



The spider fauna of Danish coastal dune habitats revisited after 25 years: evidence of faunistic impoverishment

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Abstract

Arthropod faunas have become impoverished in recent years in abundance as well as in diversity, but so far little evidence exists concerning spiders. In 2022, we repeated pitfall trap collections of spider assemblages completed 25 years previously in coastal dune habitats of the Hanstholm Reserve of National Park Thy, Denmark. Traps were placed approximately at the same spots, i.e. the habitats (white dune, grey dune, dry dune heathland, wet dune heathland, low pine plantation) were represented approximately as before. Contrary to most previous reports of insect decline, we found only weak evidence of reduction in abundance, but strong indications of reductions in faunistic value based on changes in ecological traits. Within the same period of spring and with the same number of traps, we collected 12% fewer spider individuals and 13% fewer species; rarefaction indicated that the lowered species richness was real. Species diversity had decreased and dominance increased. Changes in indices of ecological traits showed that the fauna had changed into decreased contribution of habitat specialists and species of restricted Danish distribution; the proportion of aeronauts had increased; the average body size had decreased. Indices of assemblage microclimatic niche positions and niche widths showed increased representation of shade and humidity loving species. Most of these changes were repeated in each of the habitats. Finally, we found evidence of a phenological shift towards activity earlier in spring in some species.

Implications for insect conservation We discuss possible management measures to counteract the observed trend towards reduced faunistic value.

Keywords Araneae · Conservation · Decline · Ecological traits · Faunistic value

Introduction

Lowered abundance, biomass and species diversity have been reported for several arthropod taxa during recent years from several parts of the world (e.g. Hallmann et al. 2017; Lister and Garcia 2018; Samu et al. 2023), which has been related to parallel declines of insectivorous vertebrates (e.g. Møller 2020). It has also created concern for the future of various ecosystem services, e.g. pollination and biocontrol (Wagner et al. 2021). Anthropogenic drivers of faunistic impoverishment are several, including intense land use (e.g. deforestation, drainage, urbanization), agricultural

intensifications (e.g. monocultures, insecticides), a warming climate, and other stressors derived from these (summarized by Wagner et al. 2021). Faunistic declines are observed not only in landscapes that are under heavy influence from human activities; they are seen also in nature reserves (Brooks et al. 2012; Hallmann et al. 2017; Lister and Garcia 2018; Seibold et al. 2019). This may be due to “diffuse” effects of human activities in surrounding landscapes, e.g. wind-drift of pesticides, fertilizers in rain (Brühl and Zaller 2019; Seibold et al. 2019) or generally increased temperatures (Lister and Garcia 2018; Wagner et al. 2021).

From a nature conservation point of view, the reduction in insect species richness is of concern in its own right, because reductions primarily fall on specialized species (Warren et al. 2001; Brückmann et al. 2010; Habel et al. 2016; Nolte et al. 2019), which increases the danger of both local and complete extinction. Lack of proper management especially of early successional habitats may mean that the vegetation develops, creating habitats of more benign microclimate,

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which favors generalist species (Thomas et al. 2015). At the same time, many generalists (including invasive species) increase. This exchange of specialists with generalists means that arthropod assemblages undergo a degradation in faunistic value. Apart from studies restricted to reduction in numbers and biomass of (unidentified) flying insects, declines in diversity have for years been reported especially from charismatic groups like butterflies and moths (Thomas et al. 2004; Conrad et al. 2006; Hallmann et al. 2020), dragonflies (Bowler et al. 2021), syrphid flies (Barendregt et al. 2022), carabids and other beetles (Kotze and O'Hara 2003; Desender et al. 2010; Brooks et al. 2012; Homburg et al. 2019; Hallmann et al. 2020). Other taxa are little covered. Spiders have been included in studies covering main arthropod groups (e.g. Lister and Garcia 2018; Outhwaite et al. 2020), indicating that spiders may have declined as well. In arctic Greenland, Bowden et al. (2018) found that some species had declined over 18 years while none increased. Samu et al. (2023) compared the spider fauna of an agricultural field and its margin area 23 years apart and found numerical declines of 45 and 59%, respectively; no changes in species richness or ecological traits could be detected, however. Declines of specific groups or species of spiders have also been suggested (Rix et al. 2017; Nyffeler and Bonte 2020).

Documentation of faunistic decline should preferably be based on long-term continuous registrations that make it possible statistically to distinguish normal year-to-year fluctuations from long-term trends. Unfortunately, such registrations are not available for most arthropod groups. A less optimal alternative is to repeat stand-alone studies from the past (e.g. Lister and Garcia 2018; Samu et al. 2023). Whether such studies will indicate a decline in numbers of individuals and species or not, analysis of changes in assemblage trait composition may indicate whether the faunas change in faunistic value, given criteria for such evaluations. Ecological specialists have frequently been found to be particularly vulnerable to anthropogenic disturbances and to suffer the largest population reductions and thus the largest extinction risks (Warren et al. 2001; Brückmann et al. 2010; Nolte et al. 2019). Among these, species restricted to few habitat types (habitat specialists) will generally have smaller distributions and more patchy occurrences within their distribution area, i.e. in national distribution maps they will occur in fewer districts or squares. We use “assemblage indices”, which summarize the distributions and ecological traits of all species in a local animal community, as quantifiable indicators of faunistic value. We calculate assemblage indices for ecological traits: habitat width, Danish distribution, dispersal ability, body size, and niche positions and niche widths along two environmental gradients (dry–wet, shaded–open). If specialists are exchanged with generalists, the average assemblage niche width will increase because generalists have wider niches than specialists. Otherwise

with respect to indices of assemblage niche position: if in a habitat with many microclimate specialists, e.g. a desert or a wetland, specialist species are exchanged with generalists, the average microclimatic position of the assemblage is expected to move to a more central position along the gradient. Thus, indices of assemblage niche position should be evaluated specifically for the habitats considered.

Spiders have a unique way of aerial dispersal, named ballooning (i.e. they are carried through the air on a silken thread); such aeronautic behavior are frequent in some species, while in others it has never been observed (Bell et al. 2005). Aeronautic species generally have broad niche widths and occur in more types of habitats than non-aeronauts (Bonte et al. 2003) therefore, an increasing proportion of aeronauts may also indicate that habitat generalists are taking over at the expense of specialists.

Our coastal study area consists of habitats with sparse vegetation and often extreme microclimates. Therefore, the natural fauna contains several heat and drought tolerant (xerothermic) species. Living near the northern limit of their distribution, many of these specialized species are found exclusively in dry dune habitats, some even restricted to south-facing slopes, and therefore are an especially vulnerable and threatened part of the fauna (Bonte et al. 2004). Thus, a decreased representation of xerothermic species and/or an increase in species with preferences for humid and shaded microclimates, exemplified for example by the effect of *Rosa rugosa* invasion in the yellow dune habitat (Elleriis et al. 2015), can be considered a lowered faunistic value of the fauna.

Previously (Gajdoš and Toft 2000), we analyzed changes in the spider fauna of heathland habitats over 20 years from an area only a few kilometers from the study site of the present paper. We compared pitfall trap catches from two adjacent early years (1977–1978 and 1978–1979) with those from 1997 to 1998. Overall, we found only minor changes; in particular, we found that changes between the two early years were of the same magnitude as between the early years and 20 years later, indicating that the changes were not part of a major long-term trend. Schikora (1994) also found relatively minor changes over 22 years in the spider species of a bog in spite of prominent vegetation changes due to drainage; however, the dominant spiders had changed from photophilous to skotophilous species. Our former study (Gajdoš and Toft 2000) used only changes in species composition as basis for its conclusions. Subsequently, enormous amounts of information on ecological traits of European spiders have become available, which allow us to analyze faunal changes at a much more detailed level. Here, we report on collections of spiders made by ourselves in the Hanstholm Reserve, Denmark, in 1997–1998 (Gajdoš and Toft 2002) and repeated after 25 years: we collected not only in the same area, but had our traps in approximately

the same spots. Though the trapping period was shortened from a full year to three months, we started and ended trapping on dates that formerly were trap-emptying days, i.e. we compare catches from exactly the same period of the year. It should be remembered, however, that the design of the study originally was not aimed at such a long-term comparison. We argue, however, that if the comparison reveals strong systematic patterns of change, for example in relation to ecological traits of the species, and these changes are repeated in assemblages of different habitats, then they are at least indicative of on-going trends and, in the absence of more decisive information, may serve as a warning that management action may be required. In contrast, if changes affect species randomly with respect to ecological traits, e.g. equally affect habitat generalists and specialists, large and small species etc., then they may be best considered results of natural fluctuations, even if certain species have been exchanged for others.

Because our study area lies in one of the least anthropogenically disturbed areas of Denmark, and because of the lack of evidence for major changes in our former study (Gajdoš and Toft 2000), our a priori expectation was to find a spider fauna more or less unaffected by time. During the intervening years, one of our habitats, the yellow dune, had been affected by invasion of *Rosa rugosa*, forming patches of various size in the marram grass (*Ammophila arenaria*) matrix. Since 2017, strong efforts have been made to eradicate the roses using heavy excavating machinery, leaving the former rose patches as bare sandy areas. Whereas rose invasion promoted a spider fauna with more generalists than the original dune vegetation (Elleriis et al. 2015), their eradication had the opposite effect, i.e. an increase in specialist (xerothermic) species (Toft 2020). We therefore expected a possible increase in species with specialist traits in this habitat. In other parts of the study area some vegetational succession had occurred, which had transformed bare sandy areas into grey dune vegetation, or had changed former grey dune spots into dune heath. We have accounted for this by calculating assemblage trait indices not only for the whole area, but also for each of the main habitats separately.

Study area and methods

Habitats

Forming the northern part of National Park Thy, the Hanstholm Reserve (area 3725 ha) lies at the northwestern corner of Denmark, exposed to the North Sea which forms its western border (Fig. S1 in Electronic Supplementary Material_1 (ESM_1)). Along the beach is a row of white dunes (100–200 m), to the east of which comes a mosaic of dune heathland habitats that form the main part of the reserve

(Fig. S2, S3 in ESM_1). Several sand dunes raise above the general ground level, covered with grey dune vegetation, dry heathland or planted pines (*Pinus mugo*), and oligotrophic marshes and lakes are scattered over lower parts of the area. Our study comprised the yellow dune habitat close to the beach (57.062 N, 8.526 E) and a mixture of dune and heathland habitats from an area c. 400–800 m inland. Pitfall traps (88 in 1997–8, 90 in 2022) were placed as transects centered around two adjacent dune hills (locally named Bøjebakke and Kobbelsbakke; 57.059 N, 8.532 E). The transects ran from the top of each hill (both 28 m a.s.l.) in four directions, parallel and perpendicular to the coast (i.e. NE, SE, SW, NW). At both study periods, the vegetation around each trap was registered by estimating the coverage of dominant plants within half a meter's distance from the trap. Based on these registrations, the trap sites were assigned to 7 vegetation types. These can be characterized as follows:

- Yellow dune (Fig. S4a in ESM_1): > 50% *Ammophila arenaria* was present, often as a monoculture. Most trap-sites were strongly influenced by shifting sand. The 13 traps were placed only a few meters from the slope to the beach.
- Grey dune (Fig. S4b, c in ESM_1): present on E, S and W facing dune slopes; originally created by shifting sand or as wind-breaks, this habitat has sparse vegetation with mixture of *Ammophila arenaria*, *Carex arenaria*, lichens, moss and other plants; at some trap sites, the vegetation covered < 20% of the area, leaving a bare sandy surface. We used 30 traps in both years.
- Dry heath (Fig. S5a in ESM_1): mainly present on north sides of dune hills and on level ground; dominated by *Calluna vulgaris* and *Empetrum nigrum*. We used 20/18 traps in the two sampling periods, respectively.
- Wet heath/bog (Fig. S6 in ESM_1): low-lying (restricted to elevations 9–11 m a.s.l.), more or less flooded during winter and spring. Vegetation dominated by *Erica tetralix* and *Vaccinium uliginosum* (wet heath), or by *Sphagnum* sp., *Molinia coerulea*, *Narthecium ossifragum* or *Eriophorum angustifolium* (bog). Wet heath and heath bog traps have been merged in the data analysis. We used 12/16 traps in the two sampling periods, respectively.
- Pine plantation (*Pinus mugo*) on N and W slopes of Kobbelsbakke (Fig. S3 in ESM_1), maintained at exposed slopes at less than one meter height by strong winds and low nutrient availability; at the leeward site of the dunes, it reached 2 m height. The ground was covered with dried needles or a thick layer of moss (Fig. S5b in ESM_1). In 2022, the plantation showed signs of degradation, as many of the trees had died. We used 9 traps in both sampling periods.
- *Hippophaë* shrub: two traps were placed under shrubs of c. 1 m height at the peak of Kobbelsbakke.

- *Carex* carpet: two traps were situated in a depression with dense vegetation of *Carex* sp.

We consider yellow dune, grey dune, dry heath and wet heath as the main habitat types of the area. As some of the other habitat types were represented by few traps and could not be included in a main habitat, these were omitted from several analyses. However, they were included in "whole area" analyses.

Meteorological data (temperature) were obtained from the Danish Meteorological Institute, station Silstrup, lying c. 15 km from the study area (<https://www.dmi.dk/friedata/observationer>). We calculated monthly average temperature for the trapping periods. For April, May and June mean temperatures were higher in 2022 than 1997–1998, but lower for July (1997–1998/2022: 7.1/7.5, 9.6/10.4, 13.8/14.7, 16.5/14.9 °C, respectively). Mean temperatures for the whole trapping periods were nearly identical (11.8/11.9 °C). We therefore consider that weather differences had no influence on the spider catches.

Trapping

Our 1997–8 samplings covered a full year, whereas the 2022 samplings were restricted to three months of spring and summer. We started and ended the 2022 samplings on dates where traps had been emptied previously; we thus covered exactly the same time period in both studies (12 April–19 July). Notice, however, that due to the starting date of the project in 1997, the catches of 1997–8 is combined from two separate trapping periods, i.e. 12 April–11 May 1998 and 11 May–19 July 1997. The traps were emptied at approximately fortnightly intervals in both years.

The traps differed slightly between the two collections. In 1997–8, they consisted of a plastic beaker (11 cm diameter, 20 cl) fitted into a plastic flower pot dug into the ground. The trapping fluid was a 2–3% formalin solution mixed 4:1 with ethylene glycol, with a few drops of detergent added. In 2022, we used double plastic beakers (diameter 8.8 cm, 40 cl), and the trapping fluid was concentrated salt water with detergent. In both trapping periods, the traps were covered by a wooden roof (12 × 12 cm).

All spiders from 1997–8 were identified by PG, those from 2022 by ST. Nomenclature follows the World Spider Catalog (2023). The Electronic Supplementary Material_3 (ESM_3 lists the species collected in 2022, the species collected in the same period in 1997–8, and the total species list of the 1997–8 collections, which has not been published before. The lists neglect juveniles that could not be identified at species level.

Data analysis

We evaluated the changes in species diversity by comparing diversity profiles from the two sampling periods, using PAST (Hammer et al. 2001). Diversity profiles (or Renyi curves) relate several diversity indices via a scaling parameter (α). Thus, for $\alpha=0$ they depict the number of species (S); for $\alpha=1$ and 2, their values corresponds to the Shannon and Simpson indices, respectively; and for $\alpha=4$ they correspond to the inverse of the Berger-Perker dominance index (Tothmeresz 1995; Southwood and Henderson 2000). PAST was also used for individual rarefaction analysis for evaluation of difference in species numbers.

In order to evaluate the faunistic changes between the two trapping periods, we related these changes to information on habitat width, Danish distribution, body size and climatic niches for each species; we further used information about aeronautic activity, and whether the species can be categorized as xerothermic.

Information on species' microclimatic niches were obtained from Entling et al. (2007). We calculated the mean niche positions and mean niche widths of the spider assemblage of each trap along the open-shaded and the moist-dry niche axes.

Degree of habitat specialization was analyzed based on information on species' habitat occurrence in Central Europe (including Denmark) (Hänggi et al. 1995): we counted the number of habitat types (out of 85) from which each species is known. Information on species' distribution in Denmark was obtained from https://www.zmuc.dk/entoweb/arachnology/dkchecklist_danish.htm. This lists the occurrence of Danish spiders in 11 faunistic districts. Spiders were further classified as aeronautic or non-aeronautic according to information in Bell et al. (2005). To classify species as xerotherm or non-xerotherm, we used the list of Bonte et al. (2004) with the following modifications: (1) web-spinning species that depend on vegetation for web construction were not included; (2) all salticids were included even if not mentioned by Bonte et al. (2004). Finally, we used information on adult female body sizes (total length) as reported in the main works used for species identification, i.e. Lockett and Millidge (1951, 1953), Roberts (1985, 1987) and Almqvist (2005, 2006).

Habitat specific assemblage indices were calculated as means of species' trait values for the species occurring in each habitat. They were calculated both at the individual level (using catch abundance data) and at the species level (using presence-absence data). The general formulae are $\sum T_i \times n_i/n$ and $\sum T_i/S$, respectively, where T_i is the trait value for species i , n_i is the abundance of species i , n is the total abundance of spiders in the habitat; S is the number of species in the habitat. Index values were first calculated for summed catches of each trap, then averaged for the traps

of each habitat. Ecological trait values for each species are given in Electronic Supplementary Material_2.

Phenological timing

In order to test the hypothesis that seasonal activity fell earlier in the season in 2022, we calculated the mean date of species catches for both years, using the numbers caught in each trapping period. The trapping periods were of 14 days duration and trapping dates were nearly identical. The difference in timing of activity between the two years was therefore expressed as a fraction of a fortnightly period.

Data from an intermediate year

From two of the habitat types, yellow dune and grey dune, pitfall samples were taken in 2013 from within the same area. In that year, 10 traps were operated during the period 17 May to 15 June in the same yellow dune area, and another 10 traps in one of the grey dune areas of the present investigation. Thus, for these two habitats we have an intermediate point in the 25 year interval considered in the present study, though the trapping period in 2013 covered only one month.

Statistical analysis

We used JMP v. 16 (SAS Institute Inc., Cary, NC, USA) for statistical testing. Abundance values were obtained as the cumulated catch from each trap. In the statistical analysis, abundance data have been $\log(x + 1)$ -transformed to accommodate the large differences in species abundances. Accordingly, changes in abundance between 1997-8 and 2022 have been calculated as the difference between the two log-abundances ($\log(\text{abundance}_{1997-8} + 1) - \log(\text{abundance}_{2022} + 1)$). Regression analysis was used to relate changes in species abundances to species habitat width, Danish distribution, and body size.

The indices of assemblage niche position, niche width, habitat width, Danish distribution, body size, proportion of xerothermic species, and proportion of aeronautic species were compared between 1997-8 and 2022 with ANOVA/t-test. As several data sets did not comply with the equal-variance assumption of parametric tests, we used Welch's test all through. The same test was used to compare ecological traits of aeronautic vs. non-aeronautic species.

Results

Changes in species richness and diversity

The number of identified individuals from the same number of traps (88) and the same trapping period changed from

7886 in 1997-8 to 6945 in 2022, a decrease of 11.9% (data in ESM_3). The number of identified species changed from 144 to 125, a decrease of 13.2%. Neglecting singleton and doubleton species, trends are similar though numerically less, as the decrease in both individuals and species then was 7.2%.

The diversity profile curve for 2022 lies consistently below that for 1997-8, indicating that not only species richness but all measures of diversity decreased, and dominance increased from 1997-8 to 2022 (Fig. 1a). Individual rarefaction revealed that species increase was slower in 2022 than in 1997-8, tending to level off at (mean \pm SD) 135 ± 4 species versus 165 ± 3 species, respectively (Fig. 1b). Thus, the lower species richness in 2022 is not just a consequence of a lower total catch.

Our samplings indicate that several species have decreased, while others were increased between 1997-8 and 2022. Numerically, the most remarkable species disappearance is that of the linyphiid *Hypomma bituberculatum*. It occurs exclusively in the yellow dune and is often a dominant member of the assemblage. In 1997-8, 151 specimens were caught, in 2022 none. Large changes had also taken place among species of jumping spiders (Salticidae). *Attulus saltator* had nearly disappeared (1997-8/2022: 66/1), whereas *Neon reticulatus* had become abundant (0/69). Two less common salticids had also become

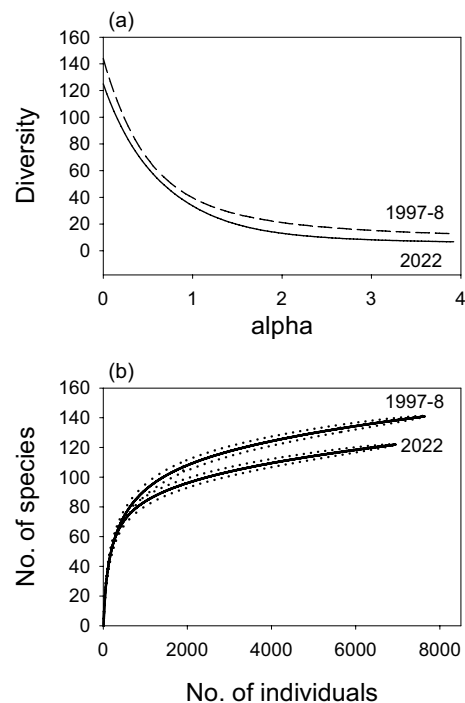


Fig. 1 **a** Comparison of diversity profiles for the total catch of spiders in 1997-8 and 2022. **b** Individual rarefaction curves for the total catch of spiders in 1997-8 and 2022. Dotted lines show 95% confidence limits

reduced (*Phlegra fasciata* 18/0, *Sitticus distinguendus* 6/0) and one had increased (*Talavera aequipes* 0/9). Two species, *Porrhoclubiona genevensis* and *Micaria dives*, have their Danish occurrence restricted to the NW faunistic district, and most of the grey dune habitat, in which they occur, lies within National Park Thy. It has therefore been suggested that National Park Thy should have a special responsibility for the protection of these species (Toft 2013). Of the two, *P. genevensis* showed a reduction in numbers (9/1), while *M. dives* increased considerably (13/46). At the same time, another rare *Micaria* species, *M. lenzi*, disappeared completely (23/0). As this species was also not recorded in the 2013 samples (S. Toft, unpublished), its absence in 2022 may be due to disappearance.

Assemblage indices: comparison of habitats

Niche positions of the spider assemblages from the habitat types along the open-shaded axis follow the trend to be expected from physico-chemical characteristics of the habitats (Fig. 2 and Fig. S8 in ESM_2): the assemblage of the grey dune shows the lowest values on the open-shaded gradient (i.e. species adapted to the most open habitats), the dry heath assemblage intermediate, and the wet heath showing the highest value (i.e. species adapted to more shaded habitats). The yellow dune assemblage was in the low to intermediate range. Likewise, the assemblage of the grey dune shows the highest positions along the moist-dry axis (i.e. species adapted to the driest habitats), and assemblages of the dry heath and yellow dune and wet heath come at increasingly lower values. The open-shaded assemblage niche widths show a similar increase from narrowest in the grey dune assemblage, intermediate in the dry heath assemblage, and broadest in the wet heath assemblage. The pattern of niche widths along the moist-dry axis is not as clearcut, except that species of the two most moisture-loving assemblages, the yellow dune and wet heath assemblages, have the most narrow niches.

Average assemblage body lengths show a strict habitat specific pattern (Fig. 3 and Fig. S9 in ESM_2): the grey dune assemblage has the highest body size index, followed in decreasing order by dry heath and wet heath, and with the yellow dune assemblage having the smallest spiders. Habitat width (# habitats) is narrow in the grey dune assemblage, increasing in the dry heath, wet heath and yellow dune assemblages. The pattern of the Danish distribution index (#districts) is similar to the habitat index, i.e. habitat generalists have a wider Danish distribution than habitat specialists. The proportion of aeronauts is lowest in the grey dune and dry heath. The proportion of xerotherms is high in the grey dune, decreasing through dry heaths and wet heath to reach a low in the yellow dune.

Changes in assemblage indices of ecological traits

Over the whole dataset (Fig. 2 and Fig. S8, Table S1 in ESM_2, column “Whole area”), assemblage indices of microclimatic niches moved to a more shaded position along the open-shaded gradient, and to a wetter position along the moist-dry niche gradient; i.e. the composition of the spider fauna had changed into increased representation of shade- and moisture-loving species. Assemblage niche widths increased along both gradients. With minor variations, the results show the same trends whether the individual or species niche indices are considered (Table S1, S2 in ESM_2).

With few exceptions (especially in the moist-dry niche widths), the trends are similar in each of the four main habitats (Fig. 2 and Fig. S8, Table S1, S2 in ESM_2). It is noted that the changes in niche position and niche widths are in the same direction and of approximately of the same magnitude, whether the habitat has a low or high position along the gradient, and whether the level of niche width was high or low (Fig. 2 and S8 in ESM_2).

Over all habitats (Fig. 3 and Fig. S9 in ESM_2, column “Whole area”), the spider fauna changed in the direction of increased representation of small species and habitat generalists of wider Danish distribution. This is associated with increased proportion of aeronauts. The proportion of xerotherms, however, remained unchanged.

The trend of decreasing body size is repeated in the assemblages of the four main habitats (Fig. 3 and Fig. S9, Table S1, S2 in ESM_2). The same is the increased habitat spectrum and the wider Danish distribution. Most habitat assemblages also show an increased proportion of aeronauts, but only the yellow dune (Fig. 3) and wet heath (Fig. S9 in ESM_2) show significant decrease in the proportion of xerotherms. It should be noted that in all cases where the results indicate an opposite trend, the differences between 1997-8 and 2022 are non-significant.

Summarizing, the trends of the ecological trait indices seen in whole data set and in each of the main habitats are: reduced body size, increased habitat width, increased Danish distribution, increased proportion of aeronauts, increased open-shade niche position, decreased moist-dry niche position, and increased niche widths along both microclimatic gradients. A decreased proportion of xerothermic species is indicated in two habitats.

Abundance changes related to habitat width, Danish distribution and body size

We found a significant relationship between the numerical change in species abundances and the species' habitat widths ($t_{158} = 2.70$, $p = 0.0077$) and Danish distribution ($t_{161} = 2.11$, $p = 0.0368$) (Fig. 4a, b). Abundance changes were most negative for species with narrow habitat widths and restricted

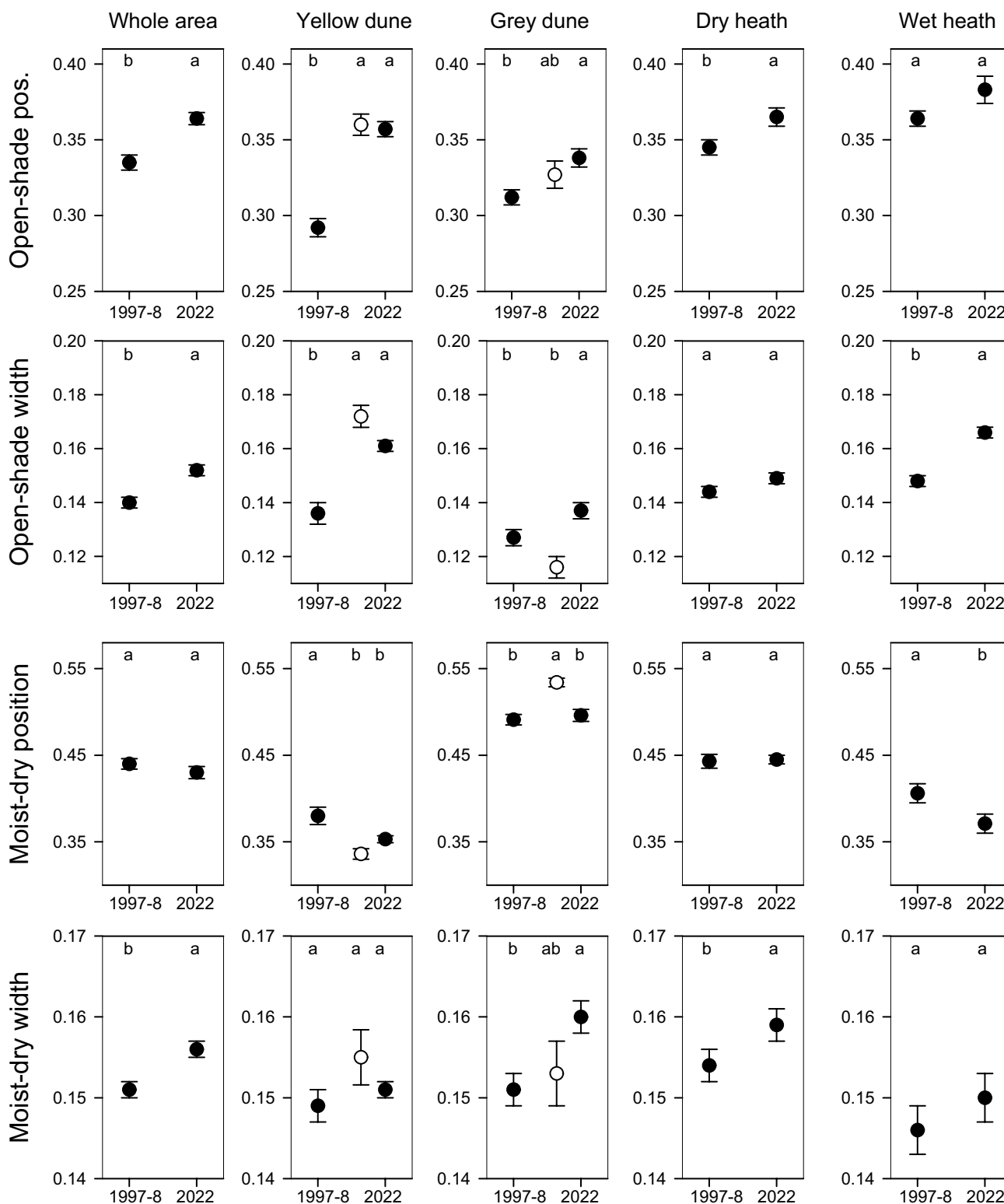


Fig. 2 Indices of niche positions and niche widths of the total catch (Whole area) and of the spider assemblages of the four main habitats (Yellow dune, Grey dune, Dry heath, Wet heath), based on presence-absence data. Open symbols (only yellow dune and grey dune):

data from 2013. A similar plot based on abundance data is presented in Fig. S8 in ESM_2. Statistical analysis is presented in Table S2 in ESM_2

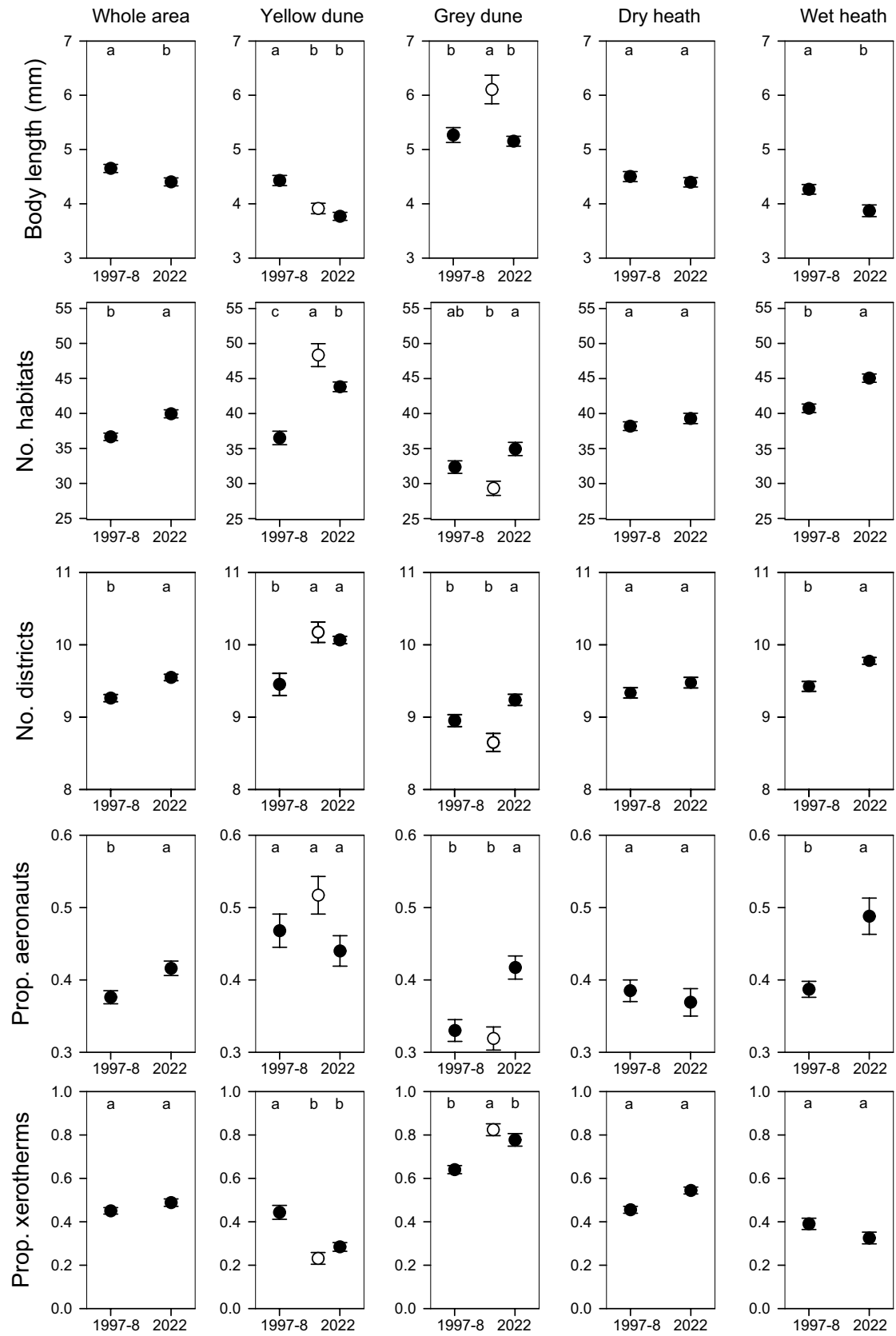


Fig. 3 Indices of ecological traits of the total catch (Whole area) and of the spider assemblages of the four main habitats (Yellow dune, Grey dune, Dry heath, Wet heath), based on presence-absence data. Open symbols (only yellow dune and grey dune): data from 2013. A similar plot based on abundance data is presented in Fig. S9 in ESM_2. Statistical analysis is presented in Table S4 in ESM_2

Danish distribution; they increased to eventually becoming slightly positive for species with the widest habitat occurrence and widest Danish distribution. Considering each habitat separately, significant regressions were repeated for habitat widths by yellow dune ($t_{73} = 2.88$, $p = 0.0053$), and for Danish distribution by yellow dune ($t_{76} = 2.18$, $p = 0.0326$) and wet heath ($t_{91} = 2.06$, $p = 0.0426$). It is further noted that, even if not significant, slopes of data from all 7 habitats are positive (Binomial test, $p = 0.004$), indicating that the same pattern exists in all habitats.

A similar analysis relating the change in species abundances to body size revealed a negative though non-significant relationship ($t_{163} = -1.30$, $p = 0.19$; Fig. 4c). The same result was obtained by comparing the body sizes of species that increased vs. those that decreased ($t_{156} = 1.10$, $p = 0.27$).

Timing of seasonal activity

The number of species whose mean seasonal activity fell earlier in 2022 than in 1997–8 was higher than the number of species whose activity fell later (16 vs. 10 species), but this difference was non-significant (binomial test, $p = 0.163$). However, the species whose activity fell earlier moved their seasonal activity more than the species whose activity fell later (t -test, $t = -2.42$, $p = 0.0251$). Thus, most of the species with later activity had changed their mean activity time by up to one week, whereas several species that changed to earlier activity had moved their mean activity time by 1–2 weeks.

We tested whether earlier/later activity timing could be related to species' ecological traits: body size, habitat width, Danish distribution, open-shade niche position and width, moist-dry niche position and width, and whether the species are aeronauts or xerothermic or not. None of these tests were significant (results not shown).

Data from 2013

How the samples from the yellow and grey dune habitats in 2013 relate to those of 1997–8 and 2022 can be seen in Figs. 2 and 3 and Fig. S8, S9 in ESM_2. In the yellow dune, trait indices of 2013 are most similar to those of 2022. In contrast, where trait indices have changed in the grey dune, 2013 is most similar to 1997–1998. In both habitats, some values are above or below those of 1997–8 and 2022.

Ecological traits in aeronauts vs. non-aeronauts

In the selection of species collected in the present study, we found that aeronautic species are slightly but not significantly smaller than non-aeronauts; however, they have broader habitat niches and are more widely distributed in Denmark (Fig. 5; Table S5 in ESM_2). They have a more moist position on the moist-dry gradient, but a less shaded position on the open-shaded gradient. They also have broader niches along both these microclimatic axes. Finally, aeronauts are less likely to be xerothermic than non-aeronauts (Contingency analysis, Fisher's Exact Test $p = 0.0030$).

Discussion

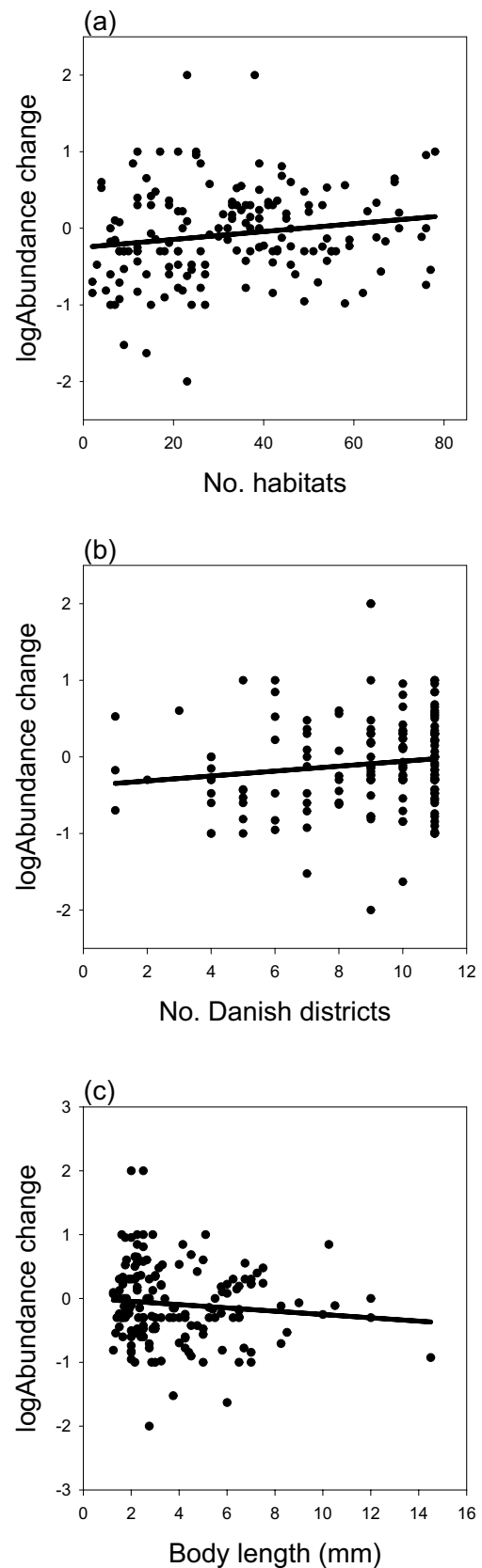
The decrease in number of individuals observed in this study is modest compared with published results on insects and spiders, and due to the lack of intermediate recordings we cannot safely conclude that total spider abundance has been reduced. However, our finding that habitat specialists with restricted national distribution were reduced the most in abundance, in contrast to widespread habitat generalists that were less reduced or had even increased (Fig. 4), is reason for concern. The same is true for the decrease in species richness and diversity (Fig. 1). The most striking evidence of faunistic degradation, however, is the systematic changes in composition of ecological traits in assemblages of most habitats between the years tested, i.e., the increased representation of habitat generalists and widespread species, the reduced body size, the increase in aeronautic species and the shifts in assemblage niche position (towards more shade and higher moisture) and larger microclimatic niche widths (Figs. 2 and 3). These trends were repeated in all habitats, independently of whether the results are analyzed on abundance or presence/absence data. Surprisingly, they were less pronounced in the grey dune assemblage than in other habitat assemblages.

The analysis of ecological traits revealed that the same trends have occurred in all habitats, no matter if the original values were high or low (Figs. 2 and 3): all assemblages showed reduced body size index, even in the yellow dune and the wet heath which originally had the smallest indices; all assemblages increased their Danish distribution index (no. faunistic districts occupied), even that of the wet heath that originally had the highest index; all assemblages changed to a higher position on the open-shaded gradient; against our expectations, even the wet heath assemblage had changed to a more moist position on the moist-dry gradient. This may indicate that the drivers of change are basically the same over the whole area, though the magnitude of effects may be modified by specific conditions of the habitats. What these drivers are, is unclear. Weather conditions in the two

Fig. 4 Relationships between species' change in abundance between 1997–8 and 2022 and their habitat width (a) and Danish distribution (b). Habitat width is the number of habitats out of 85 from which each species has been recorded in Central Europe; Danish distribution is the number of faunistic districts out of 11 that the species are known from. Statistical details: **a** $\log\text{Sum}2022 - \log\text{Sum}1997 = -0,297971 + 0,0063503 * \#\text{habitats}$; $t_{158} = 2.70$, $p = 0.0077$; **b** $\log\text{Sum}2022 - \log\text{Sum}1997 = -0,458083 + 0,039479 * \#\text{districts}$; $t_{161} = 2.11$, $p = 0.0368$; **c** $\log(\text{sum}2022 + 1) - \log(\text{sum}1997 + 1) = 0,0034738 - 0,000257 * \text{mm}$; $t_{163} = -1.30$, $p = 0.1939$

study periods were rather similar and thus cannot account for the faunistic differences. The most direct human disturbance was the mechanical eradication of *Rosa rugosa*, but this was performed only in the yellow dune habitat and only at some distance from the yellow dune trapping site; as already argued, it was further expected to have the opposite effect on the spider assemblage than the one observed (cf. Toft 2020). In the grey dune habitat, successional changes of the vegetation might explain the observed faunistic changes; they would not, however, explain the similar changes in other habitat types, and would not account for the finding that the grey dune assemblage was the least modified of all. A possible local driver of faunistic change has recently emerged, though it may have been in effect for many years, i.e. PFAS contamination (Naturstyrelsen 2023). The concentration of PFAS is extremely high in sea water foam along the North Sea coast. The foam is created by braking waves and blown inland by the prevailing westerly winds. All along the Danish west coast, grass from cattle grazed fields less than 1 km from the sea contained PFAS in amounts surpassing accepted “indicator values” (i.e. amounts creating health concerns for consumers of the meat) at 43 out of 44 sites (Naturstyrelsen 2023). The study included sample sites from a few kilometers north and south of our study area, all of which are situated less than 1 km from the coast. We know of no studies of the effects of PFAS on spiders, but several insect groups are affected negatively by these compounds (Bots et al. 2010; Mommaerts et al. 2011), and spiders are known to accumulate PFAS (Koch et al. 2021).

We expected that the assemblage of the grey dune habitat would be more vulnerable than those of the other habitats, because the species of that assemblage are the most specialized with respect to ecological traits, and several species exist at the northern border of their distribution. Instead, the grey dune assemblage was the least modified. The reason for this is uncertain, but we hypothesize that it is due to the extreme conditions of the habitat, with sparse vegetation on which to attach webs and to provide shading, and very high surface temperatures during sunny summer days. Some of the indigenous species (e.g. species of *Alopecosa* and *Arctosa*) dig into the soil, probably avoiding the extreme temperatures. Generalist species that potentially invade



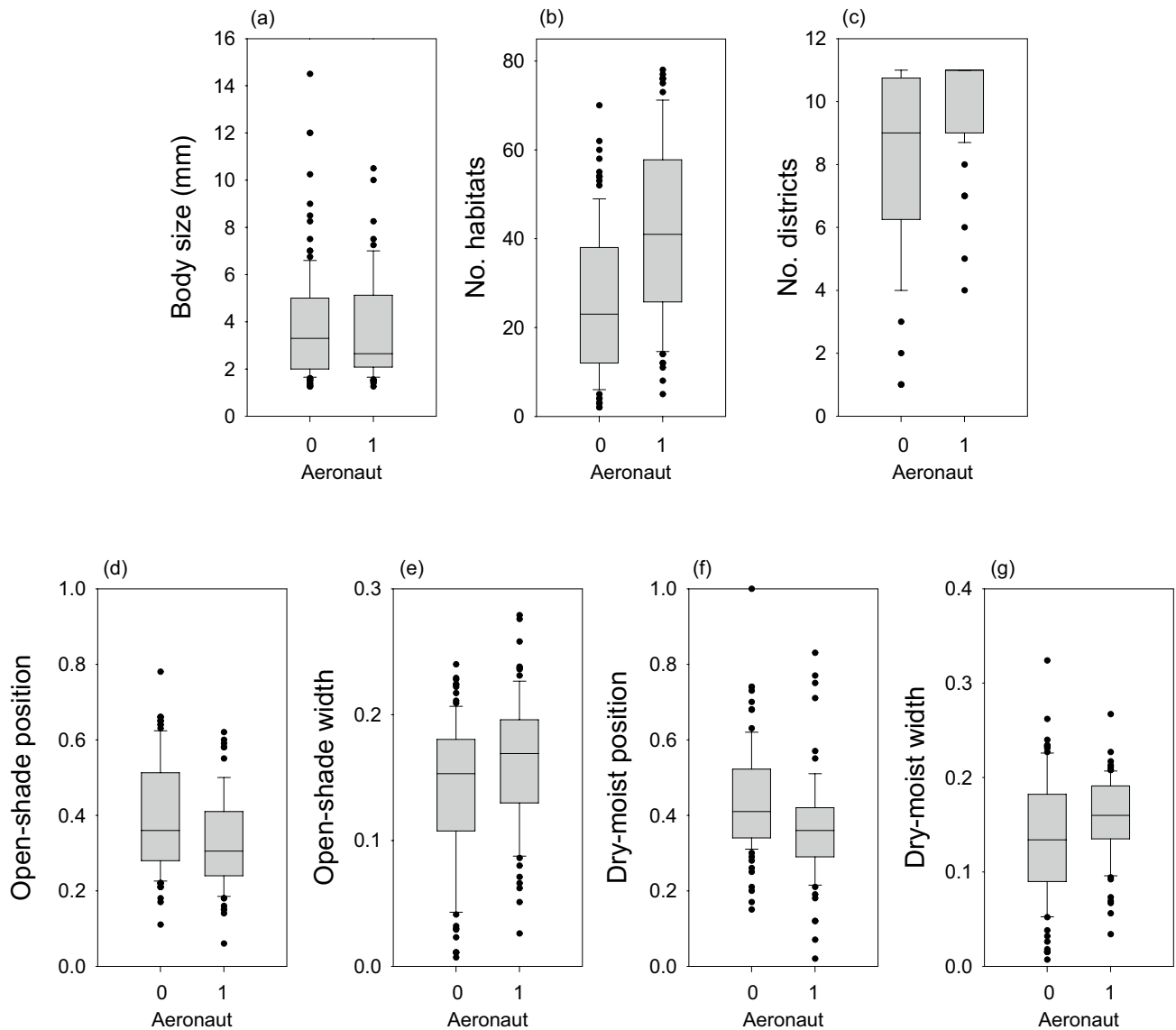


Fig. 5 Comparison of ecological traits in non-aeronautic (0) and aeronautic (1) spider species of the study area. **a** body size (mm); **b** number of habitats species are known from; **c** number of Danish faunistic districts species are known from; **d** niche position and

e niche width along the open-shaded gradient; **f** niche position and **g** niche width along the dry-moist gradient. Statistical analysis in Table S5 in ESM_2

this habitat lack this ability. The main threat to the grey dune spider assemblage is disappearance of the habitat due to encroachment of dwarf shrubs (*Calluna* and *Empetrum*) from the surrounding heath (see Fig. S7 in ESM_1), which has reduced the amount of grey dune habitat to fragmented patches.

It might be hypothesized that the changes in assemblage trait indices between 1997-8 and 2022 could be explained by increased influx and promotion of aeronauts from surrounding habitats. The analysis of ecological traits in aeronautic and non-aeronautic species shows that establishment of aeronauts would have many of the consequences seen.

Several details show, however, that this cannot be the whole explanation. For example, the assemblage positions along the open-shaded gradient increased in all habitats, whereas aeronautic species require more open habitats than non-aeronautic species. Also, in the yellow dune assemblage most trait indices changed in the same way as in the other habitats, even with no increase in the proportion of aeronauts. Aeronautic behavior is believed to be associated with living in disturbed habitats such as coasts and agricultural fields (Bell et al. 2005). The most disturbed natural habitats are coastal (beaches, salt marshes), and water is often the direct agent of the disturbance. This may explain the combination of

preference for openness and humidity in aeronautic species. In contrast, the changes of the spider assemblages combined increased preference for shadedness and humidity.

Management implications

As acknowledged in the Introduction, we cannot prove statistically that the patterns observed in this study reflect real long-term trends. Our 2013-collections in the yellow and grey dune habitats showed, however, that some assemblage trait indices had changed already in years prior to 2022; this indicates that 1997–8 and 2022 were not extreme years and that some changes had already taken place in 2013. Though we cannot describe the exact time course of the changes, we have provided evidence that the spider fauna of the Hanstholm Reserve is presently changing in a direction away from the historical state with a high proportion of specialist species, adapted to the sometimes extremely warm and dry coastal environment, into a fauna of generalists that flourish when environmental conditions are less harsh. This means that its faunistic value has diminished. The factors driving these changes are unknown, but may include a general stabilization of habitats, which is partly due to human efforts to control sand shifting, and to nutrient enrichment (through rain water) which accelerates vegetational succession; hypothetically, it may include PFAS-contamination. These factors cannot be easily eliminated, but they can possibly be counteracted by management actions that create disturbance to the area; in particular, there is a need for re-creation of more and larger open (vegetation-poor) areas, which is the habitat that houses the most specialized species (cf. Buchholz 2010; Toft 2013). There are plans to turn the Hanstholm Reserve into a so-called Nature-National Park, which involves adding large grazing mammals to the area. This type of disturbance management is expected to reduce vegetation coverage and enhance botanical diversity (Plassmann et al. 2010), which subsequently will improve conditions for habitat specialized arthropods (Kutiel 2013). Thus, Thomas et al. (2015) found that species of early heathland successional stages in the UK had benefited from a combination of climate warming and management measures aimed at promoting these early seral stages. During the last 25 years, a wild population of red deer have increased substantially in numbers, but this has not prevented the faunistic degradation that we have documented here. Studies from military training areas have shown that severe disturbance is beneficial to the arthropod fauna of heathland and similar habitats that undergo rapid succession (Warren and Büttner 2008). Our results indicate that the fauna of the Hanstholm Reserve is in need of similar habitat rejuvenation.

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Author contributions Data from 1997 to 1998 were collected by both authors. Data from 2013 to 2022 were collected by ST. ST analysed the combined data and drafted the manuscript. Both authors finished and approved the final manuscript.

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Data availability Species lists and background information on ecological traits appear in Electronic Supplementary Material 3 (ESM_3).

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval The study was completed in accordance with Danish legislation.

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