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Impact of anthropogenic disturbances on beetle communities of French Mediterranean coastal dunes

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Abstract In coastal dunes, influenced by anthropogenic activities such as tourism, it is important to determine the relative influence of environmental factors at different spatial scales to evaluate the sensitivity of local communities to disturbances. We analyzed beetle communities of 14 dunes of the French Mediterranean coast: four in the relatively preserved Camargue area, and ten in the Var department, where tourism is intensive. Beetle communities were studied three times in early spring using sand sampling. Species-environment relationships were evaluated at the regional, landscape and local scale using redundancy analysis (RDA) and variability partitioning. About 28 species were identified, of which 15 were sand-specialist species, which accounted for more than 93% of total abundance. The beetle communities of Camargue were significantly different from those of the Var department owing to the pullulation of a Tenebrionid species (*Trachyscelis aphodioides* Latr.) in the Var, except for one restored dune where the community was very similar to those of Camargue. Our results showed no longitudinal gradient between the two regions. Local factors (dune height, preservation and disturbance index) significantly explained most of the variation in the dominance of *T. aphodioides*, while some other local factors were important for other psammophilous species. This study also suggests that dune beetle communities are strongly affected on beaches intensively managed for tourism, but beetles are still abundant in much disturbed sites.

Keywords Insect · Coleoptera · Tourism · Trampling · Urbanization · Beach · Pullulation

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Introduction

Coastal dunes are original and fragile ecosystems particularly endangered on the shore of the Mediterranean Basin, where anthropogenic disturbances are exceptionally strong. Highly specialized plants and animals are characteristic of these ecosystems (Fallaci et al. 1997), which are constrained by long periods of dryness and high temperatures fluctuating over a large range (Bigot et al. 1982). Composition and structure of arthropod communities are likely to reveal disturbances affecting these ecosystems, since they respond rapidly to environmental changes and provide information on system functioning (Kremen et al. 1993; Finnamore 1996; Colombini et al. 2003). Amongst arthropods, beetles (Coleoptera) are known to be a major part of all living biodiversity (Erwin 1988; Hammond 1992; Wilson 1992), especially in dune ecosystems (Bigot et al. 1982; Ponel 1986). They are a key-element of ecosystem functioning, since they take part in all trophic levels (Burger et al. 2003) and are sensitive to environmental disturbances. Numerous species are habitat-specialist of these Mediterranean dune systems (Aloia et al. 1999; Fallaci et al. 2002).

Disturbances affecting dunes are the consequences of actions occurring on the beach itself (dune trampling, habitat fragmentation, beach cleaning) and of modifications of beach surroundings (urbanization, roads and car parks, camping sites). Most of the studies achieved on beach Coleoptera during the past 15 years were performed on the Italian coast (usually on a single site), while the last work on this topic on the French Mediterranean seashore was conducted more than 20 years ago (Ponel 1986). According to these studies, it seemed that beach Coleoptera were especially sensitive to local characteristics (sand water content, temperature, salinity and pH), which determined a spatial and temporal distribution of species from the dune to the sea (Fallaci et al. 1997, 2002; Aloia et al. 1999; Colombini et al. 1994, 2002, 2005; Colombini and Chelazzi 1996). However, none of these studies considered a larger scale than the beach itself. The influence of surrounding landscape and disturbances on beach invertebrate communities was only suggested by Colombini et al. (2003), Burger et al. (2003) and Chelazzi et al. (2005).

According to this literature, we hypothesize that beetle communities could be affected by a pool of anthropogenic disturbances, some acting at a very local scale (the dune itself) and others at a larger scale (like the surrounding landscape), and resulting in changes in the species richness or relative abundances of species. Since disturbances affect ecosystem functioning, we have tried to consider not only the species assemblages, but also the distribution of two functional groups (insect body size and trophic guild), which could reveal both the effects of environmental factors and the scale at which they are acting (Schweiger et al. 2005).

The aim of this study was, thus, to characterize beetle communities subjected to different disturbances resulting from tourism and to check the possible effects of environmental factors acting at different spatial scales.

Material and methods

Study sites and sampling

Fourteen dunes were chosen along 350 km of the French Mediterranean seashore: four in the Camargue area, where the anthropogenic pressure is low and ten in the “Var” department, where tourism is intensive (Fig. 1). No suitable site was available for this study between these two areas (“Bouches-du-Rhône” department). Dune area was highly

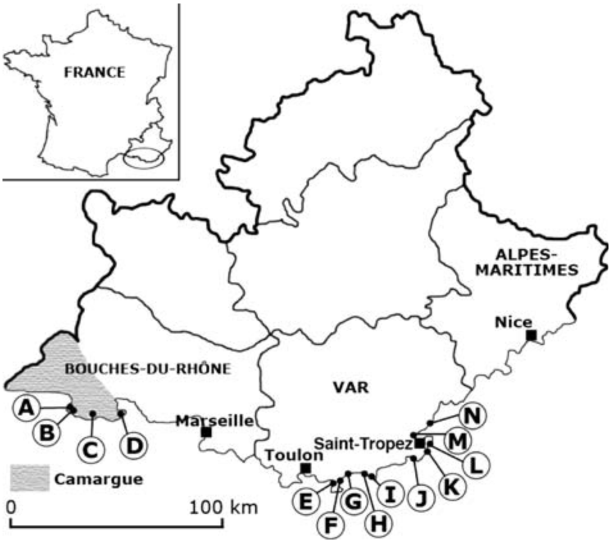

Fig. 1 Location of the 14 studied dunes on the French Mediterranean coast. A = Beauduc A; B = Beauduc B ; C = Piémanson ; D = La Gracieuse ; E = L'Almanarre ; F = Hyères Plage ; G = Les Salins d'Hyères ; H = Cabasson ; I = Le Moulin ; J = La Briande ; K = Pampelonne Sud ; L = Pampelonne Nord ; M = Cogolin ; N = Villepey

variable, from *ca.* 2 ha in Camargue to only *ca.* 100 m^2 in several relictual dunes of the Var. A 100 m^2 sampling area was used at each site, whatever the dune total area. Sampling was performed three times during the spring of 2006 (February, beginning and end of March), when the species abundance was the highest in the Var dunes (Ponel 1986). During each session, six samples (three on vegetated dune and three on adjacent bare sand) were gathered at each site, providing a total of 252 samples for the whole 14 sites. At each site, the distance between two samples never exceeded 5 m. Samples were collected with a 15 cm-wide metallic cylinder sunk into the sand down to 15 cm deep (Chelazzi et al. 2005). This auger-like technique allowed to collect a constant volume of intact sand, without bias due to sand expansion when removed. In the laboratory, insects were sorted from the sandy sediment with an elutriator made of a PVC pipe. Individuals drifted by the ascending water current out of the elutriator were collected on a set of three superimposed sieves of decreasing mesh size (1 cm, 5 mm, 800 µm) and then identified under a binocular microscope. Owing to their scarcity and to taxonomic difficulties, larvae were not taken into account.

Life traits

Species were organized into ecological groups by (i) their habitat specialization (habitat generalist or specialist species), (ii) body size and (iii) trophic guild, according to the literature. The total body length, from pygidium to forehead (excluding antenna), was measured on at least one specimen of each species. The values were, then, classified into ordinal size classes. The trophic status of each species was determined according to Caillol (1908, 1913, 1914, 1954a, b), Thérond (1975, 1976) and Ponel (1993). Six trophic guilds were distinguished: detritivorous, saprophagous, necrophagous, phytophagous, predacious, and polyphagous species. The abundance of insects belonging to each category was recorded at each site.

Environmental factors

First of all, a total of 20 environmental factors, grouped into three main sets, were considered to characterize (i) the dune itself: dune height, width and length, vegetation cover and patch size, sand organic matter content and granulometry (Ponel 1983; Aloia et al. 1999; Colombini et al. 2005). A synthetic variable "preservation" was estimated by detailed observation of each site, to obtain a global index of the dune health (general environmental quality of the site); (ii) the surrounding landscape (8 types of soil cover within a 200 m-radius around each dune, which was the maximal distance that allowed the observer to identify the landscape composition); (iii) disturbances: urbanization, tourism intensity, dune trampling, beach cleaning (i.e., removal of algal debris and organic matter deposits). For disturbances, a synthetic disturbance index (DI) was also computed as follows: the values of the four factors of the "disturbances" data set (Table 1) were reduced to the [0–1] interval using the Gover's method ($X' = (X - X_{min})/(X_{max} - X_{min})$; Legendre and Legendre 1998). The disturbance index was simply the average of these reduced values for each site. It was not used in RDA, but only for correlation. Since maps or aerial photographs were not available, each parameter was quantified on an ordinal scale ranging from 0 to 5 (Table 1) according to field observations (dune and landscape features), laboratory analyses (granulometry, organic matter) and available public statistics (tourism).

Statistical analyses

All samples were pooled over time for the analysis of vegetated *vs.* bare sand (Mann–Whitney *U*-Test), and over time and sites for all the other analyses. Non-parametric Spearman rank correlation coefficient (r_s) was used when necessary. Species richness, Shannon's diversity and evenness were computed only for beetle abundance at each site, not for functional groups. Differences in Shannon's species diversity were statistically tested using Hutcheson's *t*-test (Hutcheson 1970). Owing to the geographical distribution of sites (four in Camargue and ten in the Var department), a potentially nested structure of the data could be suspected. In that case, it would have been impossible to differentiate the effects of environmental factors (e.g. disturbances) from that of the regional species pool. This possibility was tested on both explanatory factors (Table 1) and species abundances (Table 2) by Trends Surface Analysis (second order polynomial including geographic (Euclidean) coordinates of each site). Spatial Analysis in Macroecology software (SAM v2.0, April 2007; Rangel et al. 2006) was used for this purpose. The southernmost site (Almanarre) was defined as the zero of the *Y* coordinates and Beauduc A and B (the westernmost sites), as the zero for the *X* coordinates (see Table 1). Differences in species assemblages and functional groups at each site were detected by means of Principal Component Analysis (PCA) on log-transformed data. Then, as the explanatory variables could be different for community composition and for functional groups, the three sets of environmental factors (dune morphology, landscape composition and disturbances; see Table 1) were related separately to each set of biological data by means of Redundancy analysis (RDA) with forward selection and Monte Carlo permutation tests (999 permutations) (CANOCO Software; Ter Braak and Smilauer, 2002). The resulting significant environmental factors (which were not constant across all analyses) formed a reduced set of factors, which was, then, submitted to hierarchical variability partitioning using partial RDA (Borcard et al. 1992; Legendre and Legendre 1998). The variability explained by each reduced set of environmental factors (and related significance level) were adjusted for sample size and number of predicting

Table 1 Quantification (0 to 5) of sites characteristics (dune structure, landscape composition and disturbances), average disturbance index (DI), geographical coordinates of sites (km)

		BEAU-A	BEAU-B	PIEM	GRAC	ALMA	HYER-P	SALINS	CABAS	MOUL	BRIAN	PAMP-S	PAMP-N	COGOL	VILLEP
Dune structure	Dune height	2	5	4	5	3	2	1	2	1	2	3	2	1	4
	Dune width	5	5	5	5	3	3	2	3	2	1	4	2	1	4
	Beach length	5	5	5	5	5	4	5	3	3	2	5	5	3	5
	Preservation	5	5	3	4	4	3	0	3	4	1	3	3	0	5
	Fine granulometry	5	5	1	2	2	5	2	3	3	3	1	1	1	1
	Organic matter	1	5	5	5	5	2	5	2	5	5	3	3	5	3
	Patch size	5	5	5	5	3	2	3	1	4	2	3	1	3	5
	Vegetation cover	2	4	3	2	4	5	4	3	3	1	2	3	3	4
Landscape	Sand	2	2	0	0	0	0	0	3	0	0	0	2	0	0
	Water	2	1	0	0	0	0	0	0	0	0	0	0	1	2
	Trees	0	0	0	0	0	0	0	2	5	2	0	0	0	0
	Bamboo	0	0	0	0	0	0	0	0	0	1	4	2	2	0
	Herbaceous cover	0	0	0	0	0	3	2	0	0	2	0	2	3	3
	Halophilous	2	2	5	5	3	0	3	0	0	0	0	0	0	0
	Roads/parks	0	0	0	0	3	2	1	2	0	0	3	3	3	0
	Building	0	0	0	0	0	3	0	0	0	2	1	2	3	0
Disturb.	Urbanization	0	0	0	0	2	3	2	3	0	2	3	4	5	1
	Beach use intensity	0	0	2	1	5	5	5	5	1	3	5	5	5	5
	Dune trampling	0	0	1	1	1	1	4	2	1	3	2	2	5	1
	Beach cleaning	0	0	2	0	5	5	5	3	0	0	5	5	5	5
	Disturb. Index (DI)	0	0	0.3	0.1	0.65	0.7	0.8	0.65	0.1	0.4	0.75	0.8	1	0.6
Geographical coordinates	Longitude: X (km)	0	0	15.8	24.6	124.3	126.9	130.9	140.5	141.1	165.6	168	168	162.3	173.7
	Latitude: Y (km)	35.8	36.6	30	32.3	0	1.2	4.4	2.5	1.6	10.6	15.2	17.9	20.6	36.5

Table 2 Abundance of each species (sorted by alphabetical order of family, then species) in the 14 sites, sorted according to their geographical position, from the west (Beauduc A) to the east (Villepey)

Family	Species	Species code	Beauduc A	Beauduc B	Piémanson	La Gracieuse	L'Almanarre	Hyères-Plage	Les Salis d'Hyères	Cabasson	Le Moulin	La Briande	Pampelonne Sud	Pampelonne Nord	Cogolin	Villepey	Total
Anthicidae	*Anthicus tristis*	Anth_tri	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
Aphodiidae	*Pleurophorus caesus*	Pleur_cae	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	*Psammodius basalis**	Psamm_bas	3	0	1	3	0	1	0	4	0	0	0	0	2	2	16
	*Psammodius porcicollis**	Psamm_por	6	2	4	12	6	9	3	11	0	2	6	4	2	3	70
Carabidae	*Harpalus affinis*	Harpal_aff	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Chrysomelidae	*Chaetocnema tibialis*	Chae_tib	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
	Psylliodes marcidus	Psyll_mar	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
	Tytthaspis sedecimpunctata	Tytt_sed	0	0	0	0	0	0	0	0	0	0	0	0	3	0	3
Cryptophagidae	*Cryptophagus sp.*	Crytoph	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Curculionidae	*Otiorhynchus juvencus**	Otior_juv	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
	*Philopedon plagiatum**	Philop_pla	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Elateridae	*Cardiophorus exaratus**	Cardio_exa	0	0	0	0	0	0	0	0	0	0	2	0	1	0	3
Histeridae	*Xenonychus tridens**	Xenon_tri	0	3	3	0	0	6	0	5	0	1	2	0	3	2	25
Nitidulidae	*Meligethes sp.*	Meligeth	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Staphylinidae	*Aleocharine G.*	Aleoch_1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
	Aleocharine G.	Aleoch_2	0	0	0	0	0	7	0	0	0	0	0	2	0	1	10
	Bledius unicornis	Bledi_uni	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
	Tachyporus chrysomelinus	Tachyp_chr	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
	Xantholinus sp.	Xanthol	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Tenebrionidae	*Ammobius rufus**	Ammob_ruf	0	14	38	17	1	7	10	3	0	7	25	0	26	25	173
	*Catomus consentaneus**	Catom_con	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2
	*Halammobia pellucida**	Halam_pel	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	*Phaleria bimaculata**	Phaler_bim	0	0	0	0	0	0	0	0	7	1	0	0	0	0	8
	*Phaleria provincialis**	Phaler_pro	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
	*Pimelia bipunctata**	Pimel_bip	0	0	1	0	0	0	1	0	0	0	0	0	0	0	2
	*Stenosis intermedia**	Stenos_int	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
	*Tentyria mucronata**	Tenter_muc	0	0	0	0	0	0	1	0	0	0	1	0	0	0	2
	*Trachyscelis aphodioides**	Trachy_aph	5	0	0	1	112	457	558	60	308	65	75	35	112	2	1790
		Total abundance	14	20	48	36	119	488	575	84	315	77	111	43	153	38	2121
		Richness	3	4	6	7	3	7	7	6	2	6	6	5	11	9	28

Psammophilous species are marked with *. Species codes will be used in figures factors according to Peres-Neto et al. (2006). All these above-mentioned analyses were performed with or without the dominant species (see below) when relevant.

Results

Possible regional effect

As stated before (see Material and Methods, Statistical Analyses), it was at first necessary to test for a possible regional effect before relating site characteristics to species assemblages. Except for the variable "halophilous" (occurrence of halophytes in the surroundings of dunes), which was typical of Camargue ($P = 0.03$), no spatial trend was found for all the other environmental factors. In the same way, neither the species richness, nor the total abundance of individuals, exhibited a regional trend (tests computed on all species pooled, psammophilous species alone, or allochtonous species alone). The spatial distribution of each species was also tested, which led to no significant spatial trend ($P > 0.23$ in all cases). Thus, observed differences between the species assemblages at the 14 sites could be legitimately related to local environmental factors.

Global description of the community

A total of 2,121 beetles was collected in the 252 samples coming out from the elutriation of 1.4 tons of sand. Only 30 individuals were collected in the bare sand plots. This difference of abundance between vegetated and bare sand was highly significant for all dunes (Mann–Whitney *U*-Test, $P < 0.003$). Since these few individuals from bare sand belonged to the same species as those found in vegetated sand, the samples from these two areas were pooled for further analyses.

The beetle fauna was distributed amongst 11 families, 26 genera and 28 species (Table 2). Two distinct sets of species composed the community: (i) a set of 15 species (2,096 individuals in total) which were considered as specialists of sandy habitats, according to the general literature on Coleoptera ("psammophilous" species), and (ii) a set of 13 other species (only 25 individuals in total) which were not typical of dunes, but generally found in various types of ecosystems ("habitat generalist" species, also called "allochtonous species" in this paper). Amongst the sand specialist species, the Tenebrionidae were the most numerous in terms of species richness (10 species) and abundance (more than 93% of total abundance), with *Trachyscelis aphodioides* Latr. accounting for more than 84% of total abundance (1,790 individuals). Only six species accounted for 98% of the total abundance. The other 22 species were uncommon (15 singletons, i.e., more than one half of the total species richness).

The Shannon's index of diversity (H') computed on total abundance (both psammophilous and allochtonous species pooled) resulted in three groups of sites (Table 3) according to the statistical significance of the Hutcheson *t*-test ($P < 0.05$): [a] a group where the diversity was the highest, [b] in which the diversity was intermediate (La Briande and Pampelonne Nord), and [c] where the diversity was very low. In this last group, the community was highly dominated by *T. aphodioides.* That species occurred in high number on nine of the ten dunes of the Var department, but was extremely rare in Camargue and Villepey dunes since only eight individuals of this species were caught on these five dunes. As expected, the evenness was the lowest where *T. aphodioides* was overly dominant. We can notice that the dunes of Camargue did not exhibit the highest species richness, though their

Table 3 Characteristics of species assemblages in the 14 sites

Site	Site code	Richness	Abundance	Density (ind./liter)	Psammophil. sp. (%)	Shannon H'	Evenness	Group
Beauduc A	BEAU-A	3	14	0.56	100	1.531	0.966	a
Beauduc B	BEAU-B	4	20	0.79	100	1.319	0.66	a
Piémanson	PIEM	6	48	1.83	83	1.165	0.451	a
La Gracieuse	GRAC	7	36	1.43	86	1.913	0.681	a
L'Almanarre	ALMA	3	119	4.72	100	0.358	0.226	c
Hyères Plage	HYER-P	7	488	19.37	86	0.485	0.173	c
Salins d'Hyères	HYER-S	7	575	22.82	100	0.247	0.088	c
Cabasson	CABAS	6	84	3.33	100	1.43	0.553	a
Le Moulin	MOUL	2	315	11.59	100	0.154	0.154	c
La Briande	BRIAN	6	77	2.94	100	0.902	0.349	b
Pampelonne Sud	PAMP-S	6	111	4.33	100	1.364	0.528	a
Pampelonne Nord	PAMP-N	5	43	1.71	60	1.019	0.439	b
Cogolin	COGOL	11	153	6.07	55	1.387	0.401	a
Villepey	VILLEP	9	38	1.51	56	1.91	0.602	a

Density is defined as the number of individuals per sand liter. Groups a, b and c are defined according to the Shannon's diversity index (H') and Hutcheson's *t*-test (see text). Site codes will be used in figures

diversity and evenness were high. The last two sites of Table 3 showed a high richness; however, only a few species were specialist of sandy habitats. Others were habitat generalist species.

Species assemblages

The two first axes of the PCA performed on log-transformed abundances of all psammophilous species (Fig. 2a) accounted for 80.5% of total variance. The PC1-axis was mainly structured by the Tenebrionidae *T. aphodioides* and by two Aphodiidae: *Psammodius porcicollis* Ill. and *Psammodius basalis* Muls., the two most abundant species after *T. aphodioides*. The PC2-axis was mostly defined by the Tenebrionidae *Ammobius rufus* Luc. and by the Histeridae *Xenonychus tridens* (J. du V.). This analysis clearly opposed two groups of sites on the PC1-axis: on the one hand, the sites of La Gracieuse, Beauduc A and B, Piémanson (the four sites of Camargue) and Villepey (Var) and, on the other hand, the nine other sites of the Var department. A second PCA was performed on the same set of psammophilous species, but without the overly dominant Tenebrionidae *T. aphodioides* (Fig. 2b). The two PCA-axes accounted for 73% of total inertia. The PC1-axis was defined by *A. rufus and X. tridens*, while, on the PC2-axis, *P. porcicollis* and *P. basalis* were opposed to *Phaleria bimaculata* L., which isolated the dune of "Le Moulin". On this second biplot (Fig. 2b), the projections of the dunes of Camargue were mixed with those of the dunes of the Var in two main distinct groups characterized by *Ammobius* and *Psammodius* species. Thus, the four dunes of Camargue exhibited a community structure, which varied markedly from the ones of the Var department when all the psammophilous species were considered. Moreover, the species assemblage observed at Villepey (Var) was rather similar to the communities of Camargue, although it was the most distant site from Camargue. As shown by the second PCA, this similarity resulted clearly from the low abundance of *T. aphodioides* for all these five sites while this species pullulated on all the other studied dunes of the Var. When this dominant species was neglected, the beetle communities seemed relatively similar in Camargue and in the Var, although an inter-site variability was observed. The sites of "Beauduc-A" and "Le Moulin" were, however, always distinct from the others.

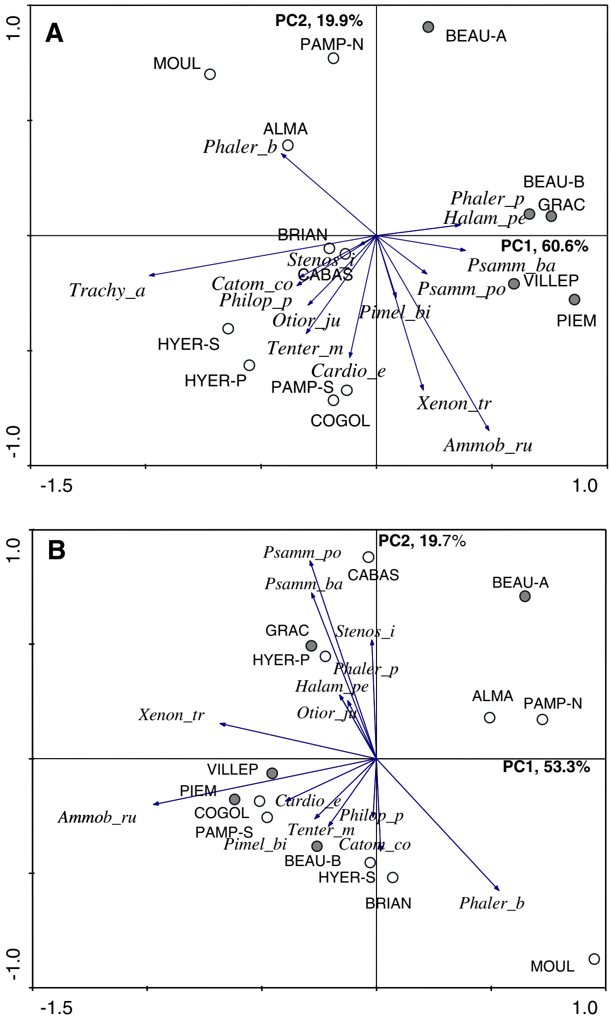

Fig. 2 Biplot of the PCA's performed on the psammophilous species abundances, with (**a**) and without (**b**) the heavily dominant species *T. aphodioides* (15 and 14 species; 2096 and 306 individuals, respectively). The four dunes of Camargue and the dune of Villepey (Var) are shown in grey

Relationships with environmental factors

Redundancy analyses (RDA) with forward selection allowed to determine which environmental factors significantly explained the variation observed in the abundance of psammophilous species, with or without the very dominant species *T. aphodioides* (Table 4). In these analyses, each one of the three explanatory sets of factors was considered independently. When all psammophilous species were taken into account, two factors of the "dune characteristics" were significant (conditional effects), respectively the dune height and preservation. Amongst the "landscape" factors, only the occurrence of trees in the dune background was found significant while urbanization was the only significant factor in the third set of explanatory factors ("disturbances"). These results changed markedly when *T. aphodioides* was omitted: the dune height was no longer significant, while the sand organic matter content explained a significant part of the variance. The importance of dune

Table 4 Amount of variance in psammophilous abundances explained by the three sets of environmental factors considered separately (RDA's with forward selection, conditional effects). Significant values are in bold and italicized. Other values just below the 10% significance level are provided for information

	All psammophilous species				Psammophilous species without *T. aphodioides*			
		Explained variance	*P*	*F*		Explained variance	*P*	*F*
Dune features	Hdune	***0.45***	***0.001***	***9.68***	Preserv	***0.23***	***0.008***	***4.03***
	Preserv	***0.1***	***0.028***	***2.65***	Organic matter	***0.16***	***0.01***	***3.3***
					Vegetation	0.08	0.09	2.18
Landscape	Trees	***0.23***	***0.012***	***4.44***	Trees	***0.2***	***0.024***	***3***
	Road / Park	0.18	0.07	2.58				
Disturbances	Urba	***0.2***	***0.043***	***3.09***	None			

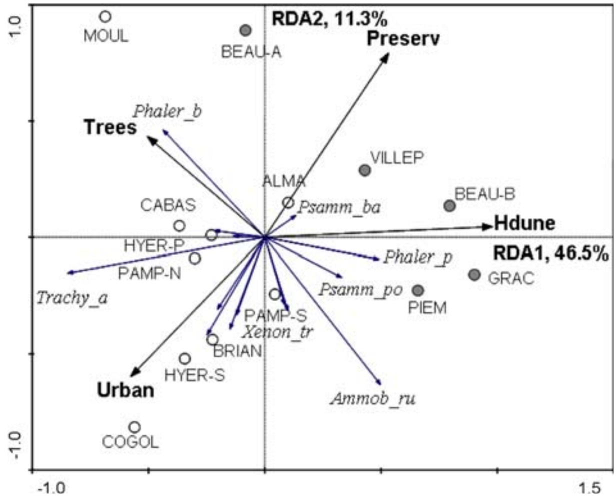

Fig. 3 Triplot of the RDA performed on psammophilous species and on the four environmental factors, which were found significant for these species (see Table 4). Only the most abundant species are found to clarify the graph. The four dunes of Camargue and the dune of Villepey (Var) are shown in grey

preservation increased, whereas the effect of trees was quite similar to that of the previous analysis. In contrast, no effect of disturbances remained significant.

The two first axes of the RDA computed on the full set of psammophilous species (Fig. 3) accounted for 57.8% of total variance. The first RDA axis clearly opposed the most preserved and high dunes (three of the dunes of Camargue and Villepey) to other dunes located in a more urbanized environment, while the occurrence of trees isolated the dune of "Le Moulin", where only two species were caught. The hugely dominant species *T. aphodioides* was associated with the most urbanized sites of the Var department while other psammophilous species (mainly *A. rufus* and *Psammodius* species) were most abundant on high and preserved dunes. On the contrary, no clear pattern appeared when *T. aphodioides* was omitted from the analysis (Figure not shown).

Although few habitat generalist species were caught (13 species, 25 individuals), we attempted to perform the same RDA analyses and forward selection. Surprisingly, three explanatory factors were found significant, i.e., the occurrence of buildings (surrounding

Table 5 Amount of variance in functional groups explained by the three sets of environmental factors considered separately (RDA's with forward selection, conditional effects)

	Body size (all species)				Body size (without *T. aphodioides*)			
	Factor	Explained variance	*P*	*F*	Factor	Explained variance	*P*	*F*
Dune features	Hdune	***0.38***	***0.001***	***7.28***	Preserv	**0.23**	**0.003**	**5.61**
	Preserv	***0.19***	***0.004***	***4.8***	Organic matter	**0.16**	**0.005**	**4.46**
Landscape	Trees	***0.2***	***0.028***	***3.04***	Trees	***0.3***	***0.015***	***5.12***
	Route/park	0.17	0.07	2.84	Sand	0.13	0.07	2.41
	Sand	0.13	0.06	2.6				
Disturbances	Trampling	0.17	0.09	2.39	None			
	Trophic guild (all species)				Trophic guild (without *T. aphodioides*)			
	Factor	Explained variance	*P*	*F*	Factor	Explained variance	*P*	*F*
Dune features	Hdune	***0.31***	***0.019***	***5.32***	Organic matter	**0.22**	***0.002***	***4.5***
	Veget	0.13	0.06	2.57	Preserv	0.18	0.058	2.89
	Organic matter	0.10	0.09	2.24				
	Preserv	0.09	0.09	2.23				
Landscape	Water	***0.22***	***0.04***	***3.45***	Trees	**0.28**	**0.019**	**4.76**
	Herbaceous	***0.21***	***0.03***	***3.87***	Halophil	0.12	0.11	2.02
Disturbances	Tourism intensity	0.23	0.06	3.6	None			

Significant values are in bold and italicized. Other values just below the 10% significance level are provided for information

landscape), and amongst the disturbance factors, the urbanization and beach trampling ($P = 0.014$, 0.036 and 0.044, respectively).

The same approach (RDA and forward selection) was used for functional groups. Both the distribution of body size and trophic guilds responded significantly to several environmental factors (Table 5). When *T. aphodioides* was included in the data set, the dune height ("Hdune") was always the most important factor, followed by dune preservation, for body size distribution. Amongst the landscape features, the occurrence of trees (for body size) and the occurrence of water and herbaceous patches (for trophic guilds) were also significant. It must be noted that the disturbance factors (dune trampling and tourism intensity) were ranked first in these analyses but remained above the 0.05 significance level. When *T. aphodioides* was omitted from the data sets, the dune height parameters was never significant, nor any of the disturbance factors. Only dune preservation, amount of organic matter (dune characteristics) and the presence of trees in the background of dune significantly explained both the distribution of beetles' body size and trophic guilds. These results were consistent with the previous RDA analyses on psammophilous species.

The last step of this study was to hierarchically partition the variability of community and functional groups between the three reduced sets of environmental factors, using partial RDA. The variability in species assemblages of psammophilous species was significantly related ($P = 0.04$) to dune characteristics (Table 6), but this effect became insignificant when the dominant species was omitted. Landscape and disturbances were not significant ($P > 0.05$).

Generalist (allochtonous) species did not respond to any dune features (no significant factor), nor to landscape ($P = 0.13$) or disturbance ($P = 0.06$) variables. This result was expected, given the low number of generalist individuals caught along this study.

Body size distribution followed the same trend as psammophilous species: dune characteristics significantly explained the variability of body size amongst the 14 studied sites

Table 6 Variability partitioning amongst the three reduced sets of significant environmental factors (dune features, landscape and disturbances) for psammophilous species and functional groups, with and without the dominant species *T. aphodioides*

		With *T. aphodioides*		Without	
		Explained variance	*P*	Explained variance	*P*
Psammophilous species	Dune	***0.160***	***0.044***	0.07	0.595
	Landscape	0.009	0.472	0.07	0.695
	Disturbances	0.002	0.389	–	–
Body size	Dune	***0.354***	***0.001***	0.044	0.242
	Landscape	0.002	0.379	***0.289***	***0.007***
	Disturbances	–	–	–	–
Trophic guild	Dune	0.117	0.055	0.004	0.664
	Landscape	0.189	0.053	***0.239***	***0.002***
	Disturbances	–	–	–	-

Explained variance and probability (*P*) are adjusted for sample size and number of predicting factors, according to Peres-Neto et al. (2006). Significant values are in bold and italicized

($P = 0.001$) when all species were considered, while only the landscape had significance otherwise. For trophic guild distribution, considering the three reduced sets of factors led to no significant variability partitioning ($P > 0.05$), but landscape seemed significant without *T. aphodioides*.

Discussion

The present study aimed at comparing beetle communities across 14 sites subjected to various anthropogenic disturbances. This survey was designed to perform a heavy sampling in early spring, the season of maximum beetle abundance in the Var dunes (Ponel 1986). As most psammophilous species are thermophilic (Fallaci et al. 1997; Aloia et al. 1999), their activity was low in early spring, allowing the use of a single method of sampling. Species quickly moving on the sand surface (e.g., Cicindelidae) were *de facto* excluded by the trapping method, but pitfall traps were not usable on the studied dunes (traps would have been filled in by wind-transported sand, or removed by people). Moreover, sand sieving allowed a better sampling of beetle's size distribution than do pitfall traps (Arneberg and Andersen 2003).

Beetle community

Analyzing the species distribution along the coast showed, at first, the lack of any significant longitudinal (regional) gradient, although there was a dichotomy between the Var and Camargue beetle communities (see Fig. 2a), as previously mentioned by Ponel (1986). However, this dichotomy was less evident when the dominant species was ignored (Fig. 2b), suggesting a common and relatively similar core of the community in the two sub-regions, although inter-site variability was observed. The second global result was the importance of dune vegetation, which appeared to be the main factor driving beetle abundance: most species and individuals were caught in vegetated areas and not in bare sand, as already observed by Colombini et al. (2003). Dune vegetation is likely to provide a shelter against high temperature and sand dryness, a refuge against predators as well as food resources for both larval and adult stages of psammophilous species, while large patches of bare sand lead to a decrease in species richness and abundance (Slobodchikoff and Doyen 1977; Ponel 1986).

As usual in this type of ecosystem (Dajoz 2002), Tenebrionidae dominated the community by their abundance and richness (Ponel 1986; Chelazzi et al. 2005). Species of this family exhibit morphological adaptations (loss of pigmentation, straight bristles, burrowing legs, winglessness) and ecophysiological adaptations (resistance to drought, and to high and largely fluctuating temperatures), which allow these very specialized species to set up permanent populations in dunes (Bigot et al. 1982; Ponel 1986). Other common species were all sand-dwelling species (*Ammobius* and *Psammodius* species). Numerous rare species were also recorded (15 singletons).

All psammophilous species found in this study were previously mentioned in the comprehensive survey (2 years) conducted by Ponel (1986) on two dunes of the region ("La Gracieuse" in Camargue and "Hyères Plage" in the Var). In spite of differences in sampling effort and duration, the density of the two common species *A. rufus* and *P. porcicollis* were found to be similar in 1986 and nowadays (i.e., 0.5–0.7 individual/sand liter). On the contrary, the current density of *T. aphodioides* was 26 times higher than in the work of Ponel (1986). The pullulation of this species on the dunes of the Var (except at Villepey) and its rarity in Camargue, was one of the most striking results of this study, although it was considered as common in Camargue by Caillol (1908). Whether its current dominance results from population fluctuations or not is still unclear. But the fact that *T. aphodioides* was the only species whose abundance was significantly correlated with the synthetic index of disturbance (Spearman rank correlation coefficient $r_s = 0.588$, $P = 0.027$) and that the species was found in huge number only in small or relictual dunes subjected to intensive tourism strongly suggests a response of the species to habitat alteration (see below). The occurrence of a very dominant species was also the reason why species evenness was very low on most of the Var dunes (except at Villepey).

The current work was too short (and probably not at the most favorable season) to be representative of habitat generalist species. It is probably the reason why few individuals were caught and why no significant results were recorded. Another explanation might be the harshness of environmental conditions prevailing on dunes, which could slow down a possible colonization by generalist species. However, the hypothesis of a possible greater occurrence of generalist species in the Var should be more extensively studied, as Colombini et al. (2003) suggested that beaches particularly degraded and heavily impacted by tourism attracted inland species that generally did not occur on beaches. This process should be studied further to provide a more reliable estimate of the abundance and potential colonizing abilities of these allochtonous (habitat generalist) species.

The significance of the variable "trees" in landscape features probably points out the species paucity at "Le Moulin" (only two species, with a huge dominance of *T. aphodioides*), which was probably related to the presence of a pinewood in the retrodunal area, as also observed on the Adriatic coast by Chelazzi et al. (2005). However, the involved mechanisms remain unclear. The second species observed at that site was the Tenebrionidae *Phaleria bimaculata* L., a scavenger species feeding mainly on dead fish. This last species was only found on the two beaches of the Var not subjected to beach-cleaning ("Le Moulin" and "Briande"). These observations suggest that very local features can induce the disappearance or survival of some species which are very sensitive to one particular factor of their environment ("lucky versus unlucky species"; Samways 2005) and that a high variability of anthropogenic disturbances (both in type and intensity) may be encountered between sites.

Relationships with environmental factors

Although the environmental factors were roughly estimated, they clearly opposed the dunes of Camargue (plus Villepey) to those of the Var, given the differences in dune characteristics, landscape features and disturbances (see Table 1). Interactions between species assemblages and environmental factors showed that dune characteristics (mainly dune height and preservation) affected significantly the community of psammophilous species. On the contrary, landscape composition and disturbances, which appeared significant when the effects of these factors were analyzed separately ("trees" and "urbanization" variables in Table 4), were no longer significant after variability partitioning (Table 6). Moreover, even the effect of dune characteristics disappeared in variability partitioning when the very dominant species was ignored. This result suggests that the population outbreak of *T. aphodioides* can be considered as the response of this species to changes in dune morphology and preservation, and that this very species is a good indicator of dune alteration (see also above its significant correlation with the average disturbance index). The dune height, which was correlated with dune width (Spearman rank correlation coefficient $r_s = 0.791$, $P = 0.001$), indicated the habitat extent, suggesting that dune fragmentation which modifies the size of dune patches also modifies the species assemblages, as already demonstrated in numerous terrestrial ecosystems. Beetle communities also largely depend on very local parameters (Colombini et al. 2003), such as dune stability, slope or exposure. Hesp (1991) underlined that beaches with higher slopes were more favorable for the settlement of pioneer vegetation which, in turn, attracted an associated fauna. In our study, dune vegetation was one of the local factors driving beetle abundance. Dune extent was also associated with dune preservation. One could infer that large dunes, like in Camargue or at Villepey (the latter was restored and protected by fences *ca.* 15 years ago), are less subjected to the anthropogenic pressure and, thus, that habitat quality is better. However, psammophilous species still occurred in fragmented and disturbed dunes of the Var department. Several aspects can explain why psammophilous species can survive in these dunes strongly impacted by tourism: (i) they are fully adapted to the harsh edaphic conditions prevailing in these ecosystems; (ii) the below-ground position of these sand-dwelling species may protect them against excessive disturbance (Driscoll and Weir 2005); (iii) although fragmented, dune patches are less disturbed than the beach itself, and psammophilous species have probably moved all year-long in the vegetated part of the dune even though the anthropogenic pressure is reduced in winter. This effect was demonstrated by Fanini et al. (2005) for the sandy flea (*Talitrus saltator* Montagu) which developed a spatio-temporal strategy to avoid tourism disturbance in summer, but disappeared completely from beaches where intensive management for tourism occurred; (iv) the short time elapsed since fragmentation or intensive disturbance (about 30 years or so) may explain why most psammophilous species are still remaining in dune fragments (Driscoll and Weir 2005). The dune parameters at a very local scale (dune height, vegetation density, preservation) are, thus, expected to indirectly express other factors such as the intensity of disturbance, leading to a confounding effect which could explain why disturbances did not explained significantly the variation partitioning for psammophilous species (Table 6).

Differing proportions of species with particular traits are likely to affect ecological functions (Diham et al. 1996). As expected, our results on beetles' body size and trophic guild distribution were strongly influenced by the dominance of *T. aphodioides* and, consequently, the same effect of dune characteristics (dune height, preservation, vegetation) was observed. However, when this species was omitted, the preservation factor remained significant, as well as the sand organic matter content, suggesting that resources differ in preserved or altered dunes, and are, thus, exploited differently by species. This aspect would greatly beneficiate from further investigations.

Conclusion

The current study allowed to compare the beetle communities of a large set of dunes subjected to different anthropogenic pressures about 20 years after the last scientific study in this region. It showed a strong relationship between ecological disturbances resulting from tourism (i.e., 10 million people a year in the Var department) and the pullulation of one Tenebrionid species, which strongly modified the beetle community structure. This situation is supposed to be detrimental to other psammophilous species since the dominant one is likely to use the most part of available resources. Furthermore, since anthropogenic disturbances are still increasing through the reduction of dune patch size, the increase of their fragmentation, isolation and exposure to trampling, there will be a major concern about the survival and conservation of these highly specialized sand beetles. Their occurrence, even in small remnant patches, hopefully supports the restoration policies combining the use of protective fences, the re-introduction of typical vegetation and the progressive extension of dune fragments, as shown at Villepey. Conservation of sand dune ecosystems must be considered as a priority, since their size and health are dramatically decreasing at most sites.

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