounding landscape do not exist; however, agriculture and forestry occurring adjacent to fens are restricted to low intensity management without fertiliser application (BUWAL 2002).

Butterflies are adequate indicators of change for many terrestrial insect groups (Thomas 2005, but see Vessby et al. 2002) and often occur in metapopulations (Hanski 1999). Several wetland specialised butterfly species occur only in distinct wetland patches in the northern Swiss Alps (Lepidoptera Specialist Group 1991). We hypothesised that these species perceive forest as a barrier, as butterflies inhabiting open habitats change their flight direction, when they encounter forest borders (Cant et al. 2005). We further hypothesise that more mobile species react to the surrounding landscape at larger spatial scales than more sedentary species (Roland and Taylor 1997).

We analysed the distribution of the three butterfly species *Boloria selene*, *Boloria titania* and *Brenthis ino* in 36 distinct wetland patches in different landscapes. We investigated the effects of landscape structure, altitude, habitat area, and management on occurrence and density of the three species. In particular, we addressed the following questions: (1) Does increased proportion of wetlands in the surrounding landscape increase the probability of occurrence and population density? (2) Does increased proportion of forest in the surrounding landscape decrease the probability of occurrence and population density? (3) Are species related to landscape composition at different spatial scales according to their dispersal ability? (4) Is grazing or mowing more suitable for the conservation of wetland-specialised butterflies? (5) How do habitat area and altitude affect the distribution of the three butterfly species?

Materials and methods

Study region and study sites

The study region (3,900 km²) is located in the Swiss Alps and Pre-Alps in the cantons of St. Gallen,

Schwyz, Glarus and Appenzell (Fig. 1). This landscape is dominated by arable land and grassland (53.4%) and by forest (28.0%). Mountains with bare rocks (7.0%), settlements (5.5%), lakes and rivers (4.8%) and wetlands (1.3%) cover smaller proportions of the region. Several high mountains of up to 2,500 m a.s.l. exist in the region. The 36 selected wetland study sites are montane calcareous fen meadow communities of the *Caricion davallianae* alliance (Wettstein and Schmid 1999; Peintinger et al. 2003). The selection of these study sites was stratified into two management practices (mowing versus grazing) equally distributed along an altitudinal gradient from 800 to 1,400 m a.s.l. to reduce correlations between these two predictor variables (Peintinger et al. 2003). Within the two management strategies and the altitudinal gradient, study sites were randomly chosen out of the Swiss wetland inventory, comprising more than 300 sites within the study region (BUWAL 1990).

Landscape analyses were conducted using “ArcGIS 9.0” (ESRI) and 1:25,000 landscape map, provided by the Swiss Federal Office of Topography (Swisstopo). The map contained “surface area objects”, which we grouped into five categories: (1) forests—tree nursery, debris in forest, debris in open forest, swamp in forest, swamp in open forest, open forest, and forest; (2) waters—river, and lake; (3) rocks—rock, debris on glacier, debris, glacier, gravel pit, clay pit, and quarry; (4) settlements—settlement, concrete dam, and embankment dam; (5) others—shrubs, debris and shrubs, grass tracks, dirt tracks, vines, swamp and shrubs, swamp, and arable land. We added a sixth category containing all wetlands (fens and bogs). The digital map of the wetlands was provided by the Swiss Federal Institute for Forest, Snow and Landscape Research (WSL).

Landscape analyses were conducted for different nested spatial scales around the centre of each study site (radii of 500 m, 1,000 m, 2,000 m, 3,000 m, 4,000 m). The spatial scales were chosen to cover the assumed dispersal range of the three study species. For each surrounding landscape scale, proportion of wetland (category 6), which is the habitat of the three fritillary butterfly species, and proportion of forest (category 1), which is a potential dispersal barrier, were chosen as predictor variables. Further potential dispersal barriers like rocks (category 3), lakes (category 2) and settlements (category 4) have very

low area coverage within the landscapes studied, and did not substantially change the results when added to the proportion of forest. Therefore, only proportion of forest was considered as a potential dispersal barrier for butterflies. The proportion of forest at the 500 m scale was correlated with the proportion of forest adjacent to (surrounding) the fen border (Spearman: $N = 36$; $r = 0.63$; $P < 0.001$). Similarly, the proportion of wetland ($\log_{10} + 1$ -transformed) at the 500 m scale was correlated with the distance to the next wetland (\log_{10} -transformed) (Spearman: $N = 36$; $r = -0.70$; $P < 0.001$). In both cases the landscape predictors were chosen as main predictor variables. For calculations of proportion of wetland within a landscape, the area of the study site was always subtracted from the landscape area to achieve independence of the two predictor variables habitat area and proportion of wetland. Further connectivity measurements were not tested, as they are inappropriate for very high proportions of nearby habitat (see Fig. 1b) and they are generally correlated with each other (Krauss et al. 2003; Winfree et al. 2005).

We measured altitude during transects with a GPS (Garmin eTrex Legend) and calculated mean altitudes for each study site. To calculate the habitat area, patches ≤ 35 m apart on the electronic map were assumed to be one patch. This distance was not set a priori but resulted from a compromise between the imprecise digital maps on this scale and the reality of patch borders in the field. Setting a critical distance at 50 or 100 m instead of 35 m resulted essentially in the same patch areas (Spearman: $0.958 \leq r \leq 0.990$; all P -values < 0.001), and in similar overall results.

Twenty of the chosen fens were managed by late-season mowing (once a year after the 1st of September), while 16 were cattle-grazed. A fen was defined as grazed, if livestock or livestock tracks were detected at least once during the site visits. Although the management history of previous years is unknown, recent management changes are unlikely (Wettstein and Schmid 1999). The proportion of plants in flower per study site was recorded during butterfly surveys by visual estimation of the area covered by flowering plants along the butterfly transect. This proportion of plants in flower pooled for the three surveys was significantly higher on mown compared to grazed fens (GLM: $F_{1,35} = 4.15$; $P = 0.049$).

Arithmetic means \pm standard errors, minima and maxima of the patch characteristics are presented in

Fig. 1 (a) The study region is located in the north-eastern part of Switzerland (small map; top left) in the cantons St. Gallen, Appenzell, Glarus and Schwyz. The location of each of the 36 fens is shown by white dots. (b) Example of one study site (shown by the arrow) with a high proportion of wetland in the surrounding landscape. (c) Example of one study site (arrow) with a low proportion of wetland in the surrounding landscape. Radii of 500, 1,000 and 2,000 m that were used in the landscape analyses are shown by circles in (b) and (c). black = wetlands; grey = forests; pale grey = other habitats; white outlined = lakes

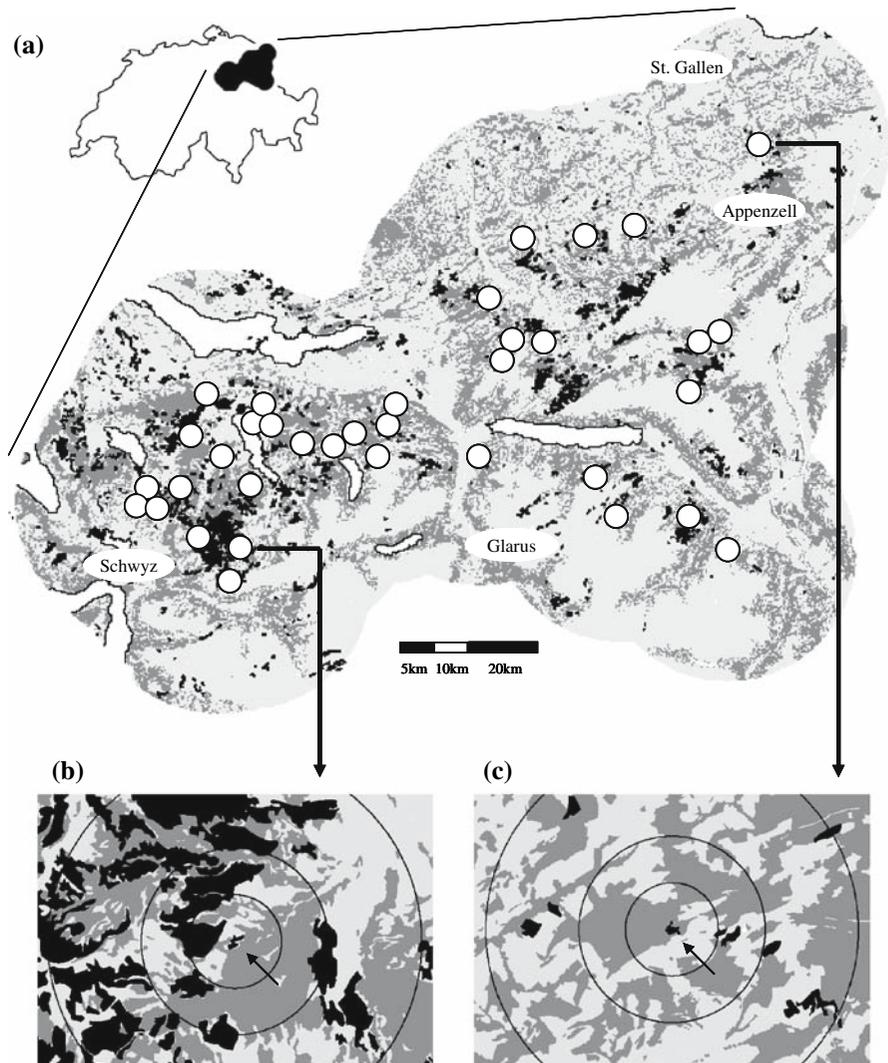


Table 1. None of the five main predictor variables (1) proportion of wetland, (2) proportion of forest, (3) altitude, (4) habitat area and (5) management were significantly intercorrelated and all correlation coefficients were smaller than 0.3 (Table 2), reducing the common problem of multi-collinearity between predictor variables (Graham 2003).

Study species

The Small Pearl-bordered Fritillary *B. selene* (Dennis and Schiffermüller), the Titania's Fritillary *B. titania* (Esper) and the Lesser Marbled Fritillary *B. ino* (Rottemburg) typically inhabit wetlands in the

montane and subalpine region of the northern Swiss Alps (Lepidoptera Specialist Group 1991). All three species occur regularly on fens, but they show different degrees of specialisation. *Boloria selene* is a characteristic fen inhabitant and its main larval food plants are March Violet *Viola palustris* and Heath Violet *V. canina*. *Boloria titania* prefers tree-rich wetlands or wetlands with nearby forest and its larvae feed on Common Bistort *Polygonum bistorta* and several *Viola* species. *Brenthis ino* prefers fens but may also occur on extensively used meadows; its larvae feed on multiple Rosaceae plant species, preferably Meadowsweet *Filipendula ulmaria*, but Great Burnet *Sanguisorba officinalis* and Marsh Cinquefoil *Potentilla palustris* can also be used

Table 1 Characteristics of 36 fen study sites located in the northern Swiss Alps

	Mean	SE	Min.	Max.
Wetland (500 m scale) in %	4.7	1.2	0.0	27.1
Wetland (4000 m scale) in %	4.8	0.7	0.3	19.9
Distance to next wetland in m	420	80	35–100	2560
Forest (500 m scale) in %	46.3	2.7	1.1	76.2
Forest (4000 m scale) in %	37.1	1.3	21.0	52.6
Adjacent (surrounding) forest in %	57.5	3.6	0	100
Altitude in m a.s.l.	1090	30	800	1410
Habitat area in ha	7.5	1.0	0.9	22.3
Plants in flower in % (grazed)	17.9	2.2	7	43
Plants in flower in % (mown)	31.6	3.6	7	68

Table 2 Spearman's correlation coefficients (r) among transformed predictor variables of the 36 study sites (* $P < 0.05$; (*) $P < 0.1$; ns = not significant)

	Wetland (4000 m)	Forest (500 m)	Forest (4000 m)	Altitude	Habitat area	Management
Wetland (500 m)	0.349*	−0.231 ns	0.055 ns	0.147 ns	0.069 ns	−0.094 ns
Wetland (4000 m)		0.027 ns	0.143 ns	0.123 ns	0.240 ns	0.011 ns
Forest (500 m)			0.226 ns	0.265 ns	0.013 ns	0.059 ns
Forest (4000 m)				0.020 ns	0.307(*)	0.307(*)
Altitude					0.065 ns	0.253 ns
Habitat area						0.199 ns

(Ebert and Rennwald 1991; Lepidoptera Specialist Group 1991). All larval food plants were common in our 36 study sites, but were not detected quantitatively in a parallel plant community study due to their low visibility on fens during the survey period in June–August (Peintinger, pers. comm.). The adults of all three butterfly species feed on a broad spectrum of flowering plant species, many of which are available on fens (Ebert and Rennwald 1991; Lepidoptera Specialist Group 1991). The three fritillary species occur in Switzerland up to about 2,000 m a.s.l., but *B. titania* is not found below 800 m a.s.l. while the other two species can occur at low altitudes. In our study sites all three butterfly species were univoltine. Finnish butterfly experts rank *B. selene* and *B. ino* as better dispersers than *B. titania* in questionnaire evaluations (Komonen et al. 2004), and Dutch and German experts assume that *B. selene* is a better disperser than *B. ino* (Bink 1992; Weidemann 1995). All three fritillary butterfly species are listed as endangered species in the red data book of Switzerland (BUWAL 1994).

Data collection

In summer 2005, all 36 study sites were surveyed for butterflies three times: 16 June–28 June, 3 July–20 July and 21 July–9 August. The relatively small time span of each survey period allowed minimal bias in butterfly distribution due to phenology. Surveys within each period were arranged to minimise travel distance and to maximise treatment combinations visited in one day. Within sites, random transects were walked for 20 min in the 13 sites, <3 ha, for 40 min in the 12 sites, 3–10 ha and for 60 min in the 11 sites, >10 ha. This assured a similar habitat area corrected probability of occurrence for each species (Krauss et al. 2003). Butterflies were recorded within a 5 m corridor, within which the detectability of the three similar species was assumed to be constant. The observer walked at a pace of ~ 2.5 km/h. The average length of each transect per study site was 820 ± 240 m for the 20 min counts, $1,800 \pm 540$ m for the 40 min counts and $2,630 \pm 730$ m for the 60 min counts. On sites <3 ha all fritillary butterflies

counted were caught and released at the end of the survey to avoid repeated counting of the same individuals. Double counts are much less likely to occur on large patches where the proportion of sampled area is lower compared to small patches.

Butterfly surveys were conducted only in appropriate weather conditions that promoted butterfly activity (temperature: $>17^{\circ}\text{C}$, wind: <3 Beaufort scale, no complete cloud cover) and at appropriate times of the day (10.00–17.00) as proposed by Pollard (1977). Temperature (Mean \pm SE: $32 \pm 1^{\circ}\text{C}$, Min: 24°C , Max: 36°C) and estimated percent sunshine (Mean \pm SE: $82 \pm 3\%$, Min: 48% , Max: 100%) during surveys in our study did not correlate with the population densities of the three butterfly species (all $P > 0.33$), which indicate that butterfly observations were not biased by weather-related variation.

Statistical analyses

The statistical analyses were performed using the software R 2.2.0 for Windows (R Development Core Team 2004). Population density of the three butterfly species was \log_{10} -transformed to meet the assumptions of normality and homoscedasticity. To increase linearity of relationships habitat area was \log_{10} -transformed and proportion of wetland was $\log_{10} + 1$ -transformed. Even though we surveyed 36 study sites, which is a relatively high replicate number in landscape studies we have a low overall power to detect strong significances. Therefore, we also consider marginally significant effects with $P \leq 0.1$ as ecological meaningful.

Occurrence data (presence versus absence) was analysed for the 36 study sites, whereas population densities were only considered for fens where a species occurred. Species were assumed to inhabit a study site if at least one individual was encountered in one of the three surveys. The length of each transect was measured with a portable GPS (Garmin eTrex Legend) and this measure was subsequently used to estimate densities expressed as individuals/ha for each species and study site. Population density of each species was summed up over the three surveys.

In pre-analyses the spatial structure of occurrence and density data of the three butterfly species was tested using Mantel test statistics based on Spearman's rank correlation with 1,000 permutations and

euclidian distances as similarity indices (Legendre and Legendre 1998). The occurrence of *B. selene* ($r = 0.130$; $P = 0.018$) and *B. ino* ($r = 0.177$; $P = 0.032$) and the density of *B. selene* ($r = 0.225$; $P = 0.023$) were spatially structured, but not the occurrence of *B. titania* ($r = 0.013$; $P = 0.310$) and densities of *B. ino* ($r = 0.034$; $P = 0.293$) and *B. titania* ($r = 0.003$; $P = 0.471$). Where the response variables were spatially structured, the predictor variable proportion of wetland was spatially structured too (all $P \leq 0.014$). Therefore, the models indirectly account for the spatial structure of the response variables, as proportion of wetland is a predictor. All other predictor variables were not spatially structured for the 36 study sites (all $P \geq 0.13$).

In further pre-analyses we estimated the detectability of the three study species separately on our study sites using the free software Presence ver 2.0 (<http://www.mbr-pwrc.usgs.gov/software/doc/presence/presence.html>) that implements the MacKenzie et al. (2002) model. AIC model selection showed that the best model for all three species was one with survey-specific detection probabilities. The estimated proportion of sites occupied did not differ substantially from our naive estimate of occupied patches without correction for detectability. *Boloria selene* had the lowest detectability (ranging from 20 to 78%, depending on the survey). The analysis suggested that the species was detected at 94.9% of the occupied patches. For *B. ino*, detectability ranged from 68 to 90% and the species was detected at 99.4% of the occupied patches. For *B. titania*, detectability ranged from 61 to 95% and the species was detected at 99.7% of the occupied patches. Therefore the detectability of the three species on our study sites was similar and almost all occupied patches were correctly identified as such. Thus, in our study imperfect detectability does not have to be accounted for in the statistical analyses.

We started the statistical analyses with single factor tests for the predictor variables with the response variables “butterfly occurrence” and “density”. Like in other studies autocorrelations among nested radii for landscape predictors are frequent and only the landscape scale showing the highest explanatory power was used in multi-factor models (following suggestions by Steffan-Dewenter et al. 2002). In a next step the predictors that showed at least marginal significances ($P \leq 0.1$) in single factor

analyses entered a multi-factor model with sequential (Type 1 SS) and adjusted (Type 2 SS) sums of squares, using generalised linear models (binomial) for occurrence data and general linear models for population density data (Crawley 2002). We only present adjusted sums of squares of multi-factor models, as sequential sums of squares with predictors in the first position showed results very similar to the results from single factor analyses. We also tested one-way interactions and squared altitude as predictors, but these predictors did not improve multi-factor models and are not presented.

Finally we conducted hierarchical partitioning analyses to estimate the relative importance of the five main predictor variables. Hereby the explained variance/deviance in multi-factor models is split into independent contributions of each predictor variable and thus allowed judging of the relative importance of each predictor variable. Hierarchical partitioning models are independent of significances (Mac Nally and Walsh 2004; Heikkinen et al. 2005).

Results

A total of 1,599 butterfly individuals of the three species *B. selene* ($n = 233$), *B. titania* ($n = 477$) and *B. ino* ($n = 889$) were recorded on the 36 wetland sites studied. *Boloria selene* and *B. titania* each occurred on 23 sites and *B. ino* occurred on 32 sites. Population densities (individuals/ha) of 12.85 ± 2.91 (range 0.76–67.90) for *B. selene*, of 30.50 ± 4.24 (range 2.04–109.30) for *B. ino* and of 25.35 ± 3.81 (range 3.05–71.84) for *B. titania* were recorded, which are presented here as sums of the three surveys per study site.

Occurrence

The occurrence of each of the three fritillary butterflies was predicted by the landscape surrounding the study sites. An increasing proportion of wetland positively affected the probability of occurrence for all three fritillary butterfly species, but the spatial scale at which butterfly occurrence was affected varied considerably among species (Table 3). The probability of occurrence of *B. selene* was best predicted at a large spatial scale of 4,000 m (Fig. 2a and b). The probability of occurrence of *B. ino*

peaked at a medium scale of 2,000 m (Fig. 2c and d) and *B. titania* at a small spatial scale of 1,000 m (Fig. 2e and f). Proportion of forest did not significantly affect *B. selene* or *B. ino* occurrence at any spatial scale. However, the probability of occurrence of *B. titania* increased with increasing proportion of forest at almost all spatial scales, peaking at a scale of 500 m (Table 3, Fig. 2g and h). Proportion of forest adjacent to (surrounding) the fen borders was an even better predictor for *B. titania* occurrence ($N = 36$; $\chi^2_1 = 13.31$; $P < 0.001$; $M_F = 28.3\%$).

Patch-specific predictors (altitude, area, management) significantly affected the occurrence of the three fritillary butterflies. The probabilities of occurrence of *B. selene* and *B. ino* were positively related to increasing habitat area, whereas *B. titania* was not significantly related to habitat area. Altitude significantly affected the occurrence of all three species with probabilities of occurrence of *B. selene* and *B. titania* increasing, and the probability of occurrence of *B. ino* decreasing with increasing altitude (Table 3). We recorded *B. selene* at all sites above 1,200 m a.s.l. but the probability to encounter *B. ino* sharply declined above 1,200 m a.s.l. to less than 40% at 1,400 m a.s.l.; *B. titania* was found at all but one study site above 1,100 m a.s.l.

Different management regimes grazing and mowing affected only the probability of occurrence of *B. selene*. Grazed fens had a significantly lower proportion of plants in flower (see methods), but a higher probability of occurrence of *B. selene* than did mown fens (Table 3, Fig. 3a). *Brenthis ino* and *B. titania* were not significantly affected by the two different management strategies.

Population density

The density of the three butterfly species was affected differently by proportion of wetland and proportion of forest. An increasing proportion of wetland at a large spatial scale of 3,000 m affected the density of *B. selene* negatively (Fig. 4a and b), whereas *B. ino* and *B. titania* were not significantly affected by proportion of wetland at any spatial scale (Table 3). Similar to the occurrence pattern, an increasing proportion of forest was positively related to density of *B. titania* at the smallest scale of 500 m (Fig. 4c and d), whereas no significant effects of proportion of forest on densities of *B. selene* and

Table 3 Generalised and general linear models on significant habitat and landscape predictors for occurrence and density of the three butterfly species *B. selene*, *B. titania* and *B. ino*

	Single factor analyses			Multi-factor analyses		
	Test-statistic	<i>P</i>	<i>M_F</i> (%)	Test-statistic	<i>P</i>	<i>M_M</i> (%)
Occurrence						
<i>B. selene</i> (<i>N</i> = 36)						
Wetland (4000 m)	$\chi^2_1 = 4.07$	0.044	8.6	$\chi^2_1 = 2.09$	0.148	–
Altitude	$\chi^2_1 = 6.76$	0.009	14.4	$\chi^2_1 = 3.33$	0.068	–
Habitat area	$\chi^2_1 = 3.39$	0.066	7.2	$\chi^2_1 = 2.79$	0.095	–
Management	$\chi^2_1 = 12.69$	<0.001	26.9	$\chi^2_1 = 10.84$	<0.001	–
Model						49.1
<i>B. ino</i> (<i>N</i> = 36)						
Wetland (2000 m)	$\chi^2_1 = 3.60$	0.058	14.3	$\chi^2_1 = 2.79$	0.095	–
Altitude	$\chi^2_1 = 7.43$	0.006	29.6	$\chi^2_1 = 11.84$	<0.001	–
Habitat area	$\chi^2_1 = 5.82$	0.016	23.3	$\chi^2_1 = 6.52$	0.011	–
Model						80.0
<i>B. titania</i> (<i>N</i> = 36)						
Wetland (1000 m)	$\chi^2_1 = 3.34$	0.067	7.1	$\chi^2_1 = 1.73$	0.188	–
Forest (500 m)	$\chi^2_1 = 5.90$	0.015	12.5	$\chi^2_1 = 3.26$	0.071	–
Altitude	$\chi^2_1 = 22.18$	<0.001	47.1	$\chi^2_1 = 13.40$	<0.001	–
Model						54.9
Density						
<i>B. selene</i> (<i>N</i> = 23)						
Wetland (3000 m)	$F_{1,21} = 5.84$	0.025	21.8	$F_{1,20} = 3.88$	0.062	–
Management	$F_{1,21} = 4.88$	0.038	18.9	$F_{1,20} = 2.20$	0.153	–
Model						30.1
<i>B. ino</i> (<i>N</i> = 32)						
Forest (500 m)	$F_{1,30} = 2.87$	0.101	8.7	–	–	–
<i>B. titania</i> (<i>N</i> = 23)						
Forest (500 m)	$F_{1,21} = 5.93$	0.024	22.0	–	–	–

Test-statistics (χ^2 or *F*) with degrees of freedom and significances (*P*) for single factor analyses and multi-factor models with adjusted Sums of Squares (see Materials and methods). *M_F* = the percentage of deviance (occurrence) or the percentage of the variance (density) explained by each predictor separately and *M_M* = the percentage of deviance (occurrence) or the percentage of variance (density) explained by the model in total

B. ino were found (Table 3). Neither habitat area nor altitude affected the density of any of the three butterfly species significantly. The density of *B. selene* was higher on grazed fens compared to mown fens (Fig. 3b), whereas the two different management strategies showed no significant effect on the densities of *B. ino* and *B. titania* (Table 3).

Multi-factor models

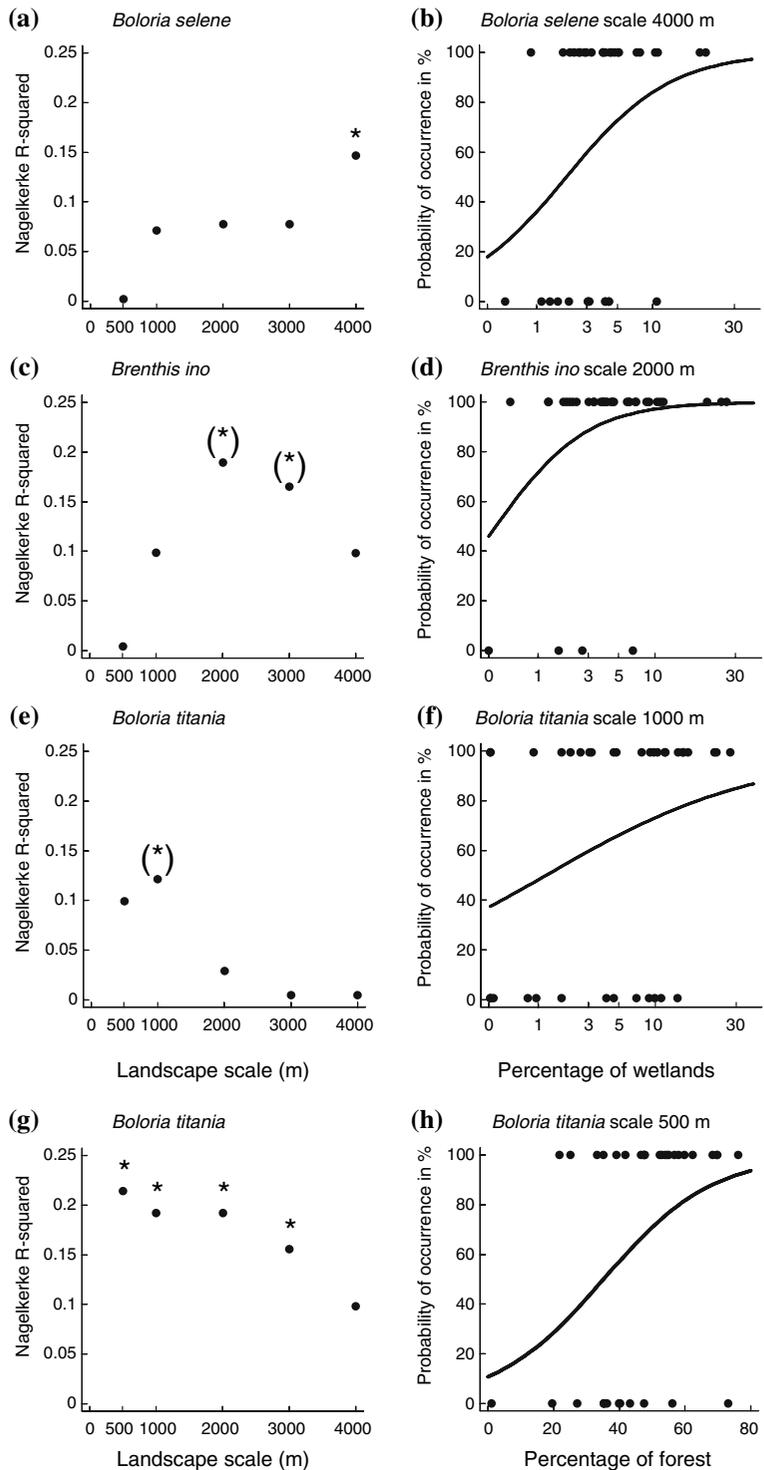
Single factor and sequential multi-factor models (Type 1 SS) with predictors in the first position

showed very similar results. Adjusted sums of squares (Type 2 SS) multi-factor models showed more differences and some predictors even became non-significant when corrected for all other significant predictor variables (Table 3).

Hierarchical partitioning

The hierarchical partitioning models, which are independent from significant levels, revealed the relative importance of all predictor variables in full multi-factor models. The independent effects of the

Fig. 2 Butterfly occurrence is affected by the surrounding landscape at different spatial scales between 500 and 4,000 m. Nagelkerke R^2 of simple logistic regressions for different spatial scales are shown for proportion of wetland (a, c, e) and proportion of forest (g). *B. selene* reacted strongest at a large spatial scale *B. ino* at a medium spatial scale and *B. titania* at a small spatial scale. Simple logistic regression plots are shown for the spatial scale showing the highest R^2 values (b, d, f, h). * P -values ≤ 0.05 ; (*) P -values ≤ 0.1



two landscape predictors in the occurrence models explain together 17.4% for *B. selene*, 25.0% for *B. ino* and 28.9% for *B. titania*, and in the

population density models they explain 50.3% for *B. selene*, 64.7% for *B. ino* and 83.1% for *B. titania* (Fig. 5).

Fig. 3 Mean (\pm SE) for (a) the probability of occurrence and (b) population density of the butterfly species *B. selene* predicted by management (grazed versus mown)

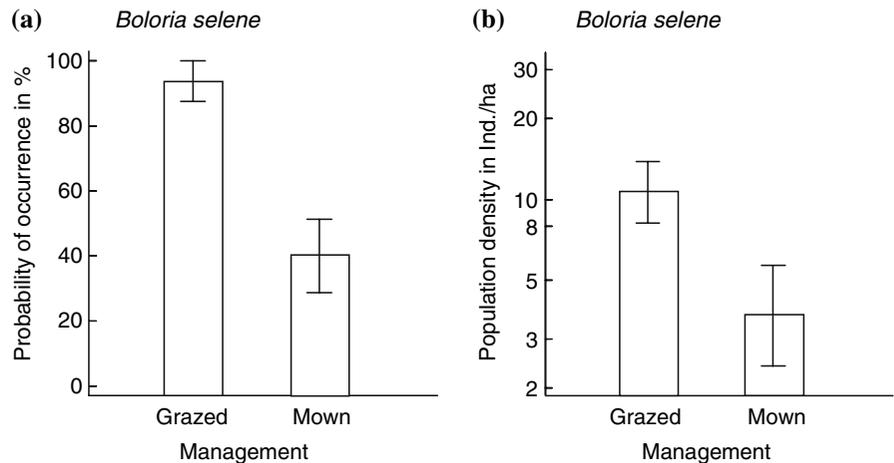
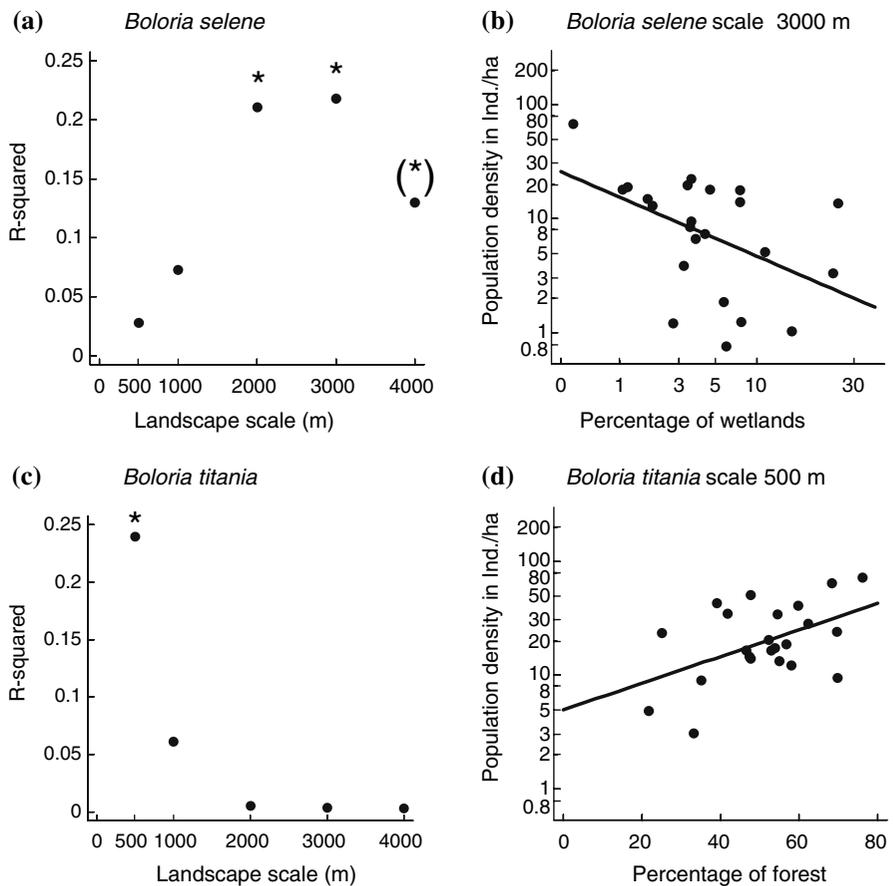


Fig. 4 Butterfly density is affected by the surrounding landscape at different spatial scales between 500 and 4,000 m. R^2 for simple regressions for different spatial scales are shown for proportion of wetland (a) and proportion of forest (c). Simple linear regression plots are shown for the spatial scale showing the highest R^2 value (b, d). * P -values ≤ 0.05 ; (*) P -values ≤ 0.1



Discussion

Our results showed that proportion of wetland and proportion of forest in the surrounding landscape, affected fritillary butterfly occurrence and density at

different spatial scales. Together, they explained an average of 66 and 24% of the variance in population density and occurrence, respectively. Patch-specific factors, such as altitude, habitat area and management were together more important explaining an average

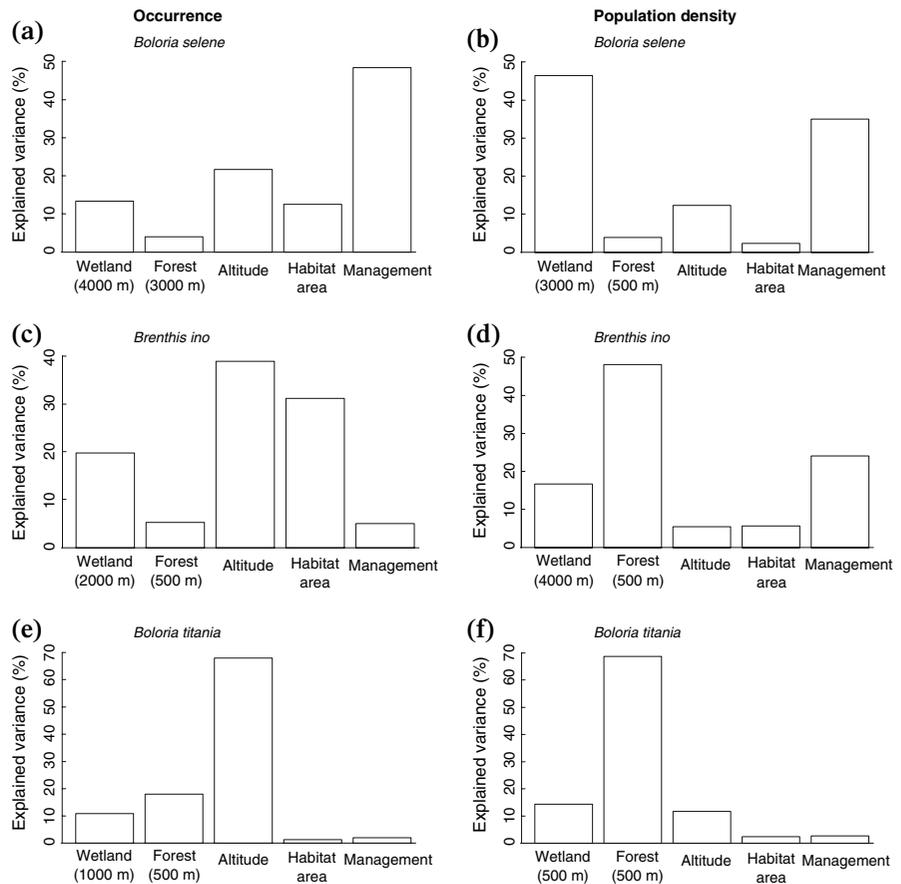
of 34 and 76% of the variance in population density and occurrence, respectively. It is surprising that the relative importance of landscape factors were less important for occurrence patterns than local patch-specific factors, even though landscape factors often affect dispersal (and hence colonisation and occurrence). In contrast landscape factors affected population density patterns strongly, even though population densities often correlate with habitat quality (Thomas et al. 2001). Under which circumstances habitat requirements outside edge-defined habitat patches are responsible for occurrence and density patterns need further investigations (Dennis et al. 2003).

Landscape effects and habitat fragmentation

In agreement with other studies, the presence of additional habitat patches in the surrounding landscape increased the probability of occurrence of

butterfly species (Wettstein and Schmid 1999; Binzenhöfer et al. 2005). However, in our study the three butterfly species reacted to the surrounding landscape at different spatial landscape scales indicating species-specific differences in dispersal ability. Experts rank *B. selene* and *B. ino* as better dispersers than *B. titania*, and *B. selene* as a better disperser than *B. ino* (Bink 1992; Weidemann 1995; Komonen et al. 2004). This is consistent with our results, where the best disperser *B. selene* reacted at the largest spatial scale, the medium disperser *B. ino* at a medium scale and the poorest disperser *B. titania* at a small spatial scale. As the effects of proportion of wetland on species distribution is at the significance level for all three species, further studies are necessary to support this scale dependency. Scale-dependent effects of the landscape structure have also been shown for whole insect communities (Weibull et al. 2000; Steffan-Dewenter et al. 2002; Krauss et al. 2003; Thies et al. 2005; Clough et al. 2005). In some studies the scale dependence of species groups was even linked with

Fig. 5 Relative importance of the five predictor variables (independent effects) estimated from hierarchical partitioning models for occurrence and population density of the three butterfly species *B. selene*, *B. titania* and *B. ino*. The explained variance shows the relative independent contribution of each predictor to the variance/deviance explained by the multi-factor model with all predictors



the dispersal ability of these species groups, assuming that better dispersers react at larger spatial scales (Steffan-Dewenter et al. 2002; Thies et al. 2005). Scale dependence for single species is less well known but was linked to estimated species-specific dispersal ability for parasitoids (Roland and Taylor 1997). As species with good dispersal ability should be able to cope better with poor landscape connectivity than poor dispersers (Kareiva and Wennergren 1995), conservation strategies aiming to increase connectivity should focus on the poorest disperser *B. titania*.

In contrast to the enhanced probability of occurrence of *B. selene* with increasing proportion of wetland, the density of *B. selene* decreased with increasing proportion of wetland. Studies presenting density–area relationships for insects show positive, negative, non-linear or non-significant relationships (Connor et al. 2000; Debinski and Holt 2000; Hambäck and Englund 2005), with population densities of species being variable through time and being dependent on landscape and species-specific factors (Matter 2003; Hambäck et al. 2007). Apart from stochastic reasons, two explanations for increasing population densities with decreasing proportion of habitats are plausible, even though more are conceivable. One possibility is crowding due to habitat loss in the past forcing individuals to move to the (few) remaining habitat patches (Debinski and Holt 2000). However, with no substantial loss of wetlands in our study region within the last 20 years (BUWAL 2002), crowding is not probable. A second explanation is that butterflies tend to have negative density–area relationships because of their largely visual searching behaviour resulting in perimeter-related instead of area-related migration rates (Hambäck and Englund 2005; Hambäck et al. 2007).

Apart from landscape analyses focusing on habitats in the surrounding landscape we assumed that forests might act as dispersal barriers. Several studies show that butterflies specialised in open habitats perceive forest as a dispersal barrier (Matter et al. 2004; Cant et al. 2005). We found no such evidence for forest to act as a dispersal barrier on any spatial scale, starting from a patch scale (adjacent forest surrounding the fen border) to a landscape scale (proportion of forest) between 500 and 4,000 m radius. A possible explanation might be that individuals experience high forest coverage—about 1/3 of

the study region was covered by forests—not as a barrier, but cross it in search of other suitable habitat patches. Whether individuals of the three fritillary species cross the forest following corridors (Haddad et al. 2003) or whether they fly over or around the forest is not known. Instead of representing barriers to dispersal that could limit butterfly occurrence, nearby forests even enhanced the probability of occurrence and population density of *B. titania*. This is in line with the habitat requirement of *B. titania* in Finland (Paukkunen et al. 1999) and Switzerland, where *B. titania* is described as a specialist of tree-rich wetlands (Lepidoptera Specialists Group 1991). For this species forest borders are an important habitat requirement as demonstrated by observations, which describe that *B. titania* females lay their eggs only in close proximity to forest borders, especially close to the spruce trees *Picea abies* (Ebert 2005). This emphasises the need to consider the distribution of species also at the patch border and in the patch surrounding landscape and not only within strictly defined habitat patches. Some butterfly species have further requirements outside edge-defined habitat sites like shelter and roosting places (Dennis et al. 2003). That habitat patch size did not significantly affect the probability of occurrence of *B. titania* in our study might be caused by the inappropriate definition of habitat and consequently of habitat size of this species. Habitat patch size is usually a good predictor for the occurrence of butterfly species showing an increased probability of occurrence with increasing habitat patch size (Krauss et al. 2004, 2005), like it was found in our study for *B. selene* and *B. ino*.

Management and altitude

Another important habitat characteristic for species distribution is the quality of a habitat patch (Thomas et al. 2001), which can be improved by species-specific management strategies (Johst et al. 2006). One aspect of habitat quality is the proportion of plants in flower, which act as the main food resource for adult butterflies (Ebert and Rennwald 1991). Case studies show that increasing proportion of plants in flower increase butterfly densities and the probability of occurrence (e.g., Quinn et al. 1998; Krauss et al. 2003). Our results show that although grazed fens had

a significantly lower coverage of plants in flower than mown fens, none of the three butterfly species showed a reduced probability of occurrence or lower densities on grazed fens. Instead, *B. selene* showed a higher probability of occurrence and higher densities on grazed fens than on mown fens. As the management strategy could not be linked to the presence of larval food plants (Peintinger, pers. comm.), the positive relationship between *B. selene* and grazing is difficult to explain. Mowing has been shown to negatively affect mean leaf area and the length of the leaf stalk of *Viola palustris* (Jensen and Meyer 2001), the main larval food plant of *B. selene*. As larvae mostly feed on leaves and stems, mowing may negatively affect the life cycle of *B. selene*, whereas grazing might be less destructive for *V. palustris* and consequently *B. selene* larvae. However, both management strategies are important for wetland conservation because they prevent plant succession into forests, and are suitable to protect wetland-specialised species (Wettstein and Schmid 1999). Apart from management strategies, we have shown the importance to consider species distribution along an altitudinal gradient, since altitude generally affects species distribution (Wettstein and Schmid 1999; Konvicka et al. 2003). *Boloria selene* and *B. tiania* had a higher probability of occurrence, and *B. ino* a lower probability of occurrence at higher altitudes. If all three fritillary butterfly species were to be preserved simultaneously, there is a need to protect wetlands both on the highlands and in the lowland regions, where human activities constantly and quickly modify the territory. In the future, high altitude habitats might become even more important if species distributions shift in response to global warming (Konvicka et al. 2003).

Implications for conservation

Our results demonstrate that not only patch-specific habitat characteristics, but also the surrounding landscapes can affect the distribution of endangered butterfly species. As the butterflies consistently reacted at spatial scales larger than a single habitat patch and as some species requirements may be met outside strictly defined habitat patches, conservation policies for butterfly species should consider whole landscapes with connected patches, which allow

dispersal between habitat patches. In such landscapes, a minimum proportion of habitat should be guaranteed that depends on the degree of mobility of each species. General habitat management recommendations for all species are difficult, but for the target species *B. selene* grazing of fens is more appropriate than mowing. The current politics in Switzerland, which supports both management strategies, may be an appropriate solution (Schmid 1996).

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