

Diversity and dynamics of coastal dune carabids

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Since 1990, populations of carabid beetles are continuously monitored in five coastal dune habitats in Belgium, situated along a transect from seaside marram dunes to inland moss dunes. In five complete year cycles about 14 000 carabids belonging to 76 species have been obtained. At most 50% of the species are continuously present in reproducing populations. The remaining species are only rarely caught, mostly outside of their normal reproductive season, and thus are presumably non-residents or vagrants. Furthermore, observations on wing and flight muscle development and on possible source areas support the hypothesis of accidental immigration rather than of local populations passing through bottlenecks. Many well-established and typical dune indicator species show strong fluctuations in their population dynamics, significantly concordant between different sampling stations and largely explained by climatological variables, either directly or indirectly. This study shows that the use of terrestrial invertebrates as bio-indicators in conservation ecology requires a population level approach.

1. Introduction

Carabid beetles are increasingly used as taxonomic study group in biodiversity and as bio-indicators in monitoring or site assessment studies for nature conservation purposes (e.g. Luff *et al.* 1989, 1992, Eyre & Luff 1990, 1994, Desender *et al.* 1991, 1992, Erwin 1991, Loreau 1994, Heijerman & Turin 1995, Dufrêne & Legendre 1996). The very high number of species, estimated some ten years ago at about 40 000 described species (Noonan 1985), as well as the well-studied pronounced habitat or even microhabitat preference of many of these (Thiele 1977) are important reasons for the increasing interest they get. Furthermore, the majority of carabid beetles (at least in temperate or subarctic climates) are relatively easily collected in a more or less standardized way

by means of pitfall trapping. Nevertheless, much discussion remains on the necessary methodologies in sampling (details of techniques, intensity and duration of trapping) as well as in data analyses (multivariate analysis techniques for community and indicator analyses, see e.g. Dufrêne & Legendre 1996) or in diversity assessment (Southwood 1978).

One problem related to the study of carabid diversity is to assess which part of the species caught at a certain site actually belongs to the local fauna and has reproducing populations. Related to this problem is the question of observed turnover in species richness from year to year on a given site. A short review of the literature shows that most authors either deny the problem (i.e. assume that all species caught on a site belong to the local fauna and/or that species caught in low numbers have a

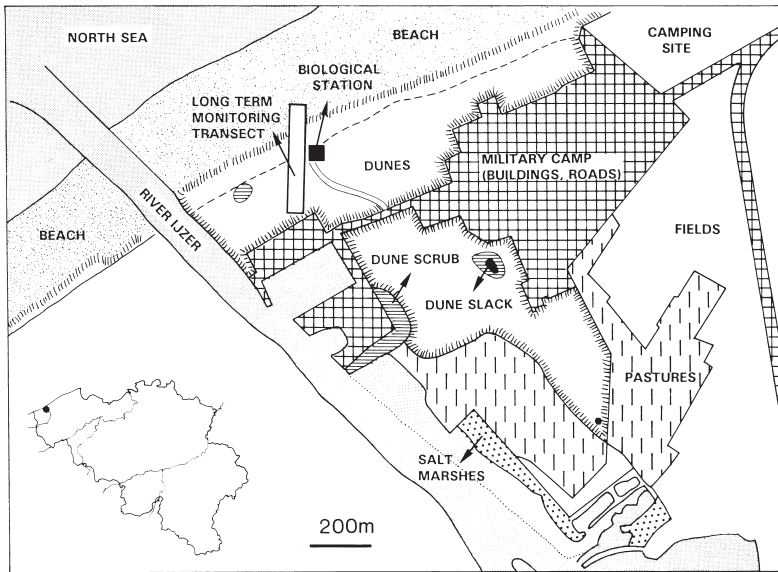


Fig. 1. Map of the study area with the sampling sites (long term monitoring transect).

small local population) or use a more or less arbitrary limit between so-called local species and accidentally caught species. Surprisingly, there have only been few attempts to discriminate between the two by means of long term population studies or by investigating additional aspects of the biology (dispersal power and reproductive characteristics) and ecology (occurrence in surrounding or nearby other habitats). A comparable problem is also encountered on a larger geographical scale, where one recently has started to distinguish between core and satellite species (e.g. Niemelä & Spence 1994).

A second problem is the lack of knowledge on year-to-year variation in numbers of many carabid species, in other words data on the magnitude of population dynamics in more or less natural situations. Such studies of course require a continuous long term sampling effort, which is probably the most obvious reason for their scarcity. If one does not take succession studies into account (which address different questions (e.g. Meijer 1980, Gruttke & Willecke 1993, Verschoor & Krebs 1995ab) but not always are able to discriminate natural dynamics from those linked to directional changes), there are indeed only a few studies where sampling has continued for over 5 years. As a result, until now relatively few authors have tried to document and explain these dynamics in carabids, and if and how these might be regulated (Weber & Klenner 1987, Den Boer 1990, 1991, Luff 1990, Van Dijk & den Boer 1992, Den Boer *et al.*

1993, Van Dijk 1994). Also, a recent paper by Den Boer and van Dijk (1994) shows that many of their long term series on carabid dynamics seem to have been influenced to a high degree by recent directional changes in environmental conditions (e.g. air pollution, changed drainage and vegetation cover) which could mean they have to be classified more as 'succession' studies.

In the above context, a long term monitoring project was started in coastal dunes in Belgium in 1990 and has been continued ever since. This study aims at understanding yearly dynamics at the community as well as the population level in order to define more precisely the possibilities and especially the constraints of such data for studies on site assessment, biodiversity and monitoring.

In this paper I will first evaluate the observed turnover in carabid species from year to year, I then will have a look at the dispersal power and reproductive state from discontinuously present species in order to find evidence in support of one of the two alternative hypotheses for their occurrence: are they accidental immigrants or do they belong to local populations passing through bottlenecks (years with very low abundance). Finally, for the well-established species, I will briefly discuss the extent of their population dynamics, whether or not their numbers fluctuate in synchrony in different populations and whether climatological data can at least partly explain the observed dynamics. Of course, analyses on the regula-

tion of population dynamics have to be viewed as preliminary because of the still relatively short nature of the available sampling series database.

2. Material and methods

Since 1990, populations of carabid beetles and spiders are continuously monitored in five coastal dune habitats, situated along a transect from seaside marram (*Ammophila arenaria*) dunes to inland moss dunes and dune grasslands.

The investigated dune habitats are located near the river IJzer estuary (Fig. 1), close to a field station of the R.B.I.N.Sc. These dunes are relatively undisturbed by tourism, which is extremely rare for Belgian standards. The transect includes seaward marram dunes (station 1), dune top (station 2) and landward side of the same marram dunes (station 3). These three habitats are all dominated by marram grass (*A. arenaria*). The remaining two sampling stations are situated more inland, one station close to the marram dunes (station 4), one station further inland (station 5). These sites are dominated by mosses, low herbs and lichens, which especially dominate in the fifth station. During the autumn of the fourth year cycle the monitoring work was disturbed due to the temporary loss of the seaward marram dune station, which vanished during several heavy northwestern storms. The authorities then decided to protect this area with a concrete wall, which was more or less covered with sand, and is now monitored again for beetles and spiders.

Other available habitats in the surroundings, which could have an influence on the investigated dune transect, have now also been sampled at least during a complete year cycle: these include some small dune scrubs, a humid dune slack, a small salt marsh area with its surrounding dikes, some pastures (partly created during the 1960's with sand from dredging the rivermouth) and cultivated fields on poor sandy soil (Fig. 1). The large database on these other sites has only been used here in order to trace the nearest likely source of possibly immigrating species in the dune transect.

Pitfall traps (3 in each sampling station; glass jam jars, diameter 9.5 cm, filled with a 10% formalin solution) are continuously in operation, emptied at fort-nightly intervals, immediately sorted and their content identified. In addition, at regular intervals, microclimate as well as vegetation cover and structure are measured on the sampling sites. Along with soil characteristics and climatological data from a nearby meteorology station, these measurements are viewed as direct or indirect environmental variables in order to attempt to explain species distributions and population dynamics.

In addition to their identification, all carabid beetles have been sexed and checked for their flight wing development. Moreover, species of rare or discontinuously occurring species have been dissected to assess the development of their flight muscles (Den Boer *et al.* 1980, Van Huizen 1977, 1990, Desender 1989). In the present study a distinction has been made between well developed and afunctional flight muscles only. Females from the same group of species were also dis-

sected in order to distinguish those in reproduction (at least carrying ripening or ripe eggs) from those out of their reproductive period (teneral, immature or spent).

The extent of population dynamics in the most abundant species was evaluated by calculating mean R values based on data for each sampling station ('coefficient of net reproduction = total number in year cycle i /number in year cycle $i-1$ ', after Den Boer 1990, Den Boer *et al.* 1993).

Analyses of concordance between yearly totals caught in different sampling stations were performed by means of Kendall's Test of Concordance (species occurring in sufficient numbers in at least three sampling stations) or Spearman Rank Correlation (species from two sampling stations only) (Siegel, 1956).

The yearly totals of the most numerous species were analysed in an ordination (Detrended Canonical Correspondence Analysis) in order to try to simplify the patterns of observed dynamics. At this stage, climatological variables were included in the analysis (temperature, precipitation, relative humidity and wind speed, all z -standardized, regrouped per season for each year or previous year, in other words including a time-lag, and after removal of redundant variables). Ordinations were performed by means of CANOCO (Ter Braak 1988).

Detailed time series are presented after interpolating the actual data to monthly totals, corrected for (small) differences in the number of days in each month.

In an earlier paper (Desender & Baert 1995) the sampling stations of this long term monitoring transect are presented in more detail along with analyses of the first four complete year cycles, with emphasis on the observed communities in different habitats or microhabitats and during different years.

In another study (Desender *et al.* 1992), we came to the conclusion that nearly every single dune habitat in the area that we monitored along the Belgian coast can be characterized by the presence of particular carabid species or assemblages. The sampling stations of this long term transect appeared to belong to two habitats with well differentiated carabid communities (and comparable results for different years, cfr. Desender & Baert 1995): on the one hand marram dunes situated close to the sea (stations 1-3), on the other hand a special kind of moss dunes with a high cover of lichens (stations 4-5).

The area that has been sampled furthermore presents a very high interest for nature conservation. In addition, many aspects of the biology and ecology of several typical carabid species occurring in the studied habitats are not well-known from the literature.

The present contribution is based on the first five complete year cycles with more than 14 000 carabid beetles from 76 species.

3. Results

3.1. Species turnover from year to year

From the 76 carabid species encountered in our complete dataset of the dune transect, only 32 were

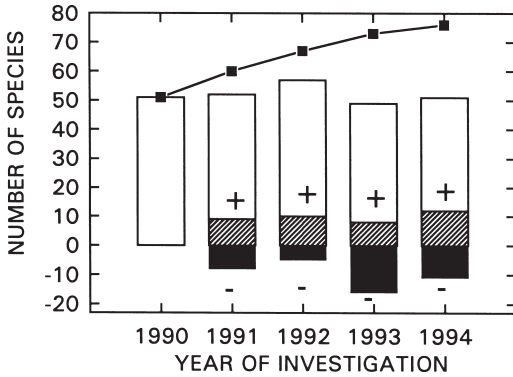


Fig. 2. Turnover in carabid species richness from year to year: each bar represents the number of species caught during a complete year cycle; hatched columns and '+' symbol: species not present in the previous year; black columns and '-' symbol: species lost as compared to previous year; line graph shows the cumulative total number of species.

caught each year in the traps (Table 1). The remaining 44 species only occur in very low numbers (a total of 161 ind., or about 1% only of all carabids caught), which is a first indication that are dealing primarily with temporarily or accidentally immigrating species.

Fig. 2 shows the total number of species caught each year along with the cumulative number of species. Year after year I observed newcomers as well as species disappearing from the stage again. On the whole, the cumulative number of species increased until the last year.

3.2. Discontinuously present species

3.2.1. Complete transect

The 44 species discontinuously present in the complete dune transect, with some exceptions only, ap-

Table 1. Number of carabid species caught during 1, 2, 3, 4 or all 5 year cycles in the investigated dune transect.

year cycles	species
1	16
2	10
3	9
4	9
5	32
total	76

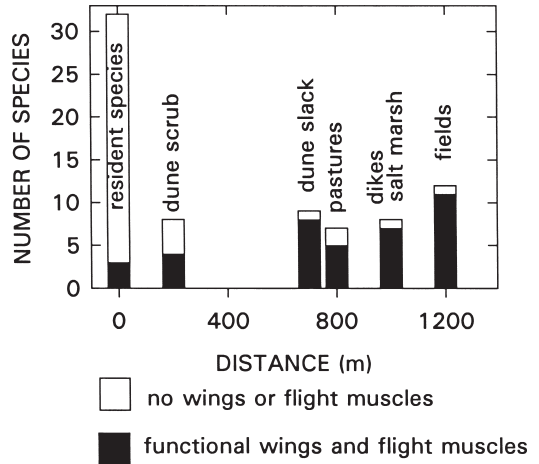


Fig. 3. Total number of carabid species from the dune transect arranged according to the distance of their presumed (nearest) habitat of origin; to the extreme left ('distance = 0') are the 32 well-established species, to the right and at increasing distance are the 44 discontinuously present species grouped according to their most probable source habitat; black bars represent species always found to possess functional wings and flight muscles in the dune transect material (see text for further explanation).

Table 2. Percentages of individuals and species with functional flight musculature for all species discontinuously found in the monitored dune transect, classified according to their most probable nearest habitat of origin (see Fig. 1 and the text for further explanation).

source habitat	total	%
dune scrub		
species	8	50
individuals	32	41
dune slack		
species	9	78
individuals	24	79
pastures		
species	7	71
individuals	31	94
dikes/salt marshes		
species	7	86
individuals	22	95
cultivated fields		
species	13	92
individuals	52	98
total		
species	44	77
individuals	161	83

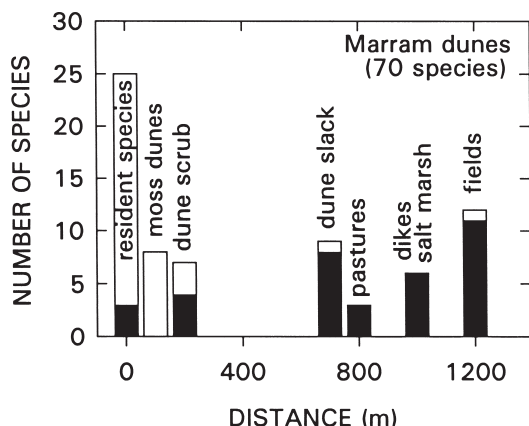


Fig. 4. Total number of carabid species from the marram dunes arranged according to the distance of their presumed (nearest) habitat of origin (see legend Fig. 3 and text for further explanation).

peared to occur in reproducing populations in the surrounding habitats. In Fig. 3, these 44 presumably non-resident species are grouped according to their most probable source habitat, that is, (1) the habitat where a population of the species is known to occur and (2) with minimal distance to the dune transect area.

The specimens of these 44 species caught in the dune transect for the majority were at the same time full-winged and in the possession of functional flight muscles and thus appeared to be able to fly (Table 2, Fig. 3). This is in sharp contrast to the resident species of the monitored dune transect: here a large majority of the species never was found to possess functional flight muscles (Fig. 3), or, for wing dimorphic species, primarily occurred in brachypterous

Table 3. Total number of individuals and percentage of macroptery in wing dimorphic carabid beetles from the monitored dune transect.

	total	% macr.
<i>Calathus cinctus</i>	1 401	2.86
<i>Calathus erratus</i>	2 632	1.48
<i>Calathus fuscipes</i>	978	0.31
<i>Calathus melanocephalus</i>	311	0.32
<i>Demetrias monostigma</i>	95	0.00
<i>Dromius linearis</i>	114	0.88
<i>Dromius notatus</i>	40	0.00
<i>Harpalus vernalis</i>	987	0.20
<i>Masoreus wetterhali</i>	42	0.00
<i>Metabletus foveatus</i>	1 033	0.97
<i>Metabletus truncatellus</i>	139	2.16

state (Table 3). Species most probably originating from the nearby small dune scrub take an intermediate position, which suggests that part of these species immigrated in the dune transect by walking instead of flying.

Except for some individuals only, females of the 44 non-resident species were immature or possessed spent ovaries, in other words were caught out of their natural reproductive period (Table 4).

3.2.2. Habitat or microhabitat spatial scale

In a further analysis, I decreased the spatial scale from the possibly somewhat unnatural level of a complete transect to habitat or microhabitat levels.

The presumably non-resident species of each habitat are again grouped according to their most probable source habitat (compare with Fig. 3).

For the marram dunes (Fig. 4) the results are comparable to those obtained for the complete transect, be it with even fewer resident species. In addition, there are low to very low numbers of all typical species belonging to the adjacent habitat, the moss dunes. From the results obtained for the com-

Table 4. Percentages of female individuals and species with immature or spent ovaries for all species discontinuously found in the monitored dune transect, classified according to their most probable nearest habitat of origin (see Fig. 1, and text for further explanation).

source habitat	total	%
dune scrub		
species	8	75
individuals	19	79
dune slack:		
species	9	89
individuals	15	80
pastures		
species	7	86
individuals	16	94
dikes/salt marshes		
species	7	100
individuals	12	100
cultivated fields		
species	12	92
individuals	41	98
total		
species	43	89
individuals	103	91

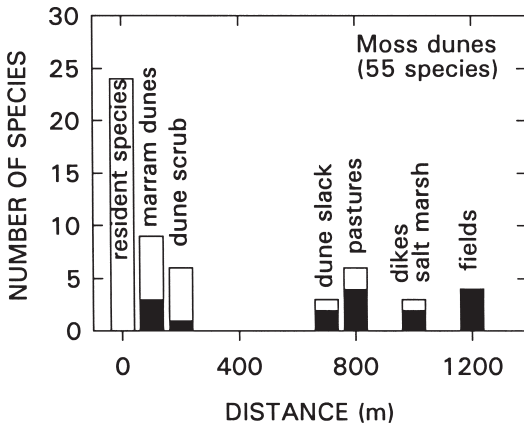


Fig. 5. Total number of carabid species from the moss dunes arranged according to the distance of their presumed (nearest) habitat of origin (see legend Fig. 3 and text for further explanation).

plete transect, it is not a surprise that in this case these carabids are nearly all non-flying species or specimens. The moss dunes (Fig. 5), in turn, show the same phenomenon.

3.3. Population dynamics of well-established species

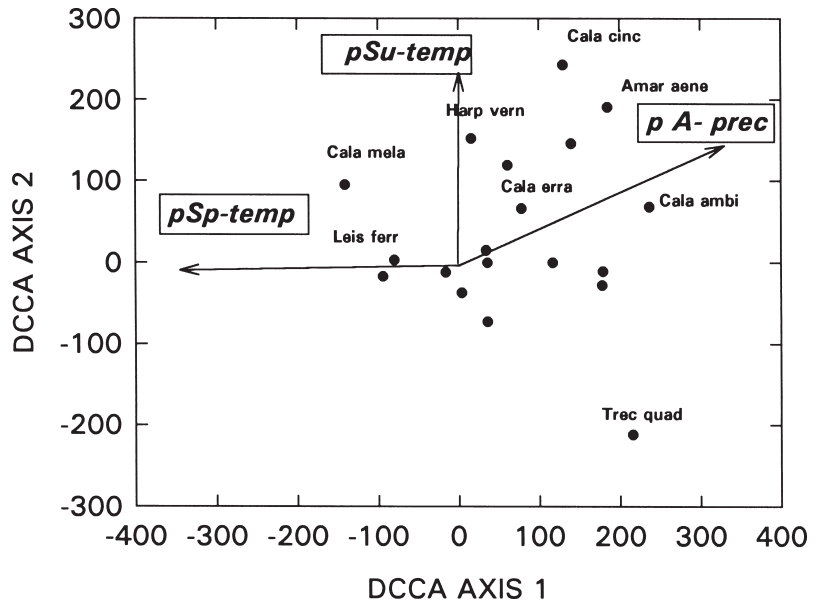
Table 5 shows the total number of individuals for the most abundant ground beetle species caught each year in the complete transect. Obviously these species account for the majority of all individuals caught. Mean *R* values (coefficients of net reproduction) based on data for each sampling station show the extent of dynamics. Added logarithmic *R* values show a distinction between species with generally increasing versus generally decreasing trends in dynamics. Although the sampling period is still relatively short, the overall mean of these values after five complete year cycles is close to zero (= 0.0078), which means that there is no overall positive or negative trend in the dynamics of these abundant species for this period.

Table 6 shows the results of comparisons of year totals over the different sampling stations for the most abundant species (analysis of concordance). The majority of the most abundant species show distinct population dynamics fluctuating in significant synchrony in different sampling stations. Twelve of these spe-

Table 5. Total number of individuals caught during each year cycle (YC) for the most abundant carabid species from the monitored dune transect (19 species accounting for the majority of total numbers of individuals caught), along with mean *R*-values (coefficient of net reproduction), mean ln(*R*) values, and *N* (number of possible comparisons for a maximum of 5 sampling stations between two consecutive years) (remark: total numbers of YC4 corrected for temporary losses of station 1 but *not* used in the calculations of *R*-values)

	YC1	YC2	YC3	YC4	YC5	sum	mean(<i>R</i>)	mean(ln(<i>R</i>))	<i>N</i>
<i>Amara aenea</i>	12	3	28	51	60	154	2.09	0.242	11
<i>Amara familiaris</i>	8	10	39	28	73	158	4.00	0.397	13
<i>Amara lucida</i>	104	22	18	14	48	206	1.58	-0.036	14
<i>Bembidion lunulatum</i>	81	29	24	15	74	223	1.44	-0.131	12
<i>Calathus ambiguus</i>	20	11	101	107	38	277	1.64	0.093	9
<i>Calathus cinctus</i>	169	37	98	393	740	1 437	2.39	0.166	12
<i>Calathus erratus</i>	913	233	524	449	628	2 747	1.37	-0.156	18
<i>Calathus fuscipes</i>	282	61	224	247	164	978	1.51	-0.098	11
<i>Calathus melanocephalus</i>	202	26	16	34	33	311	1.08	-0.673	12
<i>Calathus mollis</i>	1 035	257	502	819	1 355	3 968	1.69	0.006	18
<i>Demetrias monostigma</i>	38	14	17	8	34	111	1.45	-0.212	10
<i>Dromius linearis</i>	34	31	29	13	9	116	1.29	-0.315	15
<i>Harpalus anxius</i>	174	107	94	88	135	598	1.81	0.123	18
<i>Harpalus servus</i>	53	112	91	148	139	543	1.45	0.152	18
<i>Harpalus vernalis</i>	115	43	14	59	159	390	1.60	0.047	8
<i>Leistus ferrugineus</i>	115	36	17	6	55	229	1.47	-0.340	11
<i>Metabletus foveatus</i>	153	111	209	180	389	1 042	1.51	0.320	15
<i>Metabletus truncatellus</i>	13	26	51	43	45	178	1.79	0.154	17
<i>Trechus quadristriatus</i>	6	31	73	21	14	145	2.26	0.410	11
total	3 527	1 200	2 169	2 723	4 192	13 811			

Fig. 6. Species scores of the most abundant carabid species after DCCA on yearly totals along with z-standardized climatological variables (see text for further explanation; only variables significantly related to ordination axes are added); pSp = previous spring, pSu = previous summer, pA = previous autumn, temp = temperature, prec = precipitation; abbreviations added for some selected species: Cala mela = *Calathus melanocephalus*, Leis ferr = *Leistus ferrugineus*, Harp vern = *Harpalus vernalis*, Cala erra = *Calathus erratus*, Cala cinc = *Calathus cinctus*, Amar aene = *Amara aenea*, Trec quad = *Trechus quadristriatus*, Cala ambi = *Calathus ambiguus*.



cies show significant or highly significant concordance. For most of the remaining seven species correlation values are not significant but nevertheless largely positive, suggesting also synchronous fluctuations.

The yearly totals of the 19 most numerous spe-

cies are analysed in an ordination in order to try to simplify the patterns of observed dynamics. The species scores along with the climatological variables, associated significantly to the two most important ordination axes, are shown on Fig. 6. Axis 1

Table 6. Results of analysis of concordance between values for different year cycles in different sampling stations (Kendall's W , in the case of 5, 4 or 3 stations with sufficient numbers of the species concerned, or Spearman rank correlation values, for species occurring only in two sampling series); significance of correlation values added, along with total number of individuals.

sampling series	5	4	3	2	$p <$	N
<i>Amara aenea</i>			0.928		0.011	54
<i>Amara familiaris</i>				0.6	<i>n.s.</i>	158
<i>Amara lucida</i>				0.9	0.05	206
<i>Bembidion lunulatum</i>			0.606		<i>n.s.</i>	223
<i>Calathus ambiguus</i>				0.7	<i>n.s.</i>	277
<i>Calathus cinctus</i>	0.654				0.01	1437
<i>Calathus erratus</i>	0.600				0.01	2747
<i>Calathus fuscipes</i>			0.472		<i>n.s.</i>	978
<i>Calathus melanocephalus</i>	0.526				0.05	311
<i>Calathus mollis</i>	0.632				0.01	3968
<i>Demetrias monostigma</i>			0.817		0.01	111
<i>Dromius linearis</i>	0.482				0.05	116
<i>Harpalus anxius</i>	0.158				<i>n.s.</i>	598
<i>Harpalus servus</i>	0.214				<i>n.s.</i>	543
<i>Harpalus vernalis</i>				0.9	0.05	390
<i>Leistus ferrugineus</i>				1.0	0.01	229
<i>Metabletus foveatus</i>			0.761		0.05	1042
<i>Metabletus truncatellus</i>		0.334			<i>n.s.</i>	178
<i>Trechus quadristriatus</i>	0.578				0.01	145

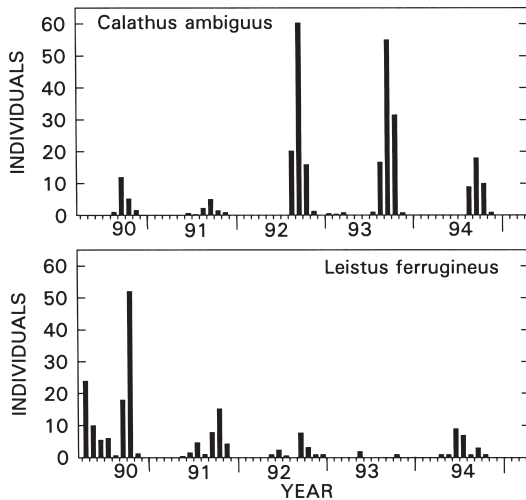


Fig. 7. Detailed time series of monthly totals (males + females) of *Calathus ambiguus* and *Leistus ferrugineus* from five complete year cycles in a dune transect.

in this analysis accounts for 55% of the total variation, whereas the second axis adds only 9% more to this explanation. A large variability is observed in the dynamics of different species. Climatic variables retained by the analysis concern temperature and precipitation values from the previous year, in other words include a time-lag.

At the right in Fig. 6 species are situated which appeared more numerous in the third and fourth year cycle. An example is the autumn breeder *Calathus ambiguus* (Fig. 7). Its peak values coincide with high autumn precipitation during the previous year, the autumn being the period in which this species lays eggs or possesses larvae. In the extreme left of the ordination *Leistus ferrugineus* (Fig. 7) shows a continuously decreasing population till the fourth year and since then appears to increase again. The pattern is highly significantly concordant between different sampling stations (Table 5), and peak years seem to coincide more or less with higher temperatures during the spring of the previous year.

4. Discussion

My results indicate that a majority of the discontinuously present species in the studied dune transect are vagrants, caught after accidental immigration by flight and that they do not really belong to the local

dune transect fauna. Based on the investigated criteria (relative abundance, dispersal power in relation to the nearest possible occurrence in surrounding habitats, reproductive state of females), only two or three species out of 44 species, would be interpreted as cases of small local populations or populations temporarily passing through bottlenecks.

Decreasing the spatial scale of my analysis from the complete transect to the level of habitat or microhabitat does not alter this conclusion: my results on a habitat scale again give more support to the hypothesis that species, that are discontinuously caught, are in majority accidental immigrants rather than individuals from small local populations.

For this reason alone, species richness and diversity measures must be used with great caution, at least in a mosaic landscape, where the influence of accidental immigrants is expected to be larger.

One interesting difference between the non-resident carabids in the marram dunes as compared to moss dunes is a relatively larger number of field-inhabiting species found in the former: this could be due to the fact that the open nature of the soil surface in fields and in marram dunes from a distance is quite comparable; another or additional explanation is the sporadic accumulation of beetles (carabids and others) along the seashore and in marram dunes due to a light southern breeze at the coast on days with exceptional climatic conditions for flight (e.g. in spring), 'stowing' flying beetles to the coastline (cfr. Palmen 1944).

Only few papers have evaluated which species of an inventory actually reproduce in a sampled habitat. Luff (1990) classified more than 50% of the carabid species in a long term study of a mosaic field/grassland site as presumed immigrants. Eversham and Telfer (1994) concluded that about 50% of the collected carabid fauna of a poor grassland road verge actually had bred there. In an earlier paper on an intensively grazed pasture (Desender & Pollet 1988) we came to a similar conclusion. Increasing the number of traps beyond 3 to 6 pitfalls (which yielded all locally reproducing species) up to 30 traps did not lead to a plateau in the cumulative number of species obtained, but gave information of immigrating species from the surroundings.

On a year cycle basis, the dune transect results have shown that the threshold for considering a species as belonging to the local fauna of a habitat

roughly is situated at least at about one individual per three traps. Increasing the sampling effort (i.e. the number of traps) per sampling station not only would give a more accurate estimate of variation in numbers of individuals for a given species in a given (micro-)habitat (Desender & Pollet 1988) and allow a better assessment of spatial distribution (e.g. Desender 1988). It also would have the disadvantage to increase the chances of adding new species to an inventory, without these actually belonging to the local fauna. The number of traps to be used in a study will thus depend on the specific questions and will not necessarily have to be very high, in contrast to suggestions made by many previous authors (e.g. Obrtel 1971)! This does, however, not preclude the need to investigate whether species caught in small numbers on a given site actually belong to the local fauna, i.e. reproduce there successfully. Simply looking at their dispersal power (wing and flight muscle development) in many cases will already suggest how to classify such species.

The majority of the most abundant species in the studied dune transect show distinct population dynamics fluctuating in significant synchrony in different sampling stations. These results suggest a dominant role of general abiotic and climatological factors in the regulation of population numbers.

A large variability is observed in the dynamics of different species. Dynamics are partly explained by climatic variables: such variables retained by the analysis include a time-lag. This could suggest a dominant role of direct or indirect effects on pre-imaginal stages in adult population regulation, a suggestion already made in several other papers (e.g. Nelemans *et al.* 1989, Van Dijk & Den Boer 1992, Van Dijk 1994).

Years with peak values for *Calathus ambiguus* coincide with high autumn precipitation during the previous year, the autumn being the period in which this species lays eggs or possesses larvae. Although very speculative, this could mean that in years with a low precipitation during autumn, the younger pre-imaginal stages of this species, paradoxically known as xerophylous, severely suffer from desiccation. Of course the influence could be indirect through for example the abundance of food or prey. The pattern of yearly dynamics for *Leistus ferrugineus* seems to coincide more or less with higher temperatures during the spring of the previous year. Interestingly, this is a carabid species with larvae showing a relatively

high soil surface activity during winter, whereas the new generation of beetles appears in spring. The larvae as well as the adults are moreover known as specialized predators on springtails, which they hunt at night. A speculative hypothesis here could be an indirect relation to temperature, related to springtail activity and abundance. On the other hand *Leistus ferrugineus* is one of the few carabid species in our dunes known to hold a summer diapause, which could explain why its dynamics seem not to be influenced by summer temperature nor precipitation.

To conclude, a high turnover from year to year is observed in the carabid species of a long term monitoring dune transect: depending on the spatial scale at most 50% of the species are continuously present in reproducing populations. Below certain observed threshold numbers, the turnover in carabid species is obvious. This indicates the limit between species with resident populations and those immigrating accidentally or temporarily. Species richness and diversity measures must therefore be used with caution, at least in a mosaic landscape. The majority of discontinuously present species appear to be full-winged with functional flight muscles, are not in reproduction (immature or spent females) and are known to occur in nearby source areas. Therefore the majority of these species do not appear to belong to small local populations but are most probably accidental immigrants or vagrants from surrounding habitats.

The abundant carabid species in the studied dune transect show important fluctuations from year to year which are mostly in synchrony in different populations. This suggests a dominant role of more general abiotic and climatological factors in the regulation of population numbers. The observed fluctuations, although based on a still relatively short time series, indeed can partly be explained by climatic fluctuations.

As a more general conclusion, data on population level (dynamics, structure, genetics, ...) are recommended for a more straightforward use of terrestrial invertebrates as bio-indicators in conservation ecology, as has recently also been proposed by Schmid and Matthies (1994).

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