
2 Using distribution patterns of five threatened invertebrates 3 in a highly fragmented dune landscape to develop 4 a multispecies conservation approach

5 *D. Maes*^{a,*}, *D. Bonte*^b

6 ^aDivision of Species Ecology and Populations, Research Institute for Nature and Forest, Kliniekstraat 25, B-1070 Brussels, Belgium

8 ^bGhent University, Department of Biology, Terrestrial Ecology Unit, K.L. Ledeganckstraat 35, B-9000 Ghent, Belgium

9

18 **Keywords:**
19 *Alopecosa fabrilis*
20 Belgium
21 Conservation
22 Dynamic grey dunes
23 Spatial distribution
24 *Hipparchia semele*
25 *Issoria lathonia*
26 Landscape effects
27 *Oedipoda caerulescens*
28 *Xysticus sabulosus*

A B S T R A C T

We analysed the patterns of occupancy of five threatened invertebrates in a highly fragmented dynamic grey dune landscape. During two years (2003–2004), 133 dune patches between Nieuwpoort (Belgium) and Bray-Dunes (France) varying in area, connectivity, eolian sand dynamics and trampling disturbance were sampled for five focal species: two spiders (*Alopecosa fabrilis* and *Xysticus sabulosus*), two butterflies (*Issoria lathonia* and *Hipparchia semele*) and one grasshopper (*Oedipoda caerulescens*). Overall diversity was highest in large and well connected patches that were characterised by high eolian sand dynamics and an intermediate trampling intensity. Patch occupancy differed greatly among species: all species significantly occurred more often in large and connected patches. High trampling intensity (by cattle and/or tourists) negatively affected the two ground dwelling spiders, but not the grasshopper or the butterfly species. High eolian sand dynamics positively affected the presence of the spider *X. sabulosus*, the grasshopper *O. caerulescens* and the butterfly *H. semele*, but had no significant effect on both other species. Colonisation was mainly explained by connectivity and never by patch area, while extinction events in *H. semele* were explained by small patch area. We discuss the implications of using a suite of focal species for management and restoration purposes in the highly fragmented dune area in Belgium and we promote the use of a multispecies approach for evaluating and monitoring conservation efforts in general.

49

50

51 1. Introduction

52 Nature conservation in many countries is largely biotope-
53 and/or ecosystem-based, i.e., sites are acquired and/or man-
54 aged for the presence of threatened biotope types (e.g., Annex
55 I of the European Union Habitat Directive) or in function of
56 ecological processes (e.g., nutrient cycles, hydrology) respec-
57 tively. But, several authors have shown that species can go ex-

tinct under such site- or ecosystem-based conservation 58
policies (Pickett et al., 1992; Simberloff, 1998). The incorpora- 59
tion of species into decisions about site selection or manage- 60
ment measures is, up to date, rather scarce, especially in 61
Flanders (north Belgium – Maes and Van Dyck, 2005). The 62
necessity and complementary nature of both species and eco- 63
system conservation simultaneously, however, can render 64
nature conservation considerably more efficient through the 65

66 use of species as tools for site selection, management evalu-
67 ation and/or the evaluation of nature conservancy policy
68 (Noss, 1990).

69 In most NW European countries, the area of coastal
70 dunes has strongly declined mainly due to building activities
71 for tourism (De Ruyck et al., 2001). In Belgium, for example,
72 the coastal dune area decreased from about 6000 ha to
73 3800 ha during the 20th century (Provoost and Bonte, 2004).
74 In addition to fixation of the seaside dunes with *Ammophila*
75 *arenaria*, sand dynamics burned out due to the lack of eolic
76 input from the beach and due to urbanisation of the coastal
77 dune area (Provoost and Bonte, 2004). This resulted in a loss
78 of natural dynamics in the dune area leading to a decrease
79 of the total area of open (sandy) habitats. Furthermore, open
80 dune habitats (e.g., dynamic grey dunes) have suffered from
81 shrub and grass encroachment (Provoost and Bonte, 2004)
82 due to the cessation of livestock grazing (mainly pony), the
83 collapse of rabbit populations after the myxomatosis epi-
84 demic in the beginning of the 1950's (Provoost and Bonte,
85 2004; Ranwell, 1960) and the atmospheric nitrogen deposi-
86 tion (Kooijman et al., 1998). Finally, recreational pressure in-
87 creased greatly during the last decades because of the
88 expanding tourism facilities. These factors resulted in a sig-
89 nificant reduction and fragmentation of the remaining dy-
90 namic grey dune complexes, accompanied with a decline
91 of many thermophilous invertebrates (e.g., Bonte, 2005; De-
92 cleer et al., 2000; Desender et al., 1995; Maelfait et al., 1998;
93 Maes and Van Dyck, 2001). Since dynamic grey dunes (i.e.,
94 fixed coastal dunes with herbaceous vegetation and shifting
95 dunes along the shoreline with *Ammophila arenaria*) are prior-
96 ity biotopes in the European Union Habitat Directive, they
97 are of high conservation concern to the Flemish government
98 (Herrier and Killemaes, 2001).

99 Present nature management in dune systems aims at
100 restoring the former species richness (both flora and fauna)
101 by using low intensity cattle grazing, the formerly applied
102 farming technique in the Belgian coastal dunes (Termote,
103 1992). Most of these grazing projects only started recently
104 and conservation biologists are only beginning to evaluate
105 its effects on typical dune species (Bonte et al., 2000; Bonte
106 et al., 2002; WallisDeVries and Ramaekers, 2001). Since graz-
107 ing is a system-approach, it will not necessarily meet the de-
108 mands of every single open dune species (grazing may fail to
109 create a sufficient area of high quality habitat) and additional
110 species-specific management measures may be necessary
111 (Lambeck, 1997).

112 An interesting short-cut to incorporate species into bio-
113 tope restoration plans and/or nature management is the
114 concept of a single focal or umbrella species (e.g., Ranius,
115 2002; Rubinoff, 2001). Such an umbrella species should rep-
116 resent the ecological demands of all other species in the
117 same biotope (Fleishman et al., 2001). But, species in the
118 same biotope type do not necessarily have the same re-
119 source demands and can differ considerably in habitat use
120 within biotopes (Dennis et al., 2003). Therefore, a single spe-
121 cies is rarely covering the ecological demands of all other
122 species in that biotope (Andelman and Fagan, 2000; Landres
123 et al., 1988; Simberloff, 1998). The use of more than one spe-
124 cies is therefore preferable to a single-species approach be-
125 cause it results in complementary information for

conservation and management purposes (e.g., Lambeck, 126
1997; Maes and Van Dyck, 2005; Root et al., 2003; Simberloff, 127
1998). Furthermore, several authors have pleaded for a more 128
prominent use of invertebrates in conservation biology than 129
is currently the case (Kotze and Samways, 1999; McGeoch, 130
1998; Samways, 1993). 131

The establishment of suitable habitat networks is an 132
important conservation measure for the conservation of spe- 133
cies. Metapopulation biology is a framework for the pro- 134
cesses allowing the persistence of species within habitat 135
networks (Hanski, 1999). Metapopulation models testing 136
the influence of spatial arrangement of suitable habitats on 137
the viability of the metapopulation, have already been suc- 138
cessfully tested on butterflies (e.g., Baguette and Schtick- 139
zelle, 2003; Hanski and Thomas, 1994), grasshoppers (e.g., 140
Appelt and Poethke, 1997; Carlsson and Kindvall, 2001) and 141
spiders (Bonte et al., 2003). Most of these studies are re- 142
stricted to a single species and very few studies incorporate 143
several studies of different taxonomic groups into metapop- 144
ulation analyses. Here, we investigate the distribution pat- 145
terns of five threatened species of dynamic grey dunes 146
along a part of the Belgian and French coast. We relate the 147
species' patterns to patch area, isolation, recreational pres- 148
sure and sand dynamics and discuss whether the five focal 149
species depend on metapopulation dynamics in our study 150
area. We discuss the implications of inter-specific differ- 151
ences in distribution patterns and vulnerability for the con- 152
servation of dynamic grey dunes and its associated typical 153
species in Belgium. 154

2. Methods 155

2.1. Studied species 156

The five studied invertebrates are the butterflies the Grayling 157
Hipparchia semele (Linnaeus 1758) and the Queen of Spain 158
Fritillary *Issoria lathonia* (Linnaeus 1758), the Blue-Winged 159
grasshopper *Oedipoda caerulescens* (Linnaeus 1758) and the 160
spiders *Xysticus sabulosus* (Hahn 1832) and *Alopecosa fabrilis* 161
(Clerck 1757). All species have a discontinuous distribution 162
in Flanders (north Belgium) with populations in the sandy 163
Campine region in the northeast and along the coast in 164
the west. The biotope types used in the two regions also dif- 165
fer: in the Campine region they mainly occur in dry heath- 166
lands while they are restricted to dynamic grey dunes in 167
the coastal area (Provoost and Bonte, 2004). All species are 168
active during the summer months (Bonte and Maelfait, 169
2001; Kleukers et al., 1997; Maes and Van Dyck, 1999). The 170
butterflies *H. semele* and *I. lathonia* are considered mobile 171
(Dennis et al., 1998; Maes et al., 2006), the grasshopper *O.* 172
caerulescens is fairly sedentary although some individuals 173
can move long distances (Appelt and Poethke, 1997; Maes 174
et al., 2006) and both spider species *A. fabrilis* and *X. sabulo-* 175
sus are believed to be very sedentary although *X. sabulosus* 176
can use ballooning as dispersal mode (Bonte et al., 2003). 177
All five species are of conservation concern in Flanders: *I.* 178
lathonia is critically endangered, *A. fabrilis* and *X. sabulosus* 179
are both endangered and *H. semele* and *O. caerulescens* are 180
vulnerable (Decler et al., 2000; Maelfait et al., 1998; Maes 181
and Van Dyck, 1999). 182

184 The study was carried out in 133 patches with dynamic grey
185 dunes along the coast between Nieuwpoort – Belgium
186 (51°08'N, 2°43'E) and Bray-Dunes – France (51°05'N, 2°33'E;

187 Fig. 1). The 133 patches were selected because they all contain
188 potential habitat for all the species, but habitat quality and
189 quantity differed among patches. The 'matrix' (the area in be-
190 tween the investigated patches) mostly consists of urban area
191 (buildings and recreation zones), roads and scrubland (*Hippop-*
192 *haerhamnoides*, *Ligustrum vulgare* and *Salix repens*). This matrix
193 is completely unsuitable habitat for all focal species (Provoost
194 and Bonte, 2004) and contains only limited resources (nectar)
195 for butterflies. For all patches, area, mean connectivity among
196 patches, trampling intensity (1 = no trampling, 2 = intermedi-
197 ate trampling and 3 = intensive trampling) and percentage
198 natural sand dynamics was calculated or estimated. The latter
199 was measured in each patch by means of five randomly lo-
200 cated sand deposition traps (jars of diameter 9 cm),
201 operational from the second half of August until the first half
202 of September. Mean patch size is 1.44 ha and ranges from
203 0.0007 ha to 22.55 ha.

204 To determine the presence of the two butterfly species and
205 the grasshopper, all sites were inspected by walking through
206 the entire patch during the first two weeks of August in
207 2003 and in 2004 under suitable weather conditions, i.e., tem-
208 perature > 20 °C, no rain and wind < 3 Beaufort (cf. Pollard and
209 Yates, 1993). Both the butterflies and the grasshopper are con-
210 spicuous animals and can be reliably inventoried in such
211 weather conditions. Presence/absence of the two spider spe-
212 cies was determined using a sufficient number of pitfall traps
213 between 20 August and 10 September in 2003 and in 2004
214 (diameter 9 cm, 6% formaldehyde-detergent solution). In all
215 surveyed patches at least five traps were randomly placed
216 with a maximum of 15 pitfalls in larger patches. The use of
217 pitfall traps has been shown to be very useful in catching this
218 typical spider species living within this biotope because of
219 their high levels of epigeic activity (Bonte et al., 2003).

2.3. Patch connectivity

220

221 Because all included species disperse by flying or ballooning,
222 and experience the matrix in a similar, hostile way, mean
223 patch connectivity was calculated using Hanski's connectivity
224 measure (after Hanski, 1994): $S_i \frac{1}{4} \sum_j \exp(-ad_{ij}) P_j$ where
225 a = a constant describing the strength of the inverse
226 relationship between numbers of migrants from patch j and
227 distance between patches, N_j = (size of patch j population
228 size at patch j) where population size is 1 in case of occupancy
229 and 0 in the case of vacancy. We did not use actual observed
230 numbers because of inter-specific differences in population
231 densities, but we considered that a population was present
232 in a patch when at least three individuals of the species were
233 observed. a was based on our own capture-mark-recapture
234 studies in the same area for four of the five species: $a = 2$ for
235 the butterfly *H. semele* (Maes et al., 2006); $a = 25$ for the grass-
236 hopper *O. caerulescens* (Appelt and Poethke, 1997; Maes et al.,
237 2006) and $a = 4$ for both spiders *A. fabrilis* and for *X. sabulosus*
238 assuming ballooning dispersal for both species (Bonte et al.,
239 2003). Although *I. lathonia* is known as a migratory/vagrant
240 butterfly in large parts of Europe, it shows similar movement
241 patterns as *H. semele* in the investigated dune area (De Weste-
242 linck, Maes and Bonte, unpublished data); we therefore attrib-
243 uted the same a -value in our analyses for *I. lathonia* ($a = 2$) as
244 for *H. semele*.

2.4. Statistical analysis

245

246 First, we looked for differences in patch area, connectivity,
247 trampling intensity and eolic sand dynamics for habitat
248 patches with different focal species diversity. Second, we ana-
249 lyzed differences in the mean values of the different patch
250 characteristics for the five focal species for patches that were
251 occupied in both years; we assume that patches that are occu-
252 pied both years represent a more suitable condition than
253 those that are only occupied one year or not occupied at all.
254 The average values of patch size, connectivity, trampling

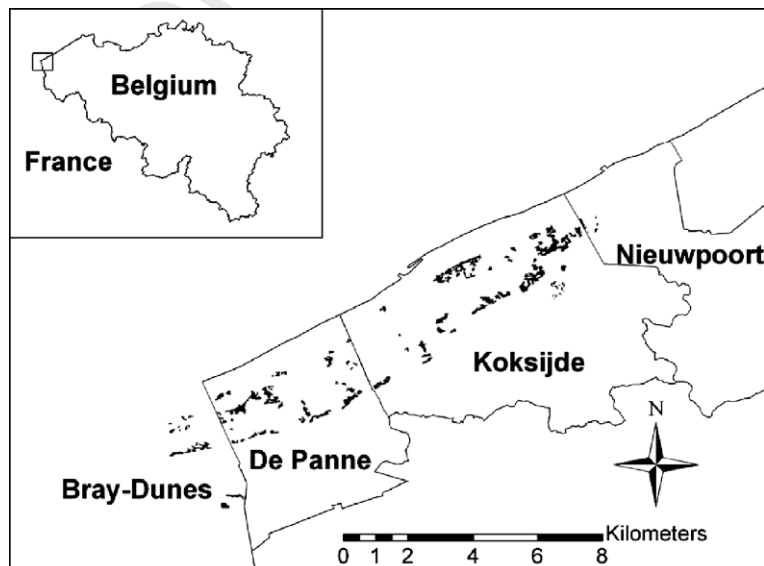


Fig. 1 – Location of the 133 investigated habitat patches in the French and Belgian dune area.

255 intensity and sand dynamics can easily be communicated to
256 and used by local terrain managers for local conservation
257 measures or restoration projects. We performed a Kruskal-
258 Wallis ANOVA for both analyses.

259 Patch occupancy was tested by mixed models with year as
260 random effect to correct for possible differences between
261 years. Colonization patterns were analysed using stepwise lo-
262 gistic regressions with colonization as dependent variable (1
263 for a colonization event and 0 for patches that remained va-
264 cant over the two years) and area (log-transformed to obtain
265 normality), connectivity (log-transformed to obtain normal-
266 ity), trampling intensity and natural sand dynamics as inde-
267 pendent variables. For extinction events, patches where
268 species went extinct were compared with patches that re-
269 mained occupied during both years.

270 3. Results

271 3.1. Overall focal species richness in relation to patch 272 characteristics

273 Patches with the highest focal species richness were on aver-
274 age large and well connected. Furthermore, they were charac-
275 terised by high eolian sand dynamics (about 55 mm sand
276 deposition) and an intermediate trampling intensity (Fig. 2).

277 3.2. Individual species distribution in relation to patch 278 characteristics

279 Patch occupancy differed greatly among species, but no sig-
280 nificant variation was observed during the two subsequent
281 sampling years ($S^2 = 0.047 \pm 0.082SE$ – Table 1). Testing patch
282 occupancy for both years separately (i.e., a kind of sensitivity
283 analysis) did not alter the outcomes of the analysis. For all five
284 species separately, patches that were occupied in both or in
285 one of the two years were significantly larger than those that
286 were vacant during both years. All species, except for *I. latho-*
287 *nia*, occupied patches that were significantly more connected
288 than vacant patches (Table 2). High trampling intensity nega-
289 tively affected the two ground dwelling spider species, but not
290 the grasshopper or the butterflies. High sand dynamics posi-
291 tively affected the spider *X. sabulosus*, the grasshopper *O. cae-*
292 *rulescens* and the butterfly *H. semele*, but had no significant
293 effect on both other species.

294 Using only patches that were occupied during both years,
295 significant differences among species were observed for area
296 (but post-hoc inter-specific comparisons were not significant;
297 $p > 0.16$) but not for sand dynamics. The connectivity measure
298 of occupied sites differed significantly among species with *H.*
299 *semele* and *I. lathonia* being more present in relatively more
300 connected patches than the other species. Trampling inten-
301 sity in occupied sites also differed significantly among species
302 with *H. semele* and *O. caerulescens* being more present in tram-
303 pled patches than the other species (Table 2).

304 Patch area was the only variable that entered in all models
305 explaining patch occupancy of the five species emphasizing
306 the importance of large patches (Table 3a). Parameter esti-
307 mates for trampling intensity were negative for *A. fabrilis*, *X.*
308 *sabulosus* and *I. lathonia* indicating that these species do not
309 support intensive trampling, but positive for *O. caerulescens*

indicating that regular disturbance is a necessary habitat 310
characteristic for this grasshopper. Connectivity parameter 311
estimates were positive for three species indicating that con- 312
nected patches were more occupied than isolated ones. Sand 313
dynamics parameter estimates were positive for *H. semele* and 314
for *O. caerulescens* emphasizing the importance of dynamic 315
environments for both species (Table 3a). 316

3.3. Colonisation and extinction 317

The number of colonization and extinction events between 318
both years are given in Tables 3b and 3c. None of the coloni- 319
zation events was explained by patch area. The spiders *A.* 320
fabrilis and *X. sabulosus* and the butterfly *H. semele* colonized 321
connected patches more easily than isolated ones (Table 3b). 322
Additionally, *A. fabrilis* patches that remained vacant had a 323
relatively high trampling intensity. *O. caerulescens* coloniza- 324
tion events were related to high sand dynamics while extinc- 325
tion events in *H. semele* were explained by small patch size 326
(Table 3c). 327

4. Discussion 328

The focal invertebrate species all occur in dynamic grey dune 329
biotope types but showed clear differences in relation to the 330
characteristics of the highly fragmented remnant dune 331
patches along the Belgian–French coast. The presence of all 332
species was positively affected by area and species were more 333
present in highly connected patches. On the other hand, 334
trampling intensity had opposite effects: the spider species 335
and one of the butterflies were negatively affected by tram- 336
pling, while the grasshopper was positively affected, indicat- 337
ing its dependency of regular disturbance. 338

Species incidence in fragmented landscapes is very often 339
positively affected by increasing patch size (Hanski, 1999; Fah- 340
rig, 2001) and all five species in our study complied to this 341
rule. But, inter-specific differences are considerable with *I.* 342
lathonia and *A. fabrilis* occurring in patches twice as large as 343
O. caerulescens. They both were consistently present in 344
patches of, on average, 4 ha, which is fairly large along the 345
strongly built-on Belgian coast. For *I. lathonia*, this is most 346
probably due to its need for patches with a mixture of rough 347
(nectar sources) and short vegetation (host plants) which 348
are both usually only present in fairly large sites. *A. fabrilis*, 349
however, is a large, burrowing spider species occurring at 350
fairly low densities. Subsequently, large patches are necessary 351
to ensure sufficiently high local population sizes and, hence, 352
to ensure local persistence under stochastic population fluc- 353
tuations (Bonte and Maelfait, 2005). 354

Patch connectivity is an important factor explaining colo- 355
nisation events in both spiders species and the butterfly *H.* 356
semele along the Belgian coast (Bonte et al., 2003; Dennis 357
et al., 1998). Only for the butterfly *I. lathonia* and for the grass- 358
hopper *O. caerulescens*, patch connectivity seems of lesser 359
importance for occupancy and colonisation events. Although 360
our connectivity measurements are based on prior, but realis- 361
tic dispersal estimates, it indicates that the butterfly *I. lathonia* 362
is mobile enough to occupy and colonise fairly isolated 363
patches (maximum colonisation distance observed between 364
2003 and 2004 is 341 m) and can probably also use nectar 365

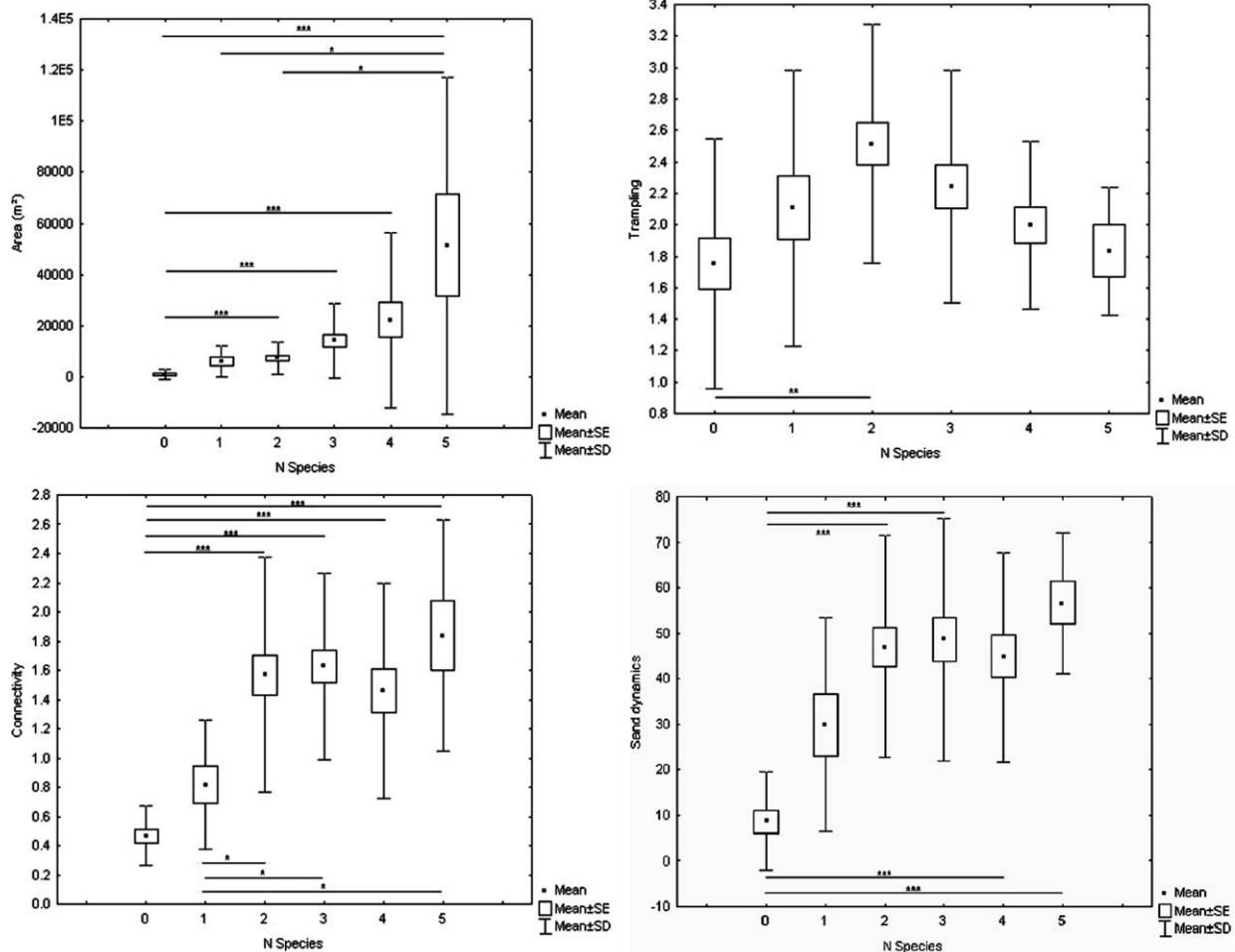


Fig. 2 – Mean (\pm SE and SD) (a) patch area (Kruskal–Wallis ANOVA $H(5, N = 133) = 53.111, p < 0.001$), (b) connectivity (Kruskal–Wallis ANOVA $H(5, N = 133) = 48.399, p < 0.001$), (c) trampling intensity (Kruskal–Wallis ANOVA $H(5, N = 133) = 17.192, p = 0.004$) and (d) eolic sand dynamics (Kruskal–Wallis ANOVA $H(5, N = 133) = 43.039, p < 0.001$) for habitat patches with different number of species (N_{Species}). Number of patches per species richness (N_{Species}) is: 0 ($n = 19$), 1 ($n = 12$), 2 ($n = 34$), 3 ($n = 32$), 4 ($n = 25$) and 5 ($n = 11$). A posteriori tests (Least significant difference test) for differences between patches are indicated by lines (only significant differences are shown): * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table 1 – Percentage occupancy ($n = 133$) of the five investigated species in 2003 and in 2004 and the difference between both years

Species	% 2003	% 2004	Difference
<i>Alopecosa fabrilis</i>	11.3	18.8	+7.5
<i>Xysticus sabulosus</i>	30.1	39.8	+9.8
<i>Oedipoda caerulescens</i>	75.2	70.7	-4.5
<i>Hipparchia semele</i>	49.6	52.6	+3.0
<i>Issoria lathonia</i>	29.3	36.1	+6.8

366 sources outside dune patches as well. *O. caerulescens*, on the
 367 other hand, is far more sedentary and the rare colonisation
 368 events only occurred in patches that were within a 100 m radi-
 369 us of an occupied patch (cf. Maes et al., 2006). Hence, iso-
 370 lated *Oedipoda*-populations are more persistent than for
 371 other species and/or species' dispersal is higher than esti-
 372 mated on individual mobility, probably by higher frequencies

of dispersing individuals. As documented earlier (Bonte et al.,
 2002), extinction events of spiders in grey dune remnants are
 highly stochastic. Only for the butterfly *H. semele*, extinctions
 could be predicted in small remnants; the lower habitat qual-
 ity or the lack of sufficient con-specifics in these small patches probably
 explain why they are only temporarily occu- pied (Dennis et al.,
 1998). But, since the different species all have different dispersal
 abilities (which is reflected in the α -value in the formula used to
 calculate connectivity – Hanski, 1994), the absolute connectivity
 values given in Table 2 cannot be directly compared among species.
 Apart from habitat quality (Thomas et al., 2001), habitat
 heterogeneity in dune areas is at least as important for the co-
 occurrence of different typical dune species (Kindvall, 1996).
 Moreover, climatic differences between years, between seasons or
 even during the day, can lead to a different habitat use by different
 species (Thomas et al., 2001). Maes et al. (2006), for example,
 have shown that *O. caerulescens* uses dif- ferent substrates
 (moss or sand) in the dune area on hot

373
 374
 375
 376
 377
 378
 379
 380
 381
 382
 383
 384
 385
 386
 387
 388
 389
 390
 391

Table 2 – Biotope and connectivity characteristics of the patches in relation to their occupancy frequency (means ± SD)

Species	Both years	One year	Never	<i>p</i>
<i>Alopecosa fabrilis</i>	13	14	106	
Area (m ²)	38367 ± 57477 ^a	22393 ± 30948 ^{ab}	10372 ± 19604 ^b	<0.001
³⁴ Connectivity	0.723 ± 0.569 ^a	0.722 ± 0.469 ^a	0.303 ± 0.389 ^b	<0.001
¹² Trampling intensity	1.08 ± 0.28 ^a	1.21 ± 0.58 ^a	1.89 ± 0.82 ^b	<0.001
Sand dynamics	45.25 ± 17.38	53.78 ± 22.23	38.57 ± 27.52	0.052
<i>Xysticus sabulosus</i>	36	21	76	
Area (m ²)	29927 ± 46901 ^a	8934 ± 13199 ^b	8510 ± 11612 ^b	<0.001
²⁴ Connectivity	1.613 ± 0.951 ^a	1.308 ± 0.750 ^a	0.322 ± 0.506 ^b	<0.001
¹ Trampling intensity	1.17 ± 0.38 ^a	1.62 ± 0.67 ^{ab}	2.04 ± 0.86 ^b	<0.001
Sand dynamics	50.65 ± 22.47 ^a	34.73 ± 23.15 ^b	37.85 ± 28.14 ^b	0.023
<i>Oedipoda caerulescens</i>	87	20	26	
Area (m ²)	19810 ± 32969 ^a	6611 ± 6942 ^a	2157 ± 4362 ^b	<0.001
³ Connectivity	0.535 ± 0.557 ^a	0.467 ± 0.431 ^a	0.092 ± 0.289 ^b	<0.001
³ Trampling intensity	1.82 ± 0.81 ^a	2.05 ± 0.89 ^a	1.23 ± 0.51 ^b	<0.001
Sand dynamics	49.15 ± 23.25 ^a	45.00 ± 24.54 ^a	9.73 ± 11.40 ^b	<0.001
<i>Hipparchia semele</i>	58	20	55	
Area (m ²)	26152 ± 38702 ^a	6675 ± 5566 ^b	4754 ± 6439 ^b	<0.001
¹ Connectivity	4.407 ± 2.172 ^a	3.451 ± 1.563 ^a	1.943 ± 1.448 ^b	<0.001
²³ Trampling intensity	1.79 ± 0.87 ^{ab}	2.20 ± 0.70 ^a	1.51 ± 0.72 ^b	0.003
Sand dynamics	57.51 ± 23.91 ^a	40.59 ± 16.95 ^a	23.32 ± 20.03 ^b	<0.001
<i>Issoria lathonia</i>	25	37	71	
Area (m ²)	40828 ± 54367 ^a	10017 ± 12261 ^b	7330 ± 7979 ^b	<0.001
² Connectivity	1.924 ± 1.016	2.061 ± 0.946	1.799 ± 0.888	0.33
¹²³ Trampling intensity	1.52 ± 0.71	1.68 ± 0.78	1.85 ± 0.86	0.23
Sand dynamics	48.00 ± 25.90	38.63 ± 23.06	39.44 ± 28.25	0.31
<i>p</i>		Area		0.028
<i>p</i>		Connectivity		<0.001
<i>p</i>		Trampling intensity		<0.001
<i>p</i>		Sand dynamics		0.15

Significant differences among occupancies are indicated by different letters in superscript (Kruskal–Wallis ANOVA). Significant differences among species (only for both years) are indicated by figures in front of the biotope characteristic.

Table 3a – Parameter estimates obtained by a logistic regression analysis on species incidence (mixed model with year as random variable)

Variables	<i>A. fabrilis</i>	<i>X. sabulosus</i>	<i>O. caerulescens</i>	<i>H. semele</i>	<i>I. lathonia</i>
Intercept	-7.812	-6.819	-7.761	-9.731	-5.746
Area ^{Log}	0.842 ⁽¹⁾	0.718 ⁽²⁾	0.888 ⁽¹⁾	0.698 ⁽³⁾	0.662 ⁽¹⁾
Trampling ^{Class}	-1.619 ⁽²⁾	-1.156 ⁽³⁾	0.512 ⁽²⁾	–	-0.018 ⁽²⁾
Sand dynamics ^{Class}	–	–	0.020 ⁽³⁾	0.027 ⁽¹⁾	–
Connectivity ^{Log}	1.843 ⁽³⁾	3.082 ⁽¹⁾	–	1.926 ⁽²⁾	–
Year	0.309 ± 0.567	0.311 ± 0.538	0.012 ± 0.111	0	0.023 ± 0.087

The number in superscript between brackets indicates the order of entrance into the model. The estimates of variance are given for the random variable ‘year’.

392 and cold days, both for thermoregulation and for crypsis.
 393 Homogenous dune patches would, therefore, not be able to
 394 sustain durable populations of this focal species.

395 For trampling intensity, patch incidence differences
 396 among species were opposite: the grasshopper *O. caerulescens*
 397 and the butterfly *H. semele* need open sand patches within the
 398 sites (for thermoregulation and territorial behaviour respec-
 399 tively – Maes et al., 2006). These ecological and behavioural
 400 ‘resources’ can be obtained by a relatively high trampling
 401 intensity. Both spider species, on the other hand, were more

present in less disturbed, more fixated sites. Being ground
 predators, high abundance of prey in more stabilised dunes
 (Bonte et al., 2002), in combination with the need of stable
 habitat for burrowing probably explained this pattern.

From our results we can conclude that apart from area and
 isolation, the two classical parameters in metapopulation
 theory, habitat quality is an important determinant for the
 distribution of the five focal species along the Belgian coast.
 The dependence on area and connectivity suggests that the
 distribution patterns of some of the focal species resemble

402
 403
 404
 405
 406
 407
 408
 409
 410
 411

Table 3b – Parameter estimates obtained by a logistic regression analysis on colonisation events

Variables	<i>A. fabrilis</i>	<i>X. sabulosus</i>	<i>O. caerulescens</i>	<i>H. semele</i>	<i>I. lathonia</i>
Colonization events	12	17	7	12	23
Vacant patches	106	76	26	55	71
Intercept	-1.433	-3.336	-4.512	-5.015	-1.127
Area	–	–	–	–	–
Trampling	-1.142 ⁽²⁾	–	–	–	–
Sand dynamics	–	–	0.123	–	–
Connectivity	2.781 ⁽¹⁾	3.770	.	2.796	–

Table 3c – Parameter estimates obtained by a logistic regression analysis on extinction events

Variables	<i>A. fabrilis</i>	<i>X. sabulosus</i>	<i>O. caerulescens</i>	<i>H. semele</i>	<i>I. lathonia</i>
Extinction events	2	4	13	8	14
Occupied patches	13	36	87	58	25
Intercept	-1.872	-2.197	-1.901	6.544	-0.580
Area	–	–	–	-0.954	–
Trampling	–	–	–	–	–
Sand dynamics	–	–	–	–	–
Connectivity	–	–	–	–	–

412 that of a metapopulation along the Belgian coast (both spider
 413 species – Bonte et al., 2003) and the butterfly *H. semele*.
 414 Although area is a strong predictor for occupancy in both
 415 the grasshopper *O. caerulescens* and in the butterfly *I. lathonia*,
 416 connectivity is not included as a factor in our models; this
 417 suggests that they are more depended on habitat quality than
 418 on classical metapopulation dynamics in the Belgian dunes.
 419 The use of a suite of focal species clearly adds to the evidence
 420 that classical metapopulation hypotheses and the impor-
 421 tance of habitat quality are certainly not mutually exclusive
 422 ones (Thomas et al., 2001). Our analyses further show that
 423 defining habitat quality in more detail (metapopulation the-
 424 ory assumes that area is a surrogate for population size that
 425 is affected by habitat quality – Hanski and Ovaskainen,
 426 2000), can help to explain distribution patterns of some of
 427 the focal species studied here.

428 4.1. Implications for conservation

429 All five invertebrates are considered as focal species for the
 430 Belgian dune region (Provoost and Bonte, 2004). Although
 431 incidence and metapopulation dynamics of the five studied
 432 species show more or less similar patterns in relation to land-
 433 scape characteristics, it is clear that local natural and anthro-
 434 pogenic disturbance affects distribution patterns in different
 435 ways.

436 Domestic grazers are currently used as ‘tools’ to convert
 437 the heterogeneous, closed landscape into open dune land-
 438 scapes, dominated by both dry grasslands and humid dune
 439 slacks (e.g., de Bonte et al., 1999; Herrier and Killemaes,
 440 2001). However, dynamic grey dunes are certainly not the pre-
 441 ferred sites for grazers because they have a very low nutri-
 442 tional value (Lamoot et al., 2005). In contrast, grey dune
 443 remnants are mainly used as corridor between more nutri-
 444 tious vegetation (Lamoot et al., personal communication)

445 and are subsequently highly trampled. As trampling appears
 446 to show contrasting effects on species incidence, with only
 447 positive effects for *O. caerulescens*, the introduction of grazers
 448 will, with exception for the latter, hardly result in the enlarge-
 449 ment of suitable habitat and patch connectivity for the inves-
 450 tigated focal species. Conservation measures for enlarging
 451 and connecting remnant grey dune patches should, therefore,
 452 aim at the restoration of eolian dynamics at a landscape
 453 scale. This will, at the same time, enlarge grey dune areas
 454 and will decrease current levels of fragmentation. The pres-
 455 ence and conservation of sand dynamics at a landscape scale
 456 also appeared to be one of the main factors in explaining spi-
 457 der assemblage structure in coastal dunes (Bonte et al., 2003).
 458 More specifically, spider assemblages in patches with similar
 459 levels of local sand dynamics, significantly differed between
 460 stabilized and dynamic landscapes. Typical coastal spider
 461 species were only present in dynamic landscapes. However,
 462 in practice, restoration of sand dynamics would imply the res-
 463 toration of natural beach-dune transitions to allow net sand
 464 replacement into the dune areas. Furthermore, connecting
 465 large dune entities is seriously hampered because it would in-
 466 volve the destruction of urban infrastructures such as roads
 467 and residential areas. Consequently, in highly populated
 468 and fragmented coastal areas, internal management actions
 469 should mainly concentrate on the reduction of over-intensive
 470 trampling disturbance (Bonte and Maes, unpublished data).
 471 As shown by Bonte et al. (2003), characteristic species can
 472 go extinct within short time frames. Therefore, efforts should
 473 focus on the conservation of sand dynamics in large dune re-
 474 serves in order to conserve the present pool of typical species.
 475 Once species go extinct due to fixation by vegetation, coloni-
 476 zation from distant dynamic dune areas can be expected to be
 477 very difficult due to limited dispersal abilities of these special-
 478 ized species (Bonte et al., 2003). Although extensive grazing is
 479 promoted as beneficial for butterflies in the dune area, addi-

480 tional specific measures for the threatened invertebrate spe-
 481 cies are necessary (WallisDeVries and Ramaekers, 2001). Since
 482 domestic grazers are not able to eliminate or open up dense
 483 shrub vegetation, it is recommended to remove dense shrub
 484 vegetations mechanically prior to grazing in order to decrease
 485 internal fragmentation of larger sites.

486 4.2. Advantages of a multispecies approach

487 Many restoration or management projects only use single
 488 indicator species (e.g., Berger, 1997; Ranius, 2002; Rubino, 2001;
 489 Watson et al., 2001) or single taxonomic groups (e.g.,
 490 Cardoso et al., 2004; Kati et al., 2004). Some authors suggest
 491 the use of a small set of ecologically similar species as indica-
 492 tor group (e.g., Martikainen et al., 1998). Our results clearly
 493 demonstrate the utility of a multispecies approach in conser-
 494 vation biology (cf. Lambeck, 1997). The single indicator use of
 495 any of the five studied species would have resulted in differ-
 496 ent management suggestions than the complementary use
 497 of all five species together (cf. Maes and Van Dyck, 2005). Fol-
 498 lowing the focal species approach of Lambeck (1997), the a
 499 priori selected five invertebrate species used here can be re-
 500 garded as an appropriate suite of indicator species for differ-
 501 ent aspects of area, connectivity, sand dynamics and
 502 recreational pressure along the French–Belgian coast. *I. latho-*
 503 *nia* and *A. fabrilis* are the most suitable indicators for patch
 504 area (and seem to be exchangeable as area indicators), *O. cae-*
 505 *rulescens*, being the least mobile of the focal species, is an
 506 appropriate connectivity indicator, and the combined pres-
 507 ence of high and low trampling intensity species (both spider
 508 species on the one hand and *O. caerulea* and *H. semele* on
 509 the other) can be considered a useful indicator of habitat het-
 510 erogeneity within patches (cf. Kindvall, 1996). Management
 511 measures or restoration projects using more than one species
 512 are, therefore, more complementary than those using only
 513 single indicator species (Fleishman et al., 2000). Our multispe-
 514 cies approach additionally has the benefit of bringing science
 515 closer to conservation practitioners using species that are
 516 easily recognizable by non-experts (Pullin and Knight, 2001;
 517 Roberge and Angelstam, 2004). Furthermore, the information
 518 content of the focal species can be explicitly used in the eval-
 519 uation or the establishment of conservation measures in a
 520 sense that the presence or absence of particular species of
 521 the multispecies group could be used as a signalling function
 522 (McGeoch, 1998). The presence of one or more of the focal
 523 species is indicative of patch quality (and not only quantity
 524 – Thomas et al., 2001) such as resource suitability, heteroge-
 525 neity etc.

526 A monitoring scheme to evaluate the effect of restoration
 527 and management measures would be cost-efficient using a
 528 multiple species approach. A well selected set of species
 529 would be very helpful in assessing the quality and quantity
 530 of the remnant dune patches along the Belgian coast. Inverte-
 531 brates are good early warning species because of their high
 532 reproductive rate (McGeoch, 1998) and other conspicuous spe-
 533 cies could be added if enough ecological information is avail-
 534 able (e.g., *Bembix rostrata*, Bonte, 2005). Including other typical
 535 dune organisms that are informative on smaller spatial scales
 536 (vascular plants, e.g., *Carlina vulgaris*, *Silene conica*, *Viola curt-*
 537 *isii*) and on larger spatial scales than invertebrates (e.g., the

toad *Bufo calamita* and the birds *Charadrius alexandrinus* and
Oenanthe oenanthe) in a multispecies monitoring scheme for
dynamic grey dunes would be advisable (Maes and Van Dyck,
2005).

Acknowledgements

We thank Ward Vercruyssen for assistance during the field
work. We are very grateful to Dirk Bauwens and Luc De Bruyn
for advice on methods and statistics and for valuable com-
ments. We also thank two anonymous reviewers for their
constructive comments on a previous version of the manu-
script. We thank Sam Provoost for his permission to use the
vegetation maps of the dune area. Koen De Smet (Head of
the Nature Department of the Flemish Nature Conservation
Ministry) granted us permission to study the legally protected
O. caerulea (licence number AMINAL/NAT/DI.832.172/
2275). Nature warden Ward De Brabandere gave us permission
to perform the study in the public nature reserves along the
Belgian coast. Dries Bonte is a postdoctoral fellow of the
Foundation of Scientific Research Flanders (FWO).

REFERENCES

- Andelman, S.J., Fagan, W.F., 2000. Umbrellas and flagships:
Efficient conservation surrogates or expensive mistakes?
Proceedings of the National Academy of Science of the United
States of America 97, 5954–5959.
Appelt, M., Poethke, H.J., 1997. Metapopulation dynamics in a
regional population of the blue-winged grasshopper (*Oedipoda*
caerulea Linnaeus, 1758). Journal of Insect Conservation 1,
205–214.
Baguette, M., Schtickzelle, N., 2003. Local population dynamics
are important to the conservation of metapopulations in
highly fragmented landscapes. Journal of Applied Ecology 40,
404–412.
Berger, J., 1997. Population constraints associated with the use of
Black Rhinos as an umbrella species for desert herbivores.
Conservation Biology 11, 69–78.
Bonte, D., 2005. Anthropogenic induced changes in nesting
densities of the dune-specialised digger wasp *Bembix rostrata*.
European Journal of Entomology 102, 809–812.
Bonte, D., Maelfait, J.-P., 2001. Life history, habitat use and
dispersal of a dune wolf spider (*Paradosa monticola* (Clerck, 1757)
Lycosidae, Araneae) in the Flemish coastal dunes (Belgium).
Belgian Journal of Zoology 131, 145–157.
Bonte, D., Maelfait, J.-P., 2005. Spatial association between a spider
wasp and its host in fragmented dune habitats. Journal of
Arachnology 33, 222–229.
Bonte, D., Maelfait, J.-P., Hoffmann, M., 2000. The impact of
grazing on spider communities in a mesophytic calcareous
dune grassland. Journal of Coastal Conservation 6, 135–
144.
Bonte, D., Baert, L., Maelfait, J.-P., 2002a. Spider assemblage
structure and stability in a heterogeneous coastal dune
system (Belgium). Journal of Arachnology 30, 331–343.
Bonte, D., Van Heuverswyn, F., Mertens, J., 2002b. Temporal and
spatial distribution of epigeic *Arthropleona springtails*
(Collembola: Hexapoda) in coastal grey dunes. Belgian Journal
of Entomology 47, 17–26.
Bonte, D., Criel, P., Van Thournout, I., Maelfait, J.-P., 2003a.
Regional and local variation of spider assemblages (Araneae)

596	from coastal grey dunes along the North Sea. <i>Journal of Biogeography</i> 30, 901–911.	
597		
598	Bonte, D., Lens, L., Maelfait, J.-P., Hoffmann, M., Kuijken, E., 2003b.	
599	Patch quality and connectivity influence spatial dynamics in a	
600	dune wolf spider. <i>Oecologia</i> 135, 227–233.	
601	Cardoso, P., Silva, I., de Oliveira, N.G., Serrano, A.R.M., 2004.	
602	Indicator taxa of spider (Araneae) diversity and their efficiency	
603	in conservation. <i>Biological Conservation</i> 120, 517–524.	
604	Carlsson, A., Kindvall, O., 2001. Spatial dynamics in a	
605	metapopulation network: recovery of a rare grasshopper	
606	<i>Stauroderus scalaris</i> from population refuges. <i>Ecography</i> 24,	
607	452–460.	
608	de Bonte, A.J., Boosten, A., van der Hagen, H.G.J.M., Sykora, K.V.,	
609	1999. Vegetation development influenced by grazing in the	
610	coastal dunes near The Hague, The Netherlands. <i>Journal of</i>	
611	<i>Coastal Conservation</i> 5, 59–68.	
612	Declerck, K., Devriese, H., Hofmans, K., Lock, K., Barenburg, B.,	
613	Maes, D., 2000. Voorlopige atlas en “rode lijst” van de	
614	sprinkhanen en krekels van België (Insecta, Orthoptera).	
615	SALTABEL i.s.m. IN en KBIN, Brussel.	
616	Dennis, R.L.H., Sparks, T.H., Shreeve, T.G., 1998. Geographical	
617	factors influencing the probability of <i>Hipparchia semele</i> (L.)	
618	(Lepidoptera: Satyrinae) occurring on British and Irish off-	
619	shore islands. <i>Global Ecology and Biogeography Letters</i> 7, 205–	
620	214.	
621	Dennis, R.L.H., Shreeve, T.G., Van Dyck, H., 2003. Towards a	
622	functional resource-based concept for habitat: a butterfly	
623	biology viewpoint. <i>Oikos</i> 102, 417–426.	
624	De Ruyck, A.M.C., Ampe, C., Langohr, R., 2001. Management of the	
625	Belgian coast: opinions and solutions. <i>Journal of Coastal</i>	
626	<i>Conservation</i> 7, 129–144.	
627	Desender, K., Maes, D., Maelfait, J.-P., Van Kerckvoorde, M., 1995.	
628	Een gedocumenteerde Rode Lijst van de zandloopkevers en	
629	loopkevers van Vlaanderen. Instituut voor Natuurbehoud,	
630	Brussel.	
631	Fahrig, L., 2001. How much habitat is enough? <i>Biological</i>	
632	<i>Conservation</i> 100, 65–74.	
633	Fleishman, E., Murphy, D.D., Brussard, P.E., 2000. A new method	
634	for selection of umbrella species for conservation planning.	
635	<i>Ecological Applications</i> 10, 569–579.	
636	Fleishman, E., Blair, R.B., Murphy, D.D., 2001. Empirical validation	
637	of a method for umbrella species selection. <i>Ecological</i>	
638	<i>Applications</i> 11, 1489–1501.	
639	Hanski, I., 1994. A practical model of metapopulation dynamics.	
640	<i>Journal of Animal Ecology</i> 63, 151–162.	
641	Hanski, I., 1999. <i>Metapopulation ecology</i> . Oxford university,	
642	Oxford.	
643	Hanski, I., Ovaskainen, O., 2000. The metapopulation capacity of a	
644	fragmented landscape. <i>Nature</i> 404, 755–758.	
645	Hanski, I., Thomas, C.D., 1994. Metapopulation dynamics and	
646	conservation: a spatially explicit model applied to butterflies.	
647	<i>Biological Conservation</i> 68, 167–180.	
648	Herrier, J.-L., Killemaes, I., 2001. Synopsis of the Flemish dune	
649	conservation policy. In: Houston, J.A., Edmonson, S.E.,	
650	Rooney, P.J. (Eds.), <i>Proceedings of the European symposium</i>	
651	<i>Coastal Dunes of the Atlantic Biogeographical Region Coastal</i>	
652	<i>dune management, shared experience of European</i>	
653	<i>conservation practice</i> . Liverpool University Press, Liverpool,	
654	pp. 316–325.	
655	Kati, V., Devillers, P., Dufrêne, M., Legakis, A., Vokou, D., Lebrun, P.,	
656	2004. Testing the value of six taxonomic groups as biodiversity	
657	indicators at a local scale. <i>Conservation Biology</i> 18, 667–675.	
658	Kindvall, O., 1996. Habitat heterogeneity and survival in a bush	
659	cricket metapopulation. <i>Ecology</i> 77, 207–214.	
660	Kleukers, R., van Niekerken, E., Odé, B., Willemsse, L., van	
661	Wingerden, W.K.R.E., 1997. <i>De Sprinkhanen en Krekels van</i>	
662	<i>Nederland (Orthoptera)</i> . Nationaal Natuurhistorisch Museum,	
663	KNNV Uitgeverij and EIS-Nederland, Leiden.	
	Kooijman, A.M., Dopheide, J.C.R., Takken, I., Verstraeten, J.M.,	664
	1998. Nutrient limitations and their implications on the effects	665
	of atmospheric deposition in coastal dunes; lime-poor and	666
	lime-rich sites in the Netherlands. <i>Journal of Ecology</i> 86, 511–	667
	526.	668
	Kotze, D.J., Samways, M.J., 1999. Support for the multi-taxa	669
	approach in biodiversity assessment as shown by the epigaeic	670
	invertebrates in a Afromontane forest archipelago. <i>Journal of</i>	671
	<i>Insect Conservation</i> 3, 125–143.	672
	Lambeck, R.J., 1997. Focal species: A multi-species umbrella for	673
	nature conservation. <i>Conservation Biology</i> 11, 849–856.	674
	Lamoot, I., Meert, C., Hoffmann, M., 2005. Habitat use of ponies	675
	and cattle foraging together in a coastal dune area. <i>Biological</i>	676
	<i>Conservation</i> 122, 523–536.	677
	Landres, P.B., Verner, J., Thomas, J.W., 1988. Ecological uses of	678
	vertebrate indicator species: a critique. <i>Conservation Biology</i>	679
	2, 316–328.	680
	Maelfait, J.-P., Baert, L., Janssen, M., Alderweireldt, M., 1998. A Red	681
	list for the spiders of Flanders. <i>Bulletin van het Koninklijk</i>	682
	<i>Belgisch Instituut voor Natuurwetenschappen, Entomologie</i>	683
	68, 131–142.	684
	Maes, D., Van Dyck, H., 1999. Dagvlinders in Vlaanderen –	685
	<i>Ecologie, verspreiding en behoud</i> . Stichting Leefmilieu i.s.m.	686
	<i>Instituut voor Natuurbehoud en Vlaamse Vlinderwerkgroep,</i>	687
	<i>Antwerpen/Brussel</i> .	688
	Maes, D., Van Dyck, H., 2001. Butterfly diversity loss in Flanders	689
	(north Belgium): Europe’s worst case scenario? <i>Biological</i>	690
	<i>Conservation</i> 99, 263–276.	691
	Maes, D., Van Dyck, H., 2005. Habitat quality and biodiversity	692
	indicator performances of a threatened butterfly versus a	693
	multispecies group for wet heathlands in Belgium. <i>Biological</i>	694
	<i>Conservation</i> 123, 177–187.	695
	Maes, D., Ghesquiere, A., Logie, M., Bonte, D., 2006. Habitat use	696
	and mobility of two threatened coastal dune insects:	697
	implications for conservation. <i>Journal of Insect Conservation</i>	698
	10, 105–115.	699
	Martikainen, P., Kaila, L., Haila, Y., 1998. Threatened beetles in	700
	white-backed woodpecker habitat. <i>Conservation Biology</i> 12,	701
	293–301.	702
	McGeoch, M.A., 1998. The selection, testing and application of	703
	terrestrial insects as bioindicators. <i>Biological Reviews of the</i>	704
	<i>Cambridge Philosophical Society</i> 73, 181–201.	705
	Noss, R.F., 1990. Indicators for monitoring biodiversity: a	706
	hierarchical approach. <i>Conservation Biology</i> 4, 355–364.	707
	Pickett, S.T.A., Parker, V.T., Fiedler, P.L., 1992. The new paradigm in	708
	ecology: implications for conservation biology above the	709
	species level. In: Fiedler, P.L., Jain, S.K. (Eds.), <i>Conservation</i>	710
	<i>biology: the theory and practice of nature conservation</i>	711
	<i>preservation and management</i> . Chapman and Hall, New	712
	York, pp. 65–88.	713
	Pollard, E., Yates, T.J., 1993. <i>Monitoring butterflies for ecology and</i>	714
	<i>conservation The British Butterfly Monitoring Scheme</i> .	715
	Chapman & Hall, London.	716
	Provoost, S., Bonte, D., 2004. <i>Levende duinen: een overzicht van de</i>	717
	<i>biodiversiteit aan de Vlaamse kust</i> . Instituut voor	718
	<i>Natuurbehoud, Brussel</i> .	719
	Pullin, A.S., Knight, T.M., 2001. Effectiveness in conservation	720
	practice: pointers from medicine and public health.	721
	<i>Conservation Biology</i> 15, 50–54.	722
	Ranius, T., 2002. <i>Osmoderma eremita</i> as an indicator of species	723
	richness of beetles in tree hollows. <i>Biodiversity and</i>	724
	<i>Conservation</i> 11, 931–941.	725
	Ranwell, D.S., 1960. Newborough Warren, Anglesey 3: Changes in	726
	the vegetation on parts of the dune system after the loss of	727
	rabbits by myxomatosis. <i>Journal of Ecology</i> 48, 385–395.	728
	Roberge, J.M., Angelstam, P., 2004. Usefulness of the umbrella	729
	species concept as a conservation tool. <i>Conservation Biology</i>	730
	18, 76–85.	731

732	Root, K.V., Akçakaya, H.R., Ginzburg, L., 2003. A multispecies	748
733	approach to ecological valuation and conservation.	749
734	Conservation Biology 17, 196–206.	750
735	Rubinoff, D., 2001. Evaluating the Californian Gnatcatcher as an	751
736	umbrella species for conservation of Southern California	752
737	coastal shrub. Conservation Biology 15, 1374–1383.	753
738	Samways, M.J., 1993. Insects in biodiversity conservation: some	754
739	perspectives and directives. Biodiversity and Conservation 2,	755
740	258–282.	756
741	Simberloff, D., 1998. Flagships, umbrellas, and keystones: Is	757
742	single-species management passé in the landscape era?	758
743	Biological Conservation 83, 247–257.	759
744	Termote, J., 1992. Wonen op het duin, de bewoningsgeschiedenis	760
745	van het duingebied tot aan de Franse Revolutie. In: ed. J.	761
746	Termote, Tussen land en zee: het duingebied van Nieuwpoort	762
747	tot De Panne. Lannoo, Tiel, 46–87.	763
	Thomas, C.D., Bodsworth, E.J., Wilson, R.J., Simmons, A.D.,	764
	Davies, Z.G., Musche, M., Conradt, L., 2001. Ecological and	
	evolutionary processes at expanding range margins. Nature	
	411, 577–581.	
	Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox,	
	D.J., Pearman, G.S., Curtis, R., Goodger, B., 2001. The quality	
	and isolation of habitat patches both determine where	
	butterflies persist in fragmented landscapes. Proceedings of	
	the Royal Society London B 268, 1791–1796.	
	WallisDeVries, M.F., Ramaekers, I., 2001. Does extensive grazing	
	benefit butterflies in coastal dunes? Restoration Ecology 9,	
	179–188.	
	Watson, J., Freudenberger, D., Paull, D., 2001. An assessment of the	
	focal-species approach for conserving birds in variegated	
	landscapes in southeastern Australia. Conservation Biology	
	15, 1364–1373.	