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Trampling and dune arthropod occurrence

Title

Trampling affects the distribution of specialised coastal dune arthropods

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Keywords: Araneae, grazing, grey dunes, Lepidoptera, multispecies metapopulation, Orthoptera, recreation, trampling

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Postprint version.
Original publication in:
Basic and Applied Ecology (2008) 9: 726-734

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Abstract

From a conservation point of view, species' tolerances towards disturbance are often generalised and lack reference to spatial scales and underlying processes. In order to investigate how average typical species react to habitat fragmentation and disturbance, we adopted a multi-species approach to address occupancy patterns of five specialised dune arthropods (butterflies *Hipparchia semele, Issoria lathonia;* grasshopper *Oedipoda caerulescens*; spiders *Alopecosa fabrilis, Xysticus sabulosus*) in recently fragmented coastal dune habitats which are subjected to varying levels and modes of local disturbance, i.e. trampling by cattle or people.

Occupancy patterns were assessed during two successive years in 133 grey dune fragments of the Flemish coastal dunes (Belgium, France). By treating species as a random factor in our models, emphasis was placed on generalisations rather than documenting species-specific patterns.

Our study demonstrates that deteriorating effects of local disturbance on arthropod incidence cannot be interpreted independent of its landscape context, and appear to be more severe when patch area and connectivity decrease. When controlled for patch area and trampling intensity, the probability of species occupancy in poorly connected patches is higher under cattle trampling than under recreation. Incidences additionally decrease with increasing intensity of cattle trampling, but increases with trampling by tourists.

This study provides empirical evidence of mode- and landscape-dependent effects of local disturbance on species occupancy patterns. Most importantly, it demonstrates that trampling of sensitive dune fragments will lead to local and metapopulation extinction in landscapes where trampling occurs in a spatially autocorrelated way, but that the outcome (spatial patterns) varies in relation to disturbance mode, indicating that effects of disturbance cannot be generalised.

Zusammenfassung

Aus Sicht des Naturschutzes werden die Toleranzen von Arten gegenüber Störungen häufig verallgemeinert und lassen einen Bezug zu räumlichen Skalen und den zugrundeliegenden Prozessen vermissen. Um zu untersuchen, wie typische Durchschnittsarten auf Habitatfragmentierung und Störung reagieren, verwendeten wir einen Vielartenansatz um die Nutzungsmuster von fünf spezialisierten Dünenarthropoden (Schmetterlinge: *Hipparchia semele, Issoria lathonia*; Heuschrecken: *Oedipoda caerulescens*; Spinnen: *Alopecosa fabrilis, Xysticus sabulosus*) in kürzlich fragmentierten Küstendünenhabitaten zu behandeln, die unterschiedlichen Arten und verschieden starken lokalen Störungen ausgesetzt waren, wie z. B. Vertritt durch Weidevieh oder Menschen. Die Nutzungsmuster wurden in zwei aufeinander folgenden Jahren in 133 Graudünenfragmenten der flämischen Küstendünen (Belgien, Frankreich) untersucht. Durch die Berücksichtigung der Arten als zufällige Faktoren legten wir den Schwerpunkt eher auf Generalisierung als auf die Dokumentation artspezifischer Muster. Unsere Untersuchung zeigt, dass die negativen Effekte lokaler Störungen auf die Arthropodenvorkommen nicht unabhängig vom Landschaftskontext interpretiert werden können, und dass sie ernster sind, wenn die Flächengröße und -vernetzung abnehmen. Wenn wir die Flächengröße und die Vertrittintensität kontrollieren, ist die Wahrscheinlichkeit des Artvorkommens in wenig vernetzten Flächen bei Beweidung größer als bei Freizeitnutzung. Die Vorkommen nehmen außerdem mit zunehmender Intensität des Weideviehvertritts ab, nehmen jedoch mit zunehmendem Vertritt durch Touristen zu. Diese Untersuchung liefert empirische Belege für art- und landschaftsabhängige Effekte lokaler Störungen auf die Nutzungsmuster von Arten. Besonders wichtig ist, dass gezeigt wird, dass der Vertritt von sensiblen Dünenfragmenten zum Aussterben von lokalen und Metapopulationen in Landschaften führen wird, wenn der Vertritt in einer räumlich autokorrelierten Form stattfindet. Das Ergebnis (die räumlichen Muster) variieren jedoch in Relation zur Störungsart und weist darauf hin, dass die Effekte von Störungen nicht generalisiert werden können.

Introduction

Both natural and anthropogenic disturbances are known to affect the viability of populations (Hansen & Clevenger 2005; Pascual & Guichard 2005). Many studies dealing with disturbance as a driving factor in metapopulation dynamics consider local disturbance as an agent that is directly responsible for local extinction events, so-called "catastrophes". In these cases, metapopulation extinction is directly affected by the degree of spatial correlation in disturbance processes and habitat geometry (Kallimanis, Kunin, Halley & Sgardelis 2005), with spatially correlated disturbances eventually leading to metapopulation extinction in the absence of long-distance dispersal. Subsequently, deterministic disturbance events may affect patch connectivity by reducing the number of populations within the dispersal range of an organism. The degree to which populations are affected by the magnitude of local disturbance and its interaction with patch geometry, however, remains largely unanswered, although recent theoretical work highlights the importance of habitat availability, disturbance regime and dispersal properties (Kallimanis et al. 2005). If the magnitude of local disturbance is inversely related to habitat quality, then source-sink models predict that patches with increasing local disturbance remain occupied only when connected to patches with a demographic excess (Kawecki 2004).

Within a conservation framework, species' tolerance towards comparable disturbances regimes is often generalised (White & Jentsch 2001). However, variation due to different spatial scales and underlying processes (Hobbs & Yates, 2003; Denny, Helmuth, Leonard, Harley, Hunt *et al*., 2004) is hardly addressed. Earlier theoretical (Henle, Davies, Kleyer, Margules & Settele. 2004) and empirical work (e.g. Krauss, Steffan-Dewenter & Tscharntje 2003; Steffan-Dewenter 2003; Brouat, Chevalier, Meusnier, Noblecourt & Rasplus 2004; Dennis, Hodgson, Grenyer, Shreeve & Roy 2004) revealed that distribution patterns are not only affected by differences in dispersal ability (which determine connectivity), but also by (often co-varying) traits related to habitat specialization. In particular, species with different life-histories do not have the same resource demands and may considerably differ in their mode of habitat use (Dennis, Shreeve & Van Dyck 2003). As a consequence, research of multi-species responses towards environmental changes may yield complementary insights for conservation and management purposes as opposed to single-species studies (e.g Lambeck 1997; Simberloff 1998; Maes & Van Dyck 2005; Maes & Bonte 2006). If a species from a particular ecosystem is at high risk, comparison of its response towards a suite of environmental parameters may enable local managers to predict how conservation efforts targeted at this single focal species can affect other species that are at less risk. However, when multi-species studies reveal contrasting patterns, it is difficult to set management priorities as beneficial actions for one species may be detrimental for another one. Instead, we argue that a compromise which generates insights into the average reaction of the species-group (the assemblage from which representative species are chosen) is more practical and that patterns revealed by the latter can be translated to management priorities that are beneficial to an entire group of species. This compromise can be expected to be a strategy for an optimal and sustainable conservation of local species richness, and not of one specific target species. Consequently, the delineation of management actions based on average reactions of species towards a particular disturbance regime may provide complementary information to the „umbrella' approach, in which conservation actions are based on responses of one species that is assumed to be representative of an entire species assemblage (Fleishman, Murphy & Brussard 2000; Fleishman, Blair & Murphy 2001).

In coastal dune ecosystems, trampling is often tolerated because of the assumed adaptation of species towards natural disturbance, i.e. aeolian dynamics (displacement of sand by wind; Bonte, Maelfait & Lens 2006). Maes and Bonte (2006) focussed in detail on the habitat demands of the selected species and landscape-related factors that influence their colonisation and extinction dynamics. We here adopt the earlier delineated „compromise' approach to study the average response of five arthropod species towards trampling variation (intensity and mode) by controlling for these earlier revealed landscape-related variation (see Maes & Bonte 2006).

Material and methods

Studied species

The set of study species comprises two butterfly species, the Grayling *Hipparchia semele* (LINNAEUS 1758) and the Queen of Spain Fritillary *Issoria lathonia* (LINNAEUS 1758), the Blue-Winged Grasshopper *Oedipoda caerulescens* (LINNAEUS 1758) and the spiders *Xysticus sabulosus* (HAHN 1832) and *Alopecosa fabrilis* (CLERCK 1757). These species are restricted to dynamic grey dunes in the coastal area (Provoost & Bonte 2004). Local distribution patterns in coastal dunes are affected by patch size, patch isolation and the intensity of trampling (Maes & Bonte 2006).

All species are active during the (late) summer (Kleukers et al. 1997; Maes & Van Dyck 1999; Bonte & Maelfait 2004, 2005). *A. fabrilis* is a burrowing species during its entire life (Bonte & Maelfait 2005), egg development of *O. caerulescens* takes place in the soil, but larval development is aboveground (Kleukers, van Nieukerke, Odé, Willemse & Van Wingerden 1997), while egg and larval development of both butterfly species (Maes & Van Dyck 1999) and *X. sabulosus* takes place in vegetation above ground-level (Bonte, unpub. data).

Species *H. semele* and *I. lathonia* are mobile (Dennis, Shreeve & Sparks 1998; Maes, Ghesquiere, Logie & Bonte 2006), *O. caerulescens* is moderately sedentary although some individuals can move for long distances (Appelt & Poethke 1997; Maes et al. 2006) and both spider species *A. fabrilis* and *X. sabulosus* are believed to be very sedentary although *X. sabulosus* can use ballooning as a dispersal mode (Bonte, Lens, Maelfait, Hoffmann & Kuyken 2003). All five species are of conservation concern in Flanders (Provoost 2004).

Methods

The study was carried out in 133 patches of dynamic grey dunes along the coast between Nieuwpoort – Belgium (51°08' N, 2°43' E) and Bray-Dunes – France (51°05' N, 2°33' E; see appendix A: Fig. 1). Like other coastal dunes in Western Europe, they comprise semi-natural landscapes that have been influenced by agro-pastoral use prior to the 1950's. Owing to the withdrawal of agro-pastoral activities, the rise of tourist activities and the dramatic decline in rabbit populations due to viral diseases, the formerly open landscape became urbanised and subject to shrub encroachment, resulting in an accelerated fragmentation of dynamic grey dunes (Provoost & Van Landuyt 2001). Grey dune habitat was discriminated from unsuitable habitat from aerial orthophotographs based on vegetation-specific red (RED) and near-infrared (NIR) reflectance values (Provoost, Ampe, Bonte, Cosyns & Hoffmann 2004). After discrimination, patches were digitised with a Geographic Information System (Arcview 3.1). Mean patch size was 1.44 ha (range: 0.0007 – 22.55 ha).

To determine the presence of the two butterfly species and the grasshopper, all sites were censused by standardised (equal search time for patch area) walks through the entire patch during the first two weeks of August in 2003 and in 2004 under suitable weather conditions (cf. Pollard and Yates 1993). Patches, independently surveyed by three different observers revealed identical presence/absence data and, hence, demonstrate the reliability of these data. Presence/absence of the two spider species was determined with pitfall traps between 20 August and 10 September in 2003 and in 2004 (diameter 9 cm, 6% formaldehyde-detergent solution). Earlier research indicated that, because of their high levels of epigeic activity and the open vegetation structure, species incidences can be determined with few pitfalls, randomly located in optimal habitat (Bonte, Baert & Maelfait 2004). Therefore at least five traps were randomly placed with a maximum of 15 pitfalls in larger patches.

For all patches, area and proportion of area that showed trampled soil and vegetation (hereafter called trampling intensity) were assessed in addition to species-specific connectivity (see further). Patches were either subjected to trampling by introduced domestical herbivores, to trampling by mass-recreation or excluded from recreation and grazing. Grazed or excluded patches were never frequented by tourists. Grey dune fragments under recreational pressure are predominantly situated within urban areas, while those under grazing are situated within nature reserves. Our measure of disturbance intensity is a relative measure that gives insight into its spatial distribution within sites. Although it does not take temporal aspects of use into account, earlier surveys indicated that its intensity is reflected in the relative proportion of damaged soil, for a specific mode of disturbance (recreation or cattle). Although trampling by tourists or by cattle result in similar trampling patterns (destruction of moss coverage; Bonte 2005), temporal aspects of trampling greatly differ: public recreation mainly occurs during the summer season (season in which specialised arthropods occur as adults) estimated to approximate 300 hours of recreation disturbance during the months July-August on the most accessible grey dunes (Bonte 2005), equalling maximal 0.1 hours/year/m² for average patches under recreation. In contrast, cattle spend yearly only 7-9% of their time on dynamic grey dunes resulting in a mean annual disturbance of less than 0.2 hours/year/m² (Lamoot, Meert & Hoffmann 2005). This grazing mainly occurs during winter and spring (Lamoot et al. 2005).

Because all surrounding habitat can be considered as being hostile, and because of the predominant aerial dispersal of the selected model species, we used simple connectivity indices based on patch-based weighted sums. These have been shown to be biologically relevant in species inhabiting landscapes with discrete habitat patches imbedded in hostile habitat and having aerial, non-directed dispersal modes (Winfree, Dushoff, Crone, Schultz, Budny et al. 2005). More specifically we used Hanski's connectivity measure (Hanski 1994) $S_i=\sum_{j\neq i}\exp(-\alpha d_{ij})N_j$ where α=a constant describing the strength of the inverse relationship between numbers of migrants from patch *j*, d_{ij} distance between patches, and N=population size at patch *j* (1 in case of occupancy, 0 in the case of vacancy). We used α-values of 2 for the butterflies *H. semele* and for *I. lathonia* (Maes et al. 2006); 25 for the grasshopper *O. caerulescens* (Appelt and Poethke 1997; Maes et al. 2006) and 4 for the spiders *A. fabrilis* and *X. sabulosus* assuming ballooning dispersal for both species (Bonte et al. 2003). These dispersal kernels are based on previous, independent empirical data sets from coastal dunes (Bonte et al. 2003; Maes et al. 2006) and are very similar to those reported in the literature. Sensitivity analysis and low variation within models of the species*connectivity interaction depict the robust influence of these constants on the patterns investigated, because connectivity is mainly affected by each species' spatial distribution within the landscape, i.e. by occupancy of neighbouring patches (Bonte & Maes, unpub. data) .

Statistical analysis

Mixed logistic models with logit-link for binomial data (0: absence; 1: presence; Procedure Glimmix; SAS statistical Package version 9.1, SAS 2003) were applied to investigate occupancy patterns of the species. Species, year and their interactions with fixed factors were included as random factors because we aimed to analyse general occupancy patterns for specialised arthropods. In a first analysis, occupancy patterns were investigated in relation to trampling intensity, patch area and patch connectivity, which were included as fixed factors. As trampling mainly originates from recreation and grazing disturbance, the nature of the disturbance was added in a second analysis as a categorical fixed factor. Because trampling intensity ranged between 0 and 50% trampled soil under grazing and from 0-100% trampled soil under recreation, we selected 75 patches within the common range of 0-50% in order to test effects of trampling (disturbance) mode on species incidence. A backward procedure was applied to eliminate non-significant factors and interactions from both models. Denominator degrees of freedom were approximated using Satterthwaite's procedure in order to correct for the unbalanced design due to species- and year-effects.

Results

Patch area, trampling intensity and species-specific connectivity measures only show weak ($r^2<0.20$) correlations (see Appendix A). Most important is the positive relationship between patch area and connectivity for all species, mainly due to the absence of small patches with high connectivity. Fragments in sites subjected to recreational trampling are smaller than those subjected to cattle (Table 1) and those excluded for both cattle and vacationers. Mean trampling intensity was lowest in the latter, higher in fragments under influence of cattle trampling and highest in those subjected to recreation.

Species incidence was affected by the interaction between patch area, patch connectivity and intensity of trampling (Table 2). The probability of occupancy increased when patches became larger or better connected. Under increasing trampling intensity, occupancy rates were high in large patches with high connectivity only. The statistical model is depicted in Appendix B.

When the type of disturbance (recreation versus grazing) was added to the model, the probability of patch occupancy was positively affected by area and the interactions between disturbance mode and connectivity and trampling intensity, respectively (Table 3). As evident from Fig. 1, probabilities of patch occupancy, controlled for mean area and trampling intensity, increased faster for patches trampled by grazing than by people. The mode of trampling, as a function of its intensity (within the common range between 0 and 50%), showed contrasting patterns in patches of similar area and connectivity (Fig. 2). In cases where trampling intensity was low, probabilities of patch occupancy were higher for sites under grazing than under recreational disturbance. With increasing trampling disturbance, however, probabilities became relatively higher for sites under recreational pressure.

Discussion

Our selected species clearly show different reactions towards landscape-ecological features and disturbance, as reflected in the high variation components of the random factors. Threshold values to ascertain the presence of these species have been documented in Maes and Bonte (2006). We here show that average occupancy patterns of dune arthropods clearly depend on the landscape structure, but also on its interaction with characteristics of local trampling disturbance. The strength of the applied analytic approach depends, however, largely on the variance among included species and their ecological affinities with the environment of interest. More specifically, only patterns that are common to all included species are retained while species-specific patterns will raise modelled variation components. This approach should therefore not be interpreted as an alternative for the multi-species approach in which patterns are analysed for several species separately. While the latter enables the assessment of necessary additive or complementary information for species conservation (e.g. Fleishman et al. 2000; 2001), our analysis provides a straightforward assessment of the average responses of the local species community towards modelled habitat-related factors.

Our habitat patches were discriminated on an objective basis that encompasses suitable habitat for all species (as revealed by previous independent research, Provoost & Bonte 2004). However, we cannot completely exclude unknown (and hence unmodelled) differences in habitat quality, which are interpreted as connectivity or disturbance effects. This may be true for e.g. factors related to microclimate and lime richness of the soil, which both show conciderable spatial autocorrelation in relation to the distance to the sea (Bonte et al. 2004). The presence of large populations of all selected species both close to the sea and close to the inner dune front renders this autocorrelation, however, unlikely. Because probabilities of species occupancy in patches under high local disturbance are only high within large areas having high connectivity, we can conclude that high levels of local disturbance give rise to mass effects (Leibold, Holyoak, Mouquet, Amarasekare, Chase et al. 2004), influenced by high effective dispersal rates from high towards low quality patches. Under high levels of isolation, high disturbance rates will be responsible for local extinction in small isolated patches. Subsequently, connectivity for the remaining populations will decrease and induce positive feedbacks on overall species incidence in case (even non-catastrophic) disturbances occur in a spatially aggregated way. If the entire metapopulation is subjected to similar levels of substantial disturbance, it will automatically lead to metapopulation extinction, as predicted by the theoretical work of Kallimanis et al. (2005). Similar results were obtained by Dunstan & Fox (1996), who found species richness to decrease with patch remnant size and increasing disturbance. As in our study, the interaction between both factors appeared to be important with small remnants being affected worst by increasing disturbance.

The magnitude of trampled area differed significantly between patches under direct influence of either mass-recreation, grazing management and those only sporadically visited by humans. Despite the general perception that effects of disturbance on species diversity can be generalised, our study provides clear evidence that different modes of disturbance affect occupancy probabilities of arthropods in a different way. Probably, temporal differences in disturbance intensity, although superficially resulting in similar environments, underly the observed patterns. Under low patch connectivity, occupancy probabilities are higher for sites under grazing management (Fig. 1). Additonally, species occupancy decreased with increased cattle trampling but increased if trampling intensity was associated with recreation (Fig. 2). These patterns may well make biological sense because trampling due to recreation peaks during few days in the summer period, while trampling by cattle appears to be a more continuous, but less intense. Recreational disturbance occurs consequently during the season when our model species are very mobile. In contrast, if cattle-trampling is fairly high in patches with a similar configuration, this indicates more continuous trampling, with peaks during the winter period, when most species are sedentary (early juveniles, eggs; Maes & Van Dyck 1999; Turin 2000) and, hence, most vulnerable to direct trampling effects. Under low trampling intensities, reverse patterns were observed, suggesting that patches under low recreational pressure are characterised by lower occupancy probabilities. Although we controlled for landscape-effects, differences in other habitat deteriorating parameters due to edge effects within different matrix-types can attribute –at least partly- for the observed patterns here. Especially the lack of sufficient amounts of natural dynamics, changes in vegetation composition and biotic interactions due to increasing abundances of invasive and garden species (Provoost 2004), may underlie these patterns, here attributed to disturbance as such. Despite the fact that our findings are purely correlative, they certainly suggest that generalizations of disturbance need to be taken very carefully.

The introduction of grazing management is a system-approach, in which grazers are introduced within delimited blocks. Spatial autocorrelation of induced trampling disturbance will consequently be responsible for declining occupancy patterns over longer time scales. This will certainly be the case in shrub dominated dune landscapes where open grey dunes are intensively frequented by cattle (Lamoot et al. 2005). Here, even intermediate trampling will have an impact on occupancy patterns because the number of occupied patches (and hence focal patch connectivity) in the surrounding will inevitably decrease due to higher average extinction probabilities. Because similar processes can be expected in urbanised areas, autocorrelated disturbance needs to be avoided by the exclusion of (larger) scattered grey dune fragments from cattle and people. Within grazing blocks, this can also be obtained by creating a sufficient amount of high-quality habitat for domestic grazers in order to lower pressure on grey dune habitats with fragile soil conditions. Additionally, as moderate trampling by people appears to be beneficial for the conservation of grey dune invertebrate habitats, soft recreation should be encouraged and even preferred above grazing in small grey dune fragments.

Acknowledgement

Ward Vercruysse provided assistance during fieldwork. We are very grateful to Roger Dennis and Luc Lens for valuable comments and linguistic streaming and to Sam Provoost for his permission to use his digital orthophotographs. Koen De Smet granted us permission to study the legally protected *O. caerulescens* (license number AMINAL/NAT/DI.832.172/2275). We are also grateful to three anonymous referees for valuable suggestions to improve the quality of this manuscript. Dries Bonte holds a post-doc fellowship at the Fund for Scientific Research – Flanders (FWO).

Appendices A, B: Supplementary Material. The online version of this article contains additional supplementary data. Please visit XXXXX.

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Table 1. Mean values of patch area, connectivity S and relative trampling intensity of grey dune fragments in relation to mode of disturbance (means ± SD). Significant differences are indicated by different letters in superscript (Tukey). Connectivity-values are given only for *O. caerulescens*, but S-values did not differ for any of the selected species

	Cattle (*N*=25)	None (*N*=14)	Recreation (*N*=94)	$F_{2,130}$	P
Area (m²)	9.43 (±1.71)^{a}	9.25 (±1.81)^{a}	8.09 (±1.65)^{b}	8.052	0.0005
S (O. caerulescens)	0.33 (±0.55)	0.48 (±0.48)	0.46 (±0.48)	0.693	0.523
Trampling intensity	27.29 (±14.5)^{a}	7.5 (±5.92)^{b}	49.24 (±24.15)^{c}	17.03	<0.0001

Table 2. Estimates, standard errors of estimates (se), denominator degrees of freedom (den. df.), F and P-values of mean effects as derived from the mixed logistic model with patch occupancy as dependent variable and patch area (area), patch connectivity (S) and trampling intensity (TI) as independent variables. Nominator degrees of freedom = 1. Species, species*environment and year-interactions were included as random factors in the model. Only those variance components lower than 0.001 are listed in the table.

Effect (fixed)	**Estimate**	**se**	**den. df.**	***F***	**P**	**Effect (random**	**s^2**	**SE**
Intercept	-11.022	1.405	181.3			Year	0.048	0.082
Area	1.198	0.144	1300	69.04	**<0.001**	Species	0.202	0.435
S	1.928	0.681	1305	8.01	**0.005**	Species*S	0.418	0.59
TI	0.084	0.03	313.9	7.59	**0.006**	Species*Area	0.013	0.014
Area*S	-0.159	0.072	1320	4.79	**0.029**	Species*S*Area	0.007	0.009
Area*TI	-0.011	0.003	1308	12.28	**<0.001**	Residual	0.823	0.032
S*TI	-0.024	0.012	1315	3.89	**0.048**			
Area*S*TI	0.003	0.001	1320	4.25	**0.039**			

Table 3. Estimates, standard errors of estimates (se), denominator degrees of freedom (den. df.), F and P-values of mean effects as derived from the reduced mixed logistic model with patch occupancy as dependent variable and patch area (area), patch connectivity (S), trampling intensity (TI) and source of trampling (TS: grazing versus recreation) as independent variables. Estimates are not given for backwards deleted effects that contributed in a non-significant way. Only patches under grazing or recreational pressure with trampling intensity less than 50% were selected (for reasoning, see text). Nominator degrees of freedom = 1. Species, species*environment and year-interactions were included as random factors in the model. Only those variance components lower than 0.001 are listed in the table.

Effect (fixed)	**Estimate**	**se**	**den. d.f.**	**F**	***P***	**Effect (random)**	**s²**	**se**
Intercept	-9.32	1.28	-	-	-	Year	0.244	0.371
Area	0.85	0.13	4.92	10.31	**0.002**	Species	5.341	5.688
S	1.21	0.32	3.42	9.89	**0.041**	Species*S	0.364	0.373
TI	0.02	0.01	3.11	0.1	0.772	Species*Area	0.596	0.595
TS	1.77	0.55	743	11.51	**<0.001**	Residual	0.871	0.046
S*TS	-0.40	0.19	729.4	7.75	**0.030**			
TI*TS	-0.04	0.01	653.8	6.54	**0.004**			
Area*S	-	-	88.62	0.22	0.641			
Area*TI	-	-	3.75	1.81	0.407			
Area*TS	-	-	742	1.33	0.249			
S*TI	-	-	53.98	1.05	0.311			
Area*S*TI	-	-	736	0.09	0.761			
Area*S*TS	-	-	738	1.60	0.278			
S*TI*TS	-	-	737	0.77	0.382			
Area*S*TI*TS	-	-	735	3.83	0.051			

Figure legends:

Figure 1. Modelled probability of patch occupancy as a function of connectivity for patches under the influence of either grazing (left panel) or recreation (right panel). Occupancy probabilities and 95% confidence limits are derived from the logistic model ln (p/(1-p))=int+b1x1+b2x2+… for which parameters estimates are given in Table 3 (for mean values of trampling intensity and area).

Figure 2. Modelled probability of patch occupancy as a function of trampling intensity for patches under influence of either grazing (left panel) or recreation (right panel). Occupancy probabilities and 95% confidence limits are derived from the logistic model ln (p/(1-p))=int+b1x1+b2x2+… for which parameters estimates are given in Table 3 (for mean values of S and area).

Figure 1.

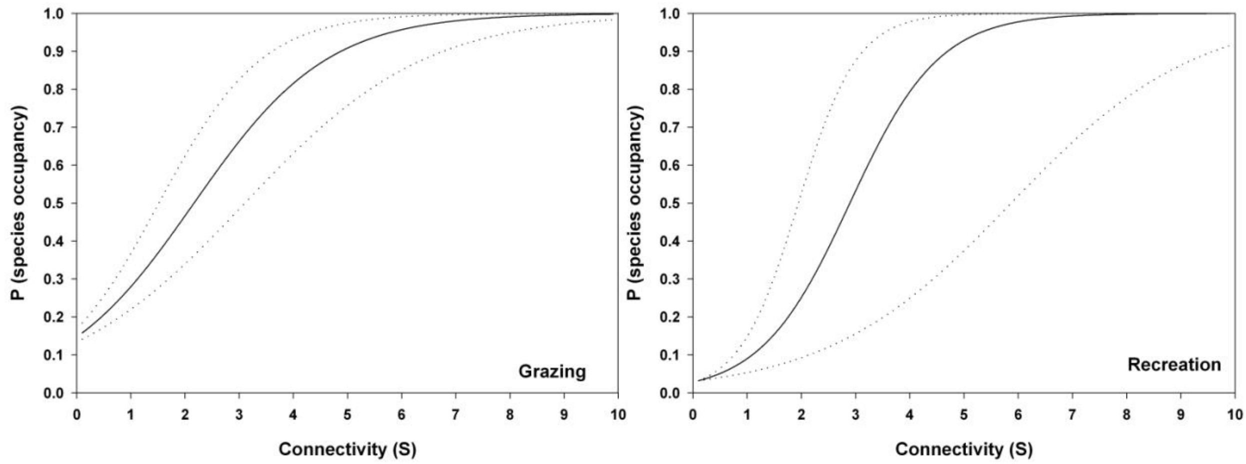
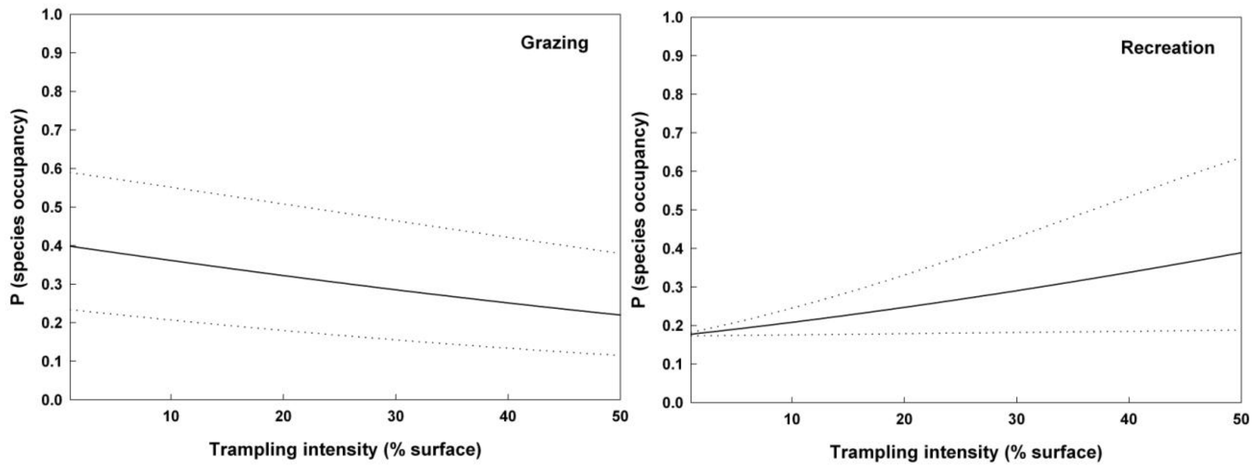


Figure 2.


Grazing
Recreation
P (species occupancy)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
10
20
30
40
50
Trampling intensity (% surface)