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Impact of invasive *Rosa rugosa* on the arthropod fauna of Danish yellow dunes

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Abstract We compared the arthropod fauna of *Rosa rugosa* patches to the adjacent native yellow dune vegetation by pitfall trapping in the National Park Thy at the Danish North Sea coast. *R. rugosa* changes the vegetation from a dune grassland (dominated by *Ammophila arenaria*) poor in flowering plants to a low monospecific shrubbery rich in large flowers. We predicted faunal responses according to the changes in resource availability and environmental conditions promoted by this particular invasive plant: increased populations of flower-visiting insects and species of the phytophagous and detritivorous guilds, and a decrease in thermophilic predator species. A matched-pairs sampling design allowed us to isolate the effects of the vegetation change from those of potentially confounding landscape gradients. The arthropod communities were significantly affected by the vegetation change (redundancy analysis). Six taxa (Opiliones, Lepidoptera larvae, Hymenoptera, Diptera, Tipulidae, Geotrupidae) increased in abundance, and three (Araneae, Staphylinidae, Auchenorrhyncha) were reduced in the rose patches. The main exception from predictions was the lack of effects on large detritivores

(isopods, diplopods). Overall, total catches were increased by 45 % in the rose patches, primarily caused by an increase in the abundance of Diptera. Arachnids and carabid beetles were analyzed at species level: the assemblage structure was significantly affected in arachnids but not in carabids. Arachnids showed reduced species richness and diversity and increased dominance in the rose patches, due to reductions among xerotherm species. The results indicate that considerable faunistic impoverishment of thermophilic dune specialist species can be expected in the future if *R. rugosa* is allowed to continue its invasion across the dune habitat.

Keywords Arachnida · Arthropoda · Biodiversity · Conservation · Carabidae · Invasive plants

Introduction

Rosa rugosa is an invasive plant that forms a monoculture by completely displacing the original vegetation in the dunes of north-western Europe (Thiele et al. 2009; Kollmann et al. 2009) and therefore affects not only the plant communities but also the animal communities in the areas they invade (Ehrenfeld 2010; Bezemer et al. 2014). Nearly one-third of all coastal dunes in Northern Europe are situated along the Danish North Sea coast, and two-thirds of these are relatively unaffected by afforestation or recreational use (Doody 1994; Damgaard et al.

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2008). In these areas, the invasion of *R. rugosa* is still in an early phase. Established c. 1950, it has been spreading across the dune habitats in recent years at an alarming pace (Kollmann et al. 2009). Originally planted as ornamentals around summer cottages, it has invaded the surrounding natural habitats (Jørgensen and Kollmann 2009). In particular, this has been the case in the yellow dunes, i.e. the habitats close to the sea (from the beach to 100–200 m inland). Yellow dunes are covered by low-diversity grassland, mostly marram grass (*Ammophila arenaria*), and are exposed to strong westerly winds with considerable sand shifting and salt spraying. A census in the National Park Thy (the area of the present investigation) in 2004 and again in 2007 revealed a doubling of the *R. rugosa* covered area in the three intervening years (Stobberup et al. 2008). It is estimated that by 2034 the cover of *R. rugosa* will have increased from <1 % to approximately 9.5 % of the dune area if no measures are taken to stop the spread (Kollmann et al. 2009). This will have serious economic consequences for local communities, because the coastal dunes are important tourist attractions: they provide access to popular bathing beaches and are used for sun-bathing and other recreational purposes themselves. If covered by *R. rugosa*, the dunes and beaches will be much less accessible as the plant forms a nearly impenetrable and thorny scrub. *Rosa rugosa* is also a threat to natural plant communities (Bruun 2005), including in the study area some red-listed dune plants such as *Ligusticum scoticum* and *Calystegia soldanella* (Stobberup et al. 2008). In the present initial phase of the invasion, the yellow dunes are particularly affected, but on longer time scales the entire dune ecosystem (including grey dunes and dune heathlands) will be threatened.

Most studies of the effects of invasive plants on animal communities find significant changes in community structure [i.e. composition of functional groups and taxa (orders/families)] and record indicator species for both the native and invasive vegetation, but they differ with respect to whether increases or decreases are found in overall changes in abundance, richness and diversity of specific taxa (Vila et al. 2011). For example, Emery and Doran (2013) found all changes in abundance and richness of particular taxa and functional groups to be positive. Several other studies reported primarily negative effects (Samways et al. 1996; Ernst and Cappuccino 2005;

Gerber et al. 2008; Zuefle et al. 2008; Hagen et al. 2010; Holmquist et al. 2011). Proches et al. (2008) found a lower abundance and diversity of herbivores on alien plants, but no effect on other feeding guilds; similar results were obtained by Engelkes et al. (2012), who argued that this might lead to a higher degree of top-down control of the herbivores on the alien plant. We expect the responses of arthropods to be idiosyncratic, i.e. depending on the focal taxon, its functional traits (trophic level, feeding mode, environmental requirements), and the types of change in the vegetation caused by the invasive species. Some animals may benefit from the invasion if the availability of particular required resources is increased and the suitability of the environment is enhanced, while others are harmed if habitat and feeding conditions deteriorate. Hence, we are not expecting a clear response from the fauna to the invasion of alien plants. However, irrespective of the faunal response (i.e. whether particular groups increase or decrease in abundance or diversity), alien plants are potentially threatening to the native fauna from a conservation point of view, especially if the plant invades a habitat that is of high local or global conservation value.

Little is known of how *R. rugosa* affects the animal communities where it prevails. The natural plant community of the yellow dunes is grass dominated, *Ammophila arenaria* being the dominant species (Frederiksen et al. 2006). It forms a mosaic of patches of varying plant density, so that areas with recent sand shifting may have open vegetation where bare sand prevails, while other areas (mostly a little further inland) have denser vegetation and litter accumulation. When *R. rugosa* invades an area, several structural and physico-chemical conditions may change. *R. rugosa* is a shrub of 0.5–1.5 m height, with a canopy of leaves at the top that effectively shades the ground (Isermann 2008). The resulting reduction in insolation and hence in temperature is expected to affect the soil-surface plant-dwelling arthropod fauna. *Rosa rugosa* produces strongly scented pollen and has many large flowers that may attract pollen feeding insects (Bruun 2005). In contrast, the native dune vegetation includes scattered flowering plants such as *Hieracium* spp. and *Lathyrus japonicus* ssp. *maritimus*. The dominance of *R. rugosa* may therefore lead to a considerable enrichment of pollinating species, which are otherwise infrequent in the yellow dune community. In addition to these

changes, *R. rugosa* may provide more nutritious leaf material for generalist phytophagous animals and possibly more palatable and/or nutritious litter for the decomposers than the siliceous *Ammophila* species; in particular, the large and abundant petals of the flowers may add a significant amount of easily decomposable litter. This may affect the structure and composition of the top soil (Hodgkin 1984). Phytophagous arthropods specialized on *Rosa* species may come from native *Rosa pimpinellifolia* inhabiting the adjacent grey dunes (Bruun 2005). We therefore expect that several guilds of arthropods (herbivores, detritivores, and in particular pollinators) will benefit from the *R. rugosa* invasion, becoming more abundant and more diverse through immigration from neighbouring habitats. In contrast, species-rich predatory groups with a large number of thermophilic species that depend on scattered vegetation with high insolation may become impoverished due to increased shading in the *R. rugosa* vegetation.

The present study aimed to analyze how *R. rugosa* affects the arthropod fauna in the yellow dunes. Our study area is part of the extensive dune system along the Danish west coast from the most northern tip of Jutland to the Wadden Sea in the south. Our overarching hypothesis was that the arthropod community composition would change as a result of the increased abundance of some functional groups and the decreased abundance of others, depending on the changes in resource availability imposed by the *R. rugosa* community invasion. We expected (1) an increased abundance of flower-visiting insect groups (e.g. Hymenoptera, Diptera) as well as of generalist herbivores and detritivores. Natural dune vegetation exhibits extreme day temperature peaks on sunny days. The increased shading in the rose patches was expected to prevent these extreme temperature events. Within the species-rich predatory assemblages (arachnids, carabids) we therefore hypothesized (2) an increased representation of shade tolerant species and a lowered abundance and species richness of diurnal xerophilic species in the rose patches. Given that mature and relatively large rose patches were selected for study, we expected *R. rugosa* to affect the physico-chemical characteristics of the soil, raising the question (3) whether faunistic changes, if any, were direct results of the vegetation change or indirect results of longer-term accumulating changes of the soil environment.

Methods

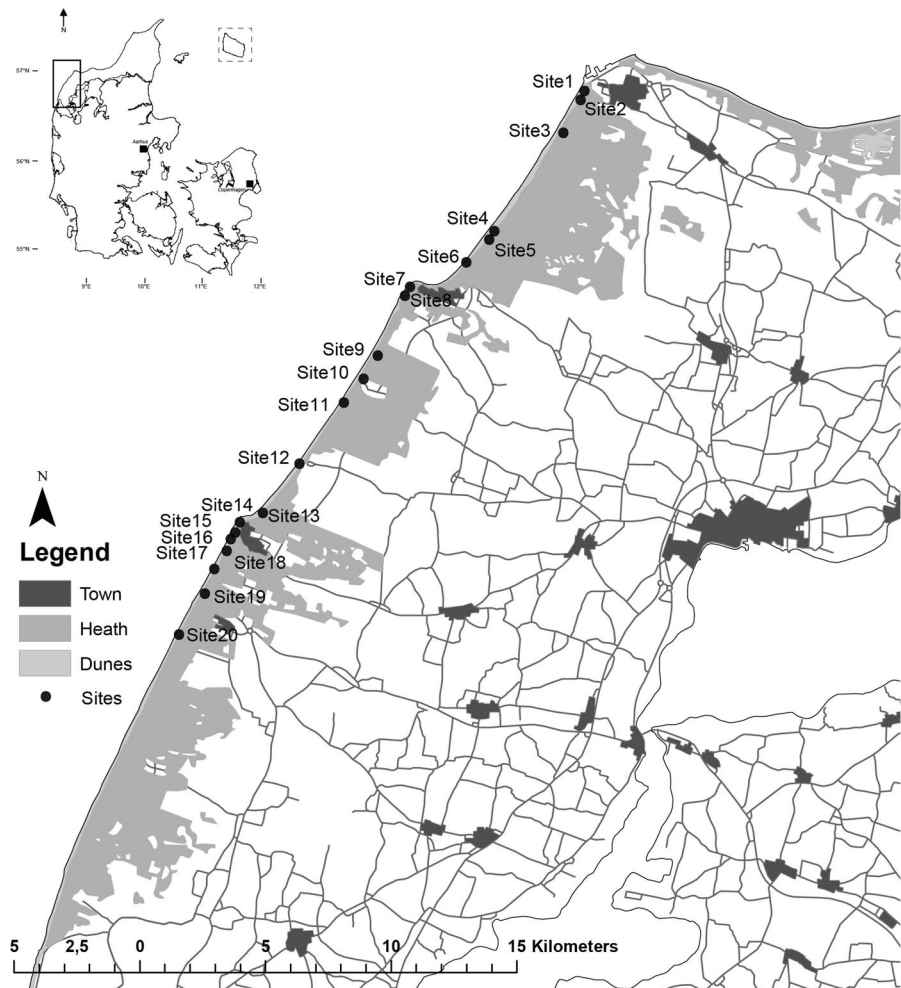
Sites

Study sites were selected based on the previous mapping of *R. rugosa* patches in the National Park Thy (Stobberup et al. 2008). Twenty patches along the coast from Hanstholm to just south of Stenbjerg were chosen (Fig. 1). Large patches (diameter mostly 25–30 m; min.–max.: 10–45 m) close to the coast and surrounded by native yellow dune vegetation were chosen. *Rosa rugosa* stand age probably varied between 10 and 25 years (Kollmann et al. 2009).

Sampling and sorting

The arthropod fauna was sampled by means of pitfall traps. This method was chosen for several reasons. Firstly, because of frequent strong winds, very few species live in the upper layers of the native dune vegetation, while the fauna on the soil surface is abundant and can be very rich in species [e.g. >100 species of spiders (Gajdos and Toft 2002)]. Secondly, some of our expectations about faunistic changes concern less abundant species that would not be adequately recorded by quantitative sampling. Thirdly, even if a few species escape pitfall traps, no other sampling method records as many species for a reasonable work load as do pitfall traps. Moreover, pitfall traps allow the collection of a large amount of biological material without extended human presence and activity in the habitat. The traps were operating during 2 months of spring and summer 2013 (25 May to 27 July) and were emptied at 2-week intervals (4 trapping periods). The traps consisted of double plastic beakers (40 cl, diameter 8.8 cm, depth 12 cm) with concentrated salt water with some drops of detergent as trapping fluid. A 15 × 15 cm roof covered the trap. As many of the traps were placed in areas with tourist activity, a note on the roof informed accidental visitors about the purpose of the project and the institutions (National Park Thy, universities) conducting it. We believe this was what completely prevented vandalism to the traps.

Four traps were placed at each site, two inside the *R. rugosa* patch (rose samples) and two outside in the native dune vegetation (reference samples). They were arranged in a line parallel to the coastline with one trap northeast of the patch, two traps inside the patch, and

Fig. 1 Map of study sites

one trap southwest of the patch. The distance between the traps in the patches was approximately 5 m, and the reference traps were placed approximately 10 m from the patch margin. This distance was considered large enough to assure that the reference catches were independent of the rose patch, while close enough to assure that the trap site conditions were similar to those of the patch-area before rose invasion.

Arthropods were identified to the level of orders or any easily recognizable lower taxonomic level (e.g. terrestrial isopods, ants, carabid beetles; see Table 2). The main feeding strategy was characterized for each taxon (pollen feeder, herbivore, detritivore, predator). Trait characterization is not always straightforward, though; predictions based on traits will therefore be fuzzy. Most of the Hymenoptera (excluding ants, which are treated separately) have parasitoid development but

feed on nectar as adults. Amongst the Diptera, the diversity in feeding habits prevents any simple categorization. Therefore, we identified Diptera families (except Acalypterae) from part of the samples: we randomly selected five trap-samples from each of the four sampling periods and both of the habitats (40 samples in total). Carabid beetles and arachnids (spiders, harvestmen, pseudoscorpions) were identified to species, using Lindroth (1985/86), Luff (2014) for carabids; Locket and Millidge (1951/53), Roberts (1985/87), Almquist (2005) for spiders; Meinertz (1962) and Toft (2004) for harvestmen and pseudoscorpions.

Vegetation and environmental parameters

The flora was registered by subjective estimation of the coverage of each plant species in a 5 m² area

around each trap. Only species with >5 % coverage were included in analyses. The average coverage of each species for the two traps inside and for the two traps outside of the rose patches, respectively, was used in subsequent analyses.

Two soil samples (of 2 l each) were taken from each site, one inside and one outside of the patch. In order to quantify soil parameters, subsamples were analyzed for water content, organic matter content, grain size distribution, and pH. Water content was measured as mass difference after drying at 105 °C (DS/CEN ISO/TS 17892-1 standard procedure). Organic matter content was measured as the mass difference of samples dried at 50 °C and subsequently combusted at 550 °C (DS 204 and DS/EN 1997-2 standard procedures). Grain size distribution was determined by sieving, using mesh sizes 4, 2, 1, 0.5, 0.25, 0.125, 0.063 mm (DS/CEN ISO/TS 17892-4 standard procedure). From the grain size distribution we calculated the median grain size, which was used in the analyses. pH was measured by an inoLab pH/Cond 720 instrument on subsamples first dried at 105 °C, then homogenized with demineralized water.

Temperature was measured both inside and outside of three rose patches (sites 6, 15, 20) by means of data loggers (Hobo/Onset Tidbit v2). These were placed at the soil surface and covered only by the vegetation. Records were taken every hour during the period 25 May to 26 June 2013. Overall average temperatures and average maximum and minimum temperatures for day time (hours 0800–2000) and night time (hours 2000–0800) were calculated and used in the analyses.

Data analyses

The total catches from the two rose traps and the two dune traps of each site were pooled, so that the data set for analysis consisted of 20 matched pairs of rose and reference samples. The matched-pairs design allowed us to test for faunistic differences between rose patches and native vegetation, thus isolating the effects from any geographical and environmental gradients not related to the roses. Paired *t* tests were used to compare the catches of each sorted taxon. Following the recommendations of Southwood and Henderson (2000) and Magurran (2004), diversity/dominance analyses were performed with the Simpson and Berger–Parker indexes, supplemented by

Whittaker plots and Renyi diversity profiles. These analyses were made in PAST (Hammer et al. 2001). The arthropod communities and arachnid and carabid assemblages were compared using redundancy analysis (RDA) in Canoco5 (ter Braak and Smilauer 2012; Smilauer and Leps 2014). “Matched-pairs RDA” was run on the faunistic data using vegetation type (rose/reference) as factor and sites as covariate. This analysis isolates the rose/reference difference by controlling for between-site factors. Standard RDA using the 4 abiotic soil factors and vegetation (coverage of the six most abundant species) as environmental factors was also run on the same faunistic data. We include the results of multiple analyses to emphasize the robustness of our conclusions that do not depend on a particular type of analysis.

To test the hypothesis that the vegetation change mostly affects diurnal thermophilic species, we used information from Hänggi et al. (1995), Bonte et al. (2004) and Almquist (2005, 2006) to identify the xerotherm spider species. The xerotherm species belong to three families: Gnaphosidae (*Micaria pulicaria*, *Zelotes clivicola*, *Z. electus*, *Z. latreillei*, *Z. longipes*, *Z. subterraneus*), Lycosidae (*Alopecosa barbipes*, *A. pulverulenta*, *Pardosa nigriceps*, *P. pullata*) and Salticidae (*Euophrys frontalis*, *Marpissa nivoyi*, *Neon reticulatus*, *Sibianor aurocinctus*, *Synageles venator*). We used paired *t* tests to compare the number of xerotherm species and the proportion of xerotherm to all species in the rose patches and in the reference vegetation. Moreover, we used the standardized “open-shaded” and “moist-dry” gradient niche position values given by Entling et al. (2007). Two indices were calculated for both environmental gradients: the average niche position per individual and the average niche position per species. These were calculated for the total catches of the reference and rose traps in each of the 20 sites. The individual-level niche position indices were calculated as

$$\sum OS_i * n_i/n$$

and

$$\sum WD_i * n_i/n,$$

where OS_i and WD_i are the niche position values of species *i* along the open-shaded and wet-dry habitat gradients, respectively; n_i is species *i*'s abundance, and n is the total abundance of spiders ($n = \sum n_i$). The

species-level indices for each gradient use presence-absence data, which reduces the formulae to

$$\sum OS_i/S$$

and

$$\sum WD_i/S,$$

where S is the number of species. Again, paired *t* tests were used to compare reference and rose trap catches.

Results

Comparison of habitat factors

The overall average temperature measured was only 0.97 °C lower in the rose patches than in the surrounding reference vegetation. This was due to the fact that the average day-time reference vegetation was 2.39 °C warmer than the rose patches, while night-time temperatures differed in the opposite direction, reference vegetation being 0.46 °C cooler than the roses. The day-time maxima were on average 4.69 °C higher, and the night-time minima were 1.10 °C lower in the reference vegetation. Temperature fluctuations were considerably reduced in the roses: on sunny days, the difference between the day-time maxima of reference vegetation and rose vegetation at sites 15 and 20 was between 10 and 17 °C (maximum 17.8 °C), and on non-sunny days it was <5 °C (some days even negative). Thus, the temperature measurements confirmed the expected differences between rose patches and reference vegetation. Overall, the climate during the study period did not deviate from the normal to any extent that would have affected the results.

No differences were found between any of the other abiotic soil factors measured in the two habitats (Table 1), i.e. the change in vegetation had no effect on soil organic matter, soil humidity, grain size or pH. Some of the measured factors were strongly intercorrelated, however. A Principal Components Analysis (PCA) produced two significant components (PC1 eigenvalue 3.15, explaining 78.7 % of the variation; PC2 eigenvalue 0.66, explaining 16.5 %). PC1 had high loadings from pH, soil humidity and organic matter, PC2 from grain size. Interestingly, a marginally significant relationship was seen between PC1 and

Table 1 Paired *t* tests and regression analysis of environmental factors measured in 20 *Rosa rugosa* patches and adjacent native reference vegetation

	Reference	Rose	<i>t</i> ₁₉	<i>P</i>
<i>Reference—rose comparisons</i>				
pH	5.8	5.9	0.59	0.56
Grain size (mm)	0.35	0.34	−0.41	0.69
Organic matter (%)	2.8	2.9	0.22	0.83
Soil humidity (%)	5.12	5.27	0.09	0.93
PC1			0.13	0.91
PC2			0.04	0.97
<i>Correlations with latitude</i>				
pH			−0.98	0.35
Grain size (mm)			0.79	0.44
Organic matter (%)			1.51	0.15
Soil humidity (%)			2.24	0.038
PC1			2.06	0.054
PC2			−1.19	0.25

the latitude of the sites as well as a significant relationship between PC1 and soil humidity (Table 1); this indicates a gradient in environmental factors along the coast. Soil humidity and organic matter content decreased from north to south, while pH increased.

The reference vegetation was dominated by *Amphiphila arenaria* supplemented by *Leymus arenarius* and other grasses (mainly *Festuca rubra*). The rose patches were a near monoculture of *Rosa rugosa* with mosses as ground cover beneath the shrubs.

Effects on the arthropod community

A total of 58,877 individuals and 27 taxa were collected during the field campaign (Table 2). Overall, the number of individuals caught was 45 % higher in the rose patches than in the reference areas. The matched-pairs RDA shows a distinct effect of rose invasion on the composition of the arthropod fauna at a higher taxon level ($F = 4.66$, $P = 0.002$) (Fig. 2). The faunistic difference was mainly due to six taxa [Opiliones, Lepidoptera larvae, Hymenoptera (excluding ants), Diptera, Tipulidae, and Geotrupidae] that occurred at higher abundances in the rose patches, and three taxa [Araneae, Staphylinidae and Auchenorrhyncha (leaf hoppers)] that were more abundant in the reference vegetation (Table 2). Diptera in particular

Table 2 Faunistic abundance differences between the *Rosa rugosa* patches and reference sites

Taxon	No. in roses	No. in reference	Matched-pairs t_{19}	<i>P</i>
Arthropods total	34,809	24,068	-3.76	0.0013
Araneae	1221	1951	4.69	0.0002
Opiliones	4526	2041	-5.87	<0.0001
Pseudoscorpiones	22	12		n.s.
Isopoda	8181	8302		n.s.
Chilopoda	74	61		n.s.
Diplopoda	122	159		n.s.
Dermaptera	13	28		n.s.
Auchenorrhyncha	165	651	5.39	<0.0001
Aphidoidea	20	229		n.s.
Heteroptera	21	21		n.s.
Lepidoptera larvae	42	16	-2.45	0.0242
Hymenoptera ^a	236	31	-3.51	0.0024
Formicoidea	4228	3270		n.s.
Diptera ^a	12,815	4308	-8.08	<0.00010
Tipulidae	97	42	-3.26	0.0041
Tipulidae larvae	26	9		n.s.
Coleoptera ^a	671	665		n.s.
Carabidae	564	475		n.s.
Curculionidae	42	42		n.s.
Elateridae	50	39		n.s.
Geotrupidae	110	29	-2.19	0.0405
Silphidae	220	287		n.s.
Staphylinidae	1301	1830	2.46	0.0235
Coleoptera larvae	146	131		n.s.
Spiders				
<i>Zelotes latreillei</i>	2	9	2.10	0.0493
<i>Hypomma bituberculatum</i>	11	0	-2.24	0.0374
<i>Palliduphantes ericaeus</i>	2	26	2.56	0.0190
<i>Pocadicnemis pumila</i>	105	500	7.38	<0.0001
<i>Tenuiphantes mingei</i>	47	101	2.54	0.0198
<i>Pardosa nigriceps</i>	7	34	3.09	0.0060
<i>Pardosa pullata</i>	2	54	4.99	<0.0001
<i>Episinus angulatus</i>	26	8	-2.59	0.0179
<i>Robertus lividus</i>	14	37	2.24	0.0376
<i>Zora spinimana</i>	25	71	2.83	0.0106
Harvestmen				
<i>Lacinius ephippiatus</i>	1811	1003	-2.85	0.0102
Leioboninae	121	40	-2.17	0.0428
<i>Phalangium opilio</i>	674	186	-2.69	0.0144
<i>Rilaena triangularis</i>	1533	572	-6.36	<0.0001
<i>Oligolophus</i> sp.	379	218	-2.52	0.0210
Ground beetles				
<i>Calathus mollis</i>	9	2	-2.33	0.0308
<i>Trechus obtusus</i>	0	7	2.33	0.0308

For Arachnida and Carabidae, only species displaying a significant difference are shown. Bold indicates the higher value for taxa with significantly different numbers

^a not including lower taxa/stages mentioned below

increased considerably. The remaining 18 taxa were unaffected by the difference in vegetation structure changes imposed by *R. rugosa*.

Most of the Diptera families increased considerably in numbers in the rose patches (Table 3). As predicted, this applied to typical flower-visiting taxa (e.g. Anthomyiidae, Muscidae) and to typical ground-living detritivores (e.g. Phoridae) alike. Also, Lepidoptera larvae as generalist herbivores and Hymenoptera as flower-visitors increased in abundance (Table 2). Sap-sucking leafhoppers decreased significantly in abundance in the roses; aphids showed a similar but not significant difference. The main detritivore taxa, Isopoda and Diplopoda, were expected to increase in abundance in the rose patches, but observations revealed no such increase.

Effects on arachnid and carabid assemblages

The sampling comprised 79 species of spiders, 8 harvestmen, 2 pseudoscorpions, and 36 carabids. Matched-pairs RDA revealed a clear separation of reference and rose samples with respect to arachnids ($F = 4.69$, $P = 0.002$) but not to carabids ($F = 0.87$, $P = 0.60$) (Fig. 3). Among spiders, two species

showed elevated abundance in the rose patches, and eight species were more abundant in the native vegetation (Table 2). Five species of harvestmen showed a significant difference in abundance between habitats, and these were all more abundant in the rose patches. Overall, the number of carabid beetles did not differ between the habitats.

Figure 4 shows RDAs with abiotic factors and vegetation included as environmental factors, and with corresponding rose and reference samples connected. Notice that for arachnids (Fig. 4a), the lines are roughly parallel and perpendicular to the (partly geographical) gradients through the sites. This pattern indicates that rose establishment changes spider assemblages in a similar way independently of their previous composition as determined by local environmental conditions, and that the impact of these environmental conditions on the arachnid assemblage composition is independent of the vegetation. The carabids showed no similar pattern (Fig. 4b).

Table 3 Catches and main feeding modes of Diptera families in randomly selected trap samples from reference and *Rosa rugosa* vegetations

	Main feeing guild	Reference	<i>Rosa</i>
Bibionidae	H/D–O	0	13
Cecidomyiidae	H/Pa/D–O	0	5
Mycetophilidae	D–O	8	8
Sciaridae	D–O	17	33
Tipulidae	D/H–O	3	21
Dolichopodidae	Pr–Pr	7	9
Empididae	Pr–Pr	8	15
Rhagionidae	Pr–Pr	9	54
Therevidae	Pr–N/Po	3	0
Sepsidae	D–O	0	6
Phoridae	D/Pa–D/Sc	160	353
Sphaeroceridae	D–D	41	22
Acalyptratae		66	140
Anthomyiidae	D/H–N/Po	27	222
Muscidae	D/Pr/Sc–N/Po	32	231
Calliphoridae	D/Sc–N/Po	0	16
Sarcophagidae	Pa/Sc–N/Po	1	3

Acalyptratae families were not distinguished. The selected samples comprised 5 traps from each of the 4 trapping periods and both habitat types

Feeding guilds (larvae–adults): *D* detritivores (including fungal feeders), *H* herbivores, *N* nectarivores, *O* not feeding as adults, *Pa* parasitoids, *Po* pollen feeders, *Pr* predators, *Sc* scavengers

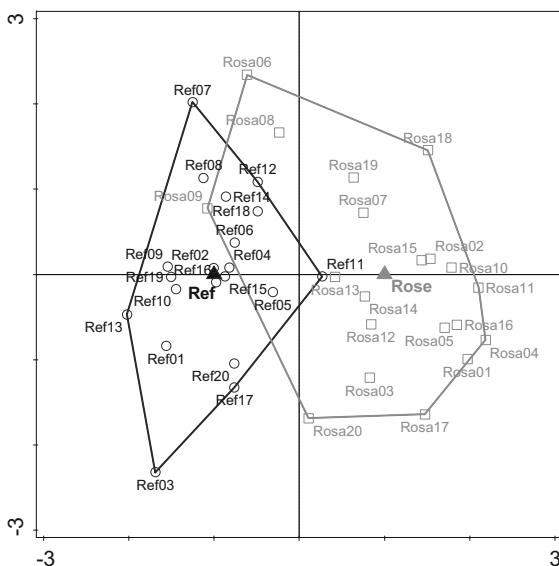


Fig. 2 “Matched-pairs” redundancy analysis of arthropod communities (order/family level) from 20 *Rosa rugosa* patches (squares) and adjacent native yellow dune vegetation reference sites (circles). Permutation test on all axes: pseudo- $F = 4.66$; $P = 0.002$; axis 1: eigenvalue 0.11, expl. var. 11.2 %; axis 2: eigenvalue 0.18, expl. var. 19.0 %

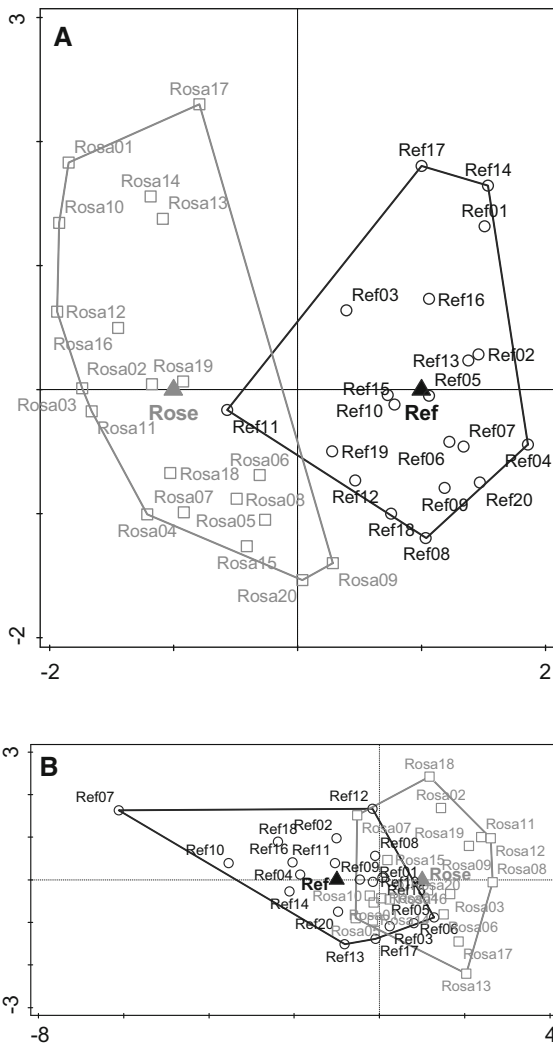


Fig. 3 “Matched-pairs” redundancy analysis of arachnids (**a**) and carabids (**b**) from 20 *Rosa rugosa* patches (squares) and adjacent native yellow dune vegetation reference sites (circles). Statistical analysis: **a** permutation test on all axes pseudo- $F = 4.69$, $P = 0.002$; axis 1 eigenvalue 0.11, expl. var. 11.2 %; axis 2 eigenvalue 0.18, expl. var. 19.1 %; **b** permutation test on all axes pseudo- $F = 0.87$, $P = 0.60$

The diversity profiles for arachnids and carabids do not cross (Fig. 5). For the arachnids, the reference profiles are clearly at a higher level than the rose patch profiles, but for carabids the two lines are almost identical. Accordingly, paired t tests of number of species, Simpson index and Berger–Parker index were significant for arachnids but not for carabids (Table 4). This difference was also illustrated in the Whittaker plots (Fig. 6). Arachnid species richness and diversity

were reduced, and dominance of abundant species was increased in the rose patches, but no similar effect was found for carabids.

The number of xerotherm spider species in the rose patches was reduced, compared to the reference vegetation. This also applied to the proportion of xerotherm species to total number of species (Table 5). Among xerotherm diurnal spiders, 5 out of 6 species of gnaphosids, 3 out of 4 species of lycosids, and all 5 species of salticids had reduced abundance in the roses. The greatest numerical reductions were seen in the two *Pardosa* species (*P. pullata* 96 %, *P. nigriceps* 79 %).

The open-shaded niche position of spiders at the individual level was significantly higher in the rose patches than in the reference vegetation, however not at the species level (Table 5). In other words, shade-loving species had become relatively more abundant in the roses. Along the wet-dry habitat gradient, the average individual preference for wetness was increased in the rose patches, and a similar marginally significant tendency was seen at the species level, i.e. wetland-preferring species had become relatively more abundant in the rose patches.

Discussion

The results of this study support several predictions: (1) established rose patches in the dunes are hosting significantly different arthropod communities than the surrounding native dune vegetation; (2) the difference is driven by an increased abundance of some functional groups and a decreased abundance of others; (3) flower-visiting insects (Hymenoptera (excluding ants), Diptera families), generalist herbivores (Lepidoptera larvae), and some detritivores (Diptera families) increased in abundance, and one species-rich predatory group (spiders) showed reduced species richness due to reduced abundance of diurnal xerotherm species. Our results also revealed changes that could not have been specifically predicted: two groups of predators (spiders and rove beetles) and one group of sap-sucking herbivores (leaf hoppers) showed lower abundance in the rose patches compared to the reference vegetation, while one family of coprophages (Geotrupidae) showed higher abundance. The main non-fulfilled prediction was the lack of

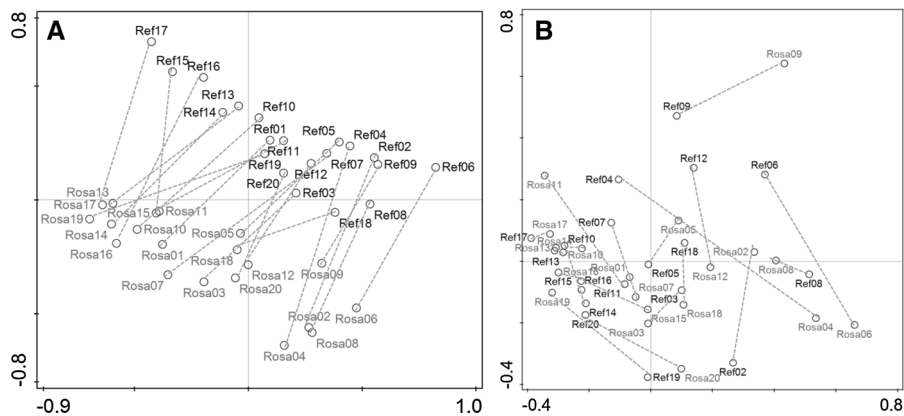


Fig. 4 Redundancy analysis of arachnids (a) and carabid beetles (b) using 4 soil factors and coverage of 6 plant species as environmental variables. Samples from the same site (i.e. *Rosa rugosa* patches and their surrounding native dune vegetation) are connected. Statistical analyses: a Permutation

test on all axes pseudo-F = 1.84, $P = 0.002$; axis 1: eigenvalue 0.15, expl. var. 15.2 %; axis 2: eigenvalue 0.10, expl. var. 10.0 %; b Permutation test on all axes pseudo-F = 0.95, $P = 0.63$

Fig. 5 Diversity profiles (Renyi curves) of arachnids (a) and carabid beetles (b) from *Rosa rugosa* patches and adjacent native yellow dune vegetation (Ref.)

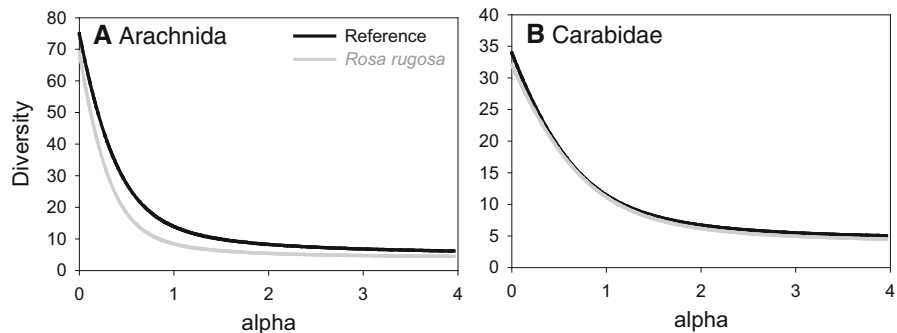


Table 4 Paired t tests of assemblage characteristics of arachnids and carabid beetles from *Rosa rugosa* patches and adjacent native yellow dune vegetation (Ref.)

	Species richness (S)				Simpson index				Berger–Parker index			
	Ref.	Rose	t_{19}	P	Ref.	Rose	t_{19}	P	Ref.	Rose	t_{19}	P
Arachnida	22.4	18.1	3.62	0.002	0.82	0.74	3.82	0.001	0.33	0.39	-2.41	0.026
Carabidae	6.7	6.9	-0.25	0.81	0.69	0.66	1.26	0.22	0.44	0.48	-1.16	0.26

effect on large detritivores, i.e. terrestrial isopods and millipedes.

The lack of difference in edaphic factors between rose patches and the surrounding reference vegetation indicates that the difference in faunal characteristics (composition, richness, diversity) between rose patches and reference vegetation can be assigned directly to the effects of vegetation change, i.e. to vegetation chemistry or structure including

microclimatic effects, rather than to the indirect effects of accumulating changes in soil factors. The RDAs that include environmental and botanical factors therefore show strong correlations of faunal composition with specific plants (rose or *Amophila/Leymus*) and no or weak correlations with abiotic factors (results not shown). These weak effects were due to the between-site gradients and not to the within-site vegetation change. The lack of within-site

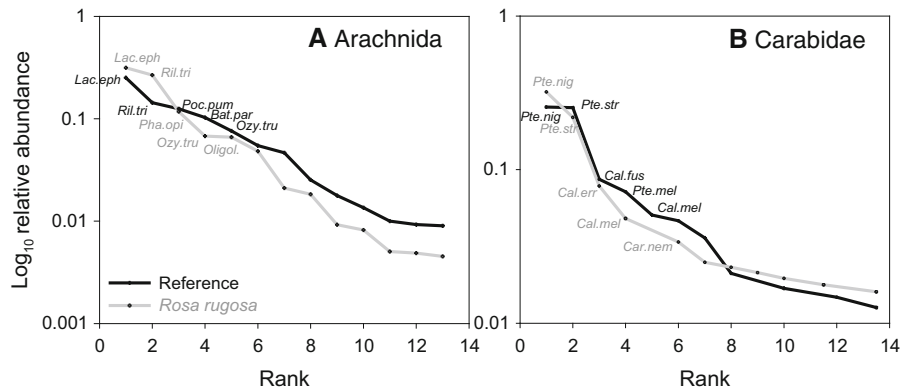


Fig. 6 Dominance-diversity (Whittaker) plots of arachnids (a) and carabid beetles (b) from *Rosa rugosa* patches and adjacent native yellow dune vegetation (Ref.). Abbreviation of species names: a Bat.par = *Bathypantes parvulus*, Lac.eph = *Lacinius ephippiatus*, Pha.opi = *Phalangium*

opilio, Poc.pum = *Pocadicnemis pumila*, Olig. = *Oligolophus/Paroligolophus* sp., Ozy.tru = *Ozyptila trux*, Ril.tri = *Rilaela triangularis*; b Cal.err = *Calathus erratus*, Cal.fus = *C. fuscipes*, Cal.mel = *C. melanocephalus*, Pte.nig = *Pterostichus niger*, Pte.str = *P. strenuus*

Table 5 Paired *t* tests of niche properties of spider assemblages from *Rosa rugosa* patches and adjacent native yellow dune vegetation (Ref.)

	Ref.	Rose	t_{19}	<i>P</i>
No. of xerotherm species/trap-pair	2.95	1.35	3.24	0.0043
Proportion xerotherm species	0.16	0.09	2.67	0.015
Open-shaded niche position/individual	0.39	0.41	2.18	0.042
Open-shaded position/species	0.38	0.39	1.53	0.14
Wet-dry niche position/individual	0.37	0.36	-3.32	0.0036
Wet-dry position/species	0.39	0.38	-1.98	0.06

Open-shaded niche position: low values show a preference for open habitats, high values show a preference for shaded habitats. Wet-dry niche positions: low values show a preference for wet habitats, high values show a preference for dry habitats

(rose/reference) differences in soil factors coupled with between-site (geographical) differences caused the matched-pairs sampling design to be the optimal choice.

Pitfall trap catches reflect activity-density and not the actual density of species (Southwood and Henderson 2000). Within species, catches can be affected by vegetation density, especially in dense grassland. At ground level, plant density is likely to be higher in the reference vegetation than in the rose patches. This difference predicts increased catches of all taxa in the rose patches, which is contrary to our findings. Another possible concern in our design is the placement of traps inside and outside of the rose patches. Long foraging distances might tend to equalize the catches; e.g. this could explain the lack of difference in abundance of ants and carabid beetles between rose

patches and reference vegetation. However, flies are the most mobile of all arthropods, and they showed the largest abundance differences of all taxa. Likewise, among spiders, the largest differences were seen among species of the most mobile families (Lycosidae, Salticidae). Therefore, we believe that habitat selection rather than mobility explains our findings.

Arthropod community structure

Both the arthropod community and the arachnid assemblages were affected significantly by the change of vegetation from native dune grassland to rose shrubbery. Increased abundances of Hymenoptera and Diptera were expected to result from the large and abundant rose flowers, but it could be questioned a priori whether this would be revealed by our sampling

technique, i.e. trapping at ground level. The increased abundance of large flower-visiting Diptera such as anthomyids, muscids and others showed that these doubts were unfounded. Other Diptera restricted to the ground layer, such as detritivores and scavengers (e.g. Sciariidae, Phoridae), increased in abundance as well. This prediction assumes a higher palatability of the rose litter, but the lack of response in numbers of woodlice and millipedes casts doubt on this explanation. Also, many of the Hymenoptera are only nectar and pollen feeders as adults but develop as parasitoids; they may have been attracted by the overall higher abundance of potential hosts in the rose patches. The reduction of leafhoppers was not predicted, and it is unknown if this finding can be extended to include the guild of sap-suckers. The increase in geotrupid beetles abundance was not predicted but may have been caused by dung provided by roe deer and hares. As the roses are slightly taller than *Ammophila*, the rose patches offer better hiding places for larger mammals. No data on mammals were collected to support this suggestion, however.

Overall, rose invasion induces a reshuffling of the relative abundances of taxa and functional groups; this is due to changes in both the resources provided to higher trophic levels and in the environmental conditions (here shading/temperature level) in the habitats. The invasion thus modulates the entire community structure and functioning through a series of linked resource changes and environmental shifts.

Arachnid and carabid assemblage structures

While the rose invasion caused only minor changes to the carabid assemblages, the arachnid fauna was significantly affected. The parallel responses of arachnid assemblages from the different sites (Fig. 3a) indicate that the driving factor was equally present at all sites, corroborating the conclusion that the response was due strictly to the vegetation change. The two abundant orders, spiders and harvestmen, changed in opposite directions: harvestmen becoming more abundant (but not richer in species), and spiders becoming less abundant and poorer in species richness in the rose patches. The latter effect was expected a priori. However, while all harvestmen showed a significant increase in abundance, spider responses were mixed: eight species were significantly reduced in the rose

patches and two became more abundant. A mixed response like this would be expected in a species rich and biologically diverse taxon such as that of spiders (Foelix 2011). Overall, spider numbers were reduced by one-third in the roses. As a partly open grassland, the native dune vegetation provides a natural habitat for a high contingency of thermophilic spider species, which are susceptible to the changes in insolation and temperature brought about by rose encroachment. Bonte et al. (2006) identified such species as the most endangered habitat specialists of the dunes. Our results confirmed the disappearance of these thermophilic specialist dune species in addition to an increased abundance of shade tolerant species in the rose patches, resulting in overall reduced spider species richness and diversity. In fact, the spider assemblages changed towards an increased relative abundance of shade and humidity loving species. The impact of rose encroachment on spiders can be compared to the results obtained by Isermann (2008) for flowering plants, where only a few shade-tolerant taxa remained below the rose shrubs.

The abundance of harvestmen is also most likely related to the shading effect of the roses and the consequent lower temperature (and probably higher humidity) of the habitat. Harvestmen require high humidity because they are susceptible to dehydration (Todd 1949; Curtis and Machado 2007) and they are not dependent on or associated with specific plants. The harvestmen may also have been attracted by the increased prey availability in the rose patches.

The significant negative impacts on the arthropod fauna documented in this study can only be a weak trace of the potential future effects if the roses are allowed to spread in the area. Firstly, in the study area *R. rugosa* is only in an initial phase of increase and covers only a minor fraction of the dunes (c. 1 %, Kollmann et al. 2009). In only a few places have the rose patches merged to form a coherent shrubbery over large areas of land. Therefore, edge effects tend to favor the original dune fauna that may trespass the rose patches. Secondly, so far rose patches cover mostly east-facing dune slopes; here the native dune vegetation is rather dense with accumulating litter on the ground. More exposed dune slopes with scarcer vegetation and open sand areas, i.e. the parts that house most of the xerotherm specialist species expected to be threatened the most by the rose invasion, are so far little affected.

Conclusion

The study has demonstrated a significant impact of invasive *R. rugosa* on the arthropod fauna in Danish yellow dunes. Many of the changes were expected, given the radical shifts seen in environmental conditions, resource availability and vegetation structure. Although some of the changes represent faunistic enrichment, mainly caused by enhanced resource availability, there is cause for concern about the pauperization of the fauna brought about mainly by the changes in abiotic conditions. Increased shading and reduced patchiness of habitat characteristics may be a generic consequence of plant invasions, because shading is a powerful competition strategy for a plant. We see clear effects among the spiders, which are a group with many dune habitat specialists (Hänggi et al. 1995; Gajdos and Toft 2002; Bonte et al. 2006; Schirmel and Buchholz 2011). Spider species richness and diversity were significantly reduced in the rose patches, and reductions were found in particular among diurnal, xerotherm hunting species; in contrast, the species increasing in abundance in the rose patches were less specialized vegetation-dependent web-builders. Several previous studies agree that the most endangered specialist dune spiders are those depending on active sand dynamics (Bonte et al. 2006; Warren and Büttner 2008; Schirmel and Buchholz 2011; Wunsch et al. 2012; Brunbjerg et al. 2015). However, being a woody shrub, *R. rugosa* coverage will act to inhibit the natural sand dynamics of the coastal dunes (Provoost et al. 2011; Muñoz-Vallés et al. 2014). *Rosa rugosa* may therefore not only have a negative effect on the dune fauna directly in the rose-covered parts; it will also indirectly affect the potentially much larger areas of native vegetation by protecting this against sand shifting and Aeolian dynamic processes.

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