How do alterations in habitat structure by an invasive grass affect salt-marsh resident spiders?

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In European salt marshes, recent invasions by the grass *Elymus athericus* raise questions regarding subsequent habitat modification and its effects on the resident biota. In this study, we studied the effects of modified salt-marsh structure on occurring spider assemblages, especially on salt exposure and flood resistance. We showed that locations having tall and deep-rooted invasive vegetation contained more species able to resist tidal floods as compared with locations with natural vegetation. Dominant species displayed different temporal trends between habitat types after flooding, with some species being less affected by floods either in invaded or in natural habitats. Some cursorial species were able to (re)colonize salt marshes after a spring flood as salinity levels decreased. Finally, stand characteristics of *E. athericus* did not affect the distribution of halotolerant spiders. As a habitat structure relates to flood resistance and/or risk-avoiding strategies, our results indicate that the status of salt-marsh resident species should be considered according to their habitat affinity.

Introduction

Salt marshes are considered one of the rarest ecosystems in the world (Lefeuvre *et al.* 2003), characterized by a sporadic and linear distribution along coastlines. As a consequence of harsh environmental conditions due to tidal flooding and a high salinity, they contain an impoverished flora and fauna. Resident species, however, show original ecological strategies in response to these regular disturbances. Consequently, salt marshes are of high interest in terms of biodiversity conservation (Gibbs 2000, Adam 2002, Bakker *et al.* 2002).

Soil salinity and flood frequency and intensity roughly covary according to the position along a coastline–sea gradient, affecting species occurrence patterns accordingly (Pétillon *et al.* 2008). However, the temporal scales of these constraints are different. At the scale of a tidal cycle, the abrupt changes in soil salinity constitute important constraints for osmotic regulation

(Verschoor & Krebs 1995a, 1995b, Bruyndoncx *et al.* 2002). Additionally, periodic succession of flood events are potentially detrimental to terrestrial organisms as they may be scoured or drowned by the tidal flows (*see* the review of Plum 2005 for floodplains). Such physical limitations necessitate special physiological adaptations (e.g. concentration of hemolymph ions: Moloney & Nicolson 1984) or behavioural responses (e.g. risk-avoiding behaviour: Lambeets *et al.* 2008a). Regular inundation of salt marshes leads to spatial heterogeneity of soil salinity, increasing from high to low marshes. As a consequence, abundance and distribution patterns of resident salt-marsh species depend on their ability to cope with these constraints; species without appropriate biological or ecological life-history traits being filtered out (Levin & Talley 2000).

Vegetation and underground structures are known to influence the flood resistance (Foster & Treherne 1976, Kneib 1984) and flood avoidance (Cooke 1962, Adis 1997) of terrestrial invertebrates by, for instance, providing suitable refuges. Between spring floods, however, spiders may (re-)colonize new habitats according to their intrinsic mobility. Moreover, the trade-off between a strategy of submersion tolerance or flood avoidance depends on habitat specialization and dispersal ability (Rothenbücher & Schaefer 2006, Lambeets *et al.* 2008b).

In European salt marshes, habitat structures are highly modified due to native invasions by *Elymus athericus*, a nitrophilous Poaceae (Bockelmann & Neuhaus 1999). This species differs from other salt-marsh plants by its typical architectural characteristics (mainly higher vegetation height and deeper litter: Pétillon *et al.* 2005a) and is therefore likely to alter the distribution of the present biota and its biodiversity. As non-coastal spider species only recently colonized these salt marshes and were shown to benefit from the *Elymus* invasion (Pétillon *et al.* 2005a), the latter might increase their resistance to tidal floods and enable the establishment of resident populations. With it, changes in spider communities were related to important habitat changes, mainly the establishment of a higher, deep-rooted vegetation with an extensive litter layer. The status of salt-marsh resident species, defined as a combi-

nation between salinity tolerance and propensity to withstand floods (Pétillon *et al.* 2004), will be affected by such invasions. Pétillon *et al.* (2006) already showed that structural characteristics of salt marshes, mainly soil interstices and vegetation height, globally interact with flood resistance of spider predatory guilds. Considering the role of abiotic structures for flood resistance of salt-marsh resident spiders, and potentially for their salinity tolerance, it is likely that their distribution patterns are affected by these modified habitat structures.

In the Mont Saint-Michel bay (France), salt marshes are currently invaded by *E. athericus*, which started 10 years ago and nowadays, some marshes are covered up to the mean sea-tide level (Valéry *et al.* 2004). Generally, the invasion is related to an increase in edaphic nitrogen due to numerous human activities in the surrounding landscape (Leport *et al.* 2006). The presence of areas with or without the invasive grass provides a good opportunity to unravel structuring mechanisms of community patterns and the impact of habitat modifications on salt-marsh biodiversity. Here, we analyzed whether habitat modification due to the invasion by *E. athericus* modified the exposure of spiders to specific environmental constraints, i.e. tidal floods and salinity. We assessed (i) the influence of both vegetation and salinity on the distribution of salt-marsh species, and (ii) temporal changes in species richness and abundance during flood events in natural as well as invaded habitats. Under these hypotheses respectively, we expect (i) spider distribution to be more determined by habitat structure than by salinity, and (ii) differences in temporal trends between habitat types, with an improved flood resistance of spiders in invaded habitats.

Material and methods

Study sites and sampling design

In order to study the relationships between stand characteristics (salinity and vegetation structure) and spider communities, we sampled the latter from April until November 2002 (13 sampling dates) at the 'Ferme Foucault' site (48°37´N, 1°32´W), situated near the Mont St-Michel

(located between Brittany and Normandy in NW France). The seven sampling sites (sampling methods: *see* below) comprised one control site located on a dike (i.e. a seawall) two meters above the sea level during high tide. This site was unaffected by tidal floods and consequently by salinity except for possible eolic deposits. The other sites, i.e. three dominated by the invasive plant *Elymus athericus* and three by the natural plant *Atriplex portulacoides* (Chenopodiaceae), were located along a sea–land transect (1200 meters) and subject to inundations during spring floods. To standardize the number of sampled sites per habitat and with respect to the distribution of vegetation, sites were distributed in both upper (two invaded and one natural sites; between 0 and 350 m from the dike) and low (two natural and one invaded sites; between 850 and 1200 m from the dike) marshes. We chose sites to be rather homogeneous with regard to vegetation composition and salinity and large enough to avoid edge effects (Bonte *et al.* 2002).

In order to determine whether habitat change modifies species' flood resistance, we sampled spider communities in April 2004 (four sampling dates) at the 'Vivier-sur-Mer' site (48°42´N, 1°58´W). Three invaded sites (dominated by *E. athericus*) and three natural sites (dominated by *A. portulacoides*) were studied in the high marsh. To test the immediate effects of flooding, sites were sampled twice for three-days starting four days before and two days after (i.e. the time necessary to completely drain seawater) the spring flood (tidal range: 13.35 meters). Then, to study salt-marsh colonization after the spring flood, both salt-marsh and control sites were sampled twice for three-days starting seven and fifteen days after the spring flood.

Variations in soil salinities across the marsh and along time

According to Pétillon *et al.* (2008), the salt-marsh elevation is indicative for the degree of salinity. Here, this assumption was verified by comparing soil salinities and the distance from the dike at the 'Ferme Foucault' site. Soil salinities were synchronically assessed at the seven sampling sites in August 2002. The distance

of the traps to the dike was measured to the nearest meter using a geographical information system (Arcview 3.1; "Distance and Bearing" extension). At the 'Vivier-sur-Mer' site, temporal changes in soil salinity were assessed at six sites, one, two and three weeks after the spring flood (April 2004).

For both study sites, soil salinities were estimated by measuring pore water electric conductivity (mS m^{-1}) using a W.E.T. Sensor connected to a moisture meter HH2 with a specific clay-soil calibration (Delta-T Devices Ltd., Cambridge, U.K.). Conductivity was measured two times around each pitfall trap (i.e. eight times per site).

Sampling methods and spider identification

To study the effects of stand characteristics, we used ground-living spiders as a model system since they are more likely to be affected by variations in soil salinity than web-building spiders living higher in the vegetation. Their distributions, i.e. occurrence patterns depending on local habitat conditions and salt-marsh elevation, were determined by means of pitfall traps which are suitable to sample ground-living spiders (Scott *et al.* 2006). To unravel the effects of tidal floods, pitfall-trap captures were completed with hand-collection two times per sample period (1.5 hour per site before and after the spring flood). This way, temporal changes in species richness and abundances (cf. recolonization processes) could be accurately estimated (Green 1990, Standen 2000).

Four pitfall traps were installed at each site at both locations, which represents a sufficient number of replicates to study spider communities in herbaceous areas (Bonte *et al.* 2000). Traps consisted of polypropylene cups (diam. 10 cm, depth 17 cm) filled with ethylene-glycol which is assumed to be unattractive for spiders (Schmidt *et al.* 2006). A wooden cover prevented overflow by rainfall. Pitfall traps were spaced 10 m apart to avoid mutual interference between traps (Topping & Sunderland 1992). Therefore, traps were considered to be true replicates per sample site. To standardize sampling effort, pitfall trap catches were divided by trapping dura-

tion and pitfall perimeter (Luff 1975, Curtis 1980). After collection, spiders were preserved in 70% ethanol and adult spiders were identified to species level. Nomenclature followed Canard (2005), except for *Pardosa purbeckensis*, absent from this list but now considered to be a valid species (A. Canard pers. comm.).

Data analyses

The relationship between the salt-marsh elevation and the degree of salinity was verified using a regression analysis between soil salinities and the distance from the dike. We compared mean soil salinities after the flood between habitats and time intervals using an analysis of variance for repeated measures (R-ANOVA; habitat type as fixed factor and date as within subject effect) followed by a Tukey post-hoc test (*p* values after Bonferroni adjustment for multiple comparisons).

We grouped the sample sites based upon their similarity of spider occurrences, using a hierarchical cluster analysis (Ward method, Bray-Curtis dissimilarities), resulting in a spider-based typology. To test whether these groups could be characterized by indicator species, indicator values (IndVal) were calculated (Dufrêne & Legendre 1997). The IndVal method is useful and efficient to define ecological indicators according to different habitat factors, notably for spiders (Bonte *et al*. 2002, 2003, Cattin *et al*. 2003, Larrivée *et al*. 2008). The IndVal of species *i* in habitat type *j* is calculated using species total abundance *N* at each site as follows: IndVal$_{ij}$ = $A_{ij} \times B_{ij} \times 100$, where A_{ij} ($= N_{ij}/N_{i.}$) is a measure of the specificity of species *i* to the habitat type *j* and B_{ij} ($= N_{\mathrm{samples}ij}/N_{\mathrm{samples}.j}$) is a measure of the fidelity of species *i* to habitat type *j* (McCune & Grace 2002). Only significant IndVal > 25 were taken into account which implies that the species is present in at least 50% of the sampled sites of the considered habitat type, and that this type contains at least 50% of the total data of the species. The IndVal software can be downloaded from http://mrw.wallonie.be/dgrne/sibw/outils/indval/home.html.

To assess the effects of flooding disturbance on total species richness only species represented by at least 5 individuals (both sampling methods combined) were taken into account (cf. Ugland *et al*. 2005). We finally compared temporal abundances of species represented by more than 30 individuals (in pitfall traps) before the flood with a *t*-test for dependent samples. These statistics were carried out using MINITAB 12.1 for Windows.

Results

Soil salinities across the marsh and over time

Mean soil salinities significantly increased with the distance from the dike: *y* (mS m⁻¹) = 179 + 0.809*x* (m) (regression analysis: R^2_{adj} = 73.6%, *p* < 0.001).

Mean soil salinities significantly decreased 14 days after the spring flood in both natural and invaded habitats (Fig. 1; Tukey post-hoc test following R-ANOVA: both comparisons at *p* < 0.001, df = 46). During the next seven days, salinities slightly increased in natural habitats, similar to salinities measured 7 and 14 days after the flood, but remained constant in invaded habitats. Seven days after the spring flood, mean soil salinities did not differ between invaded and natural habitats, whereas 14 and 21 days after the flood, natural habitats had higher salinities than invaded ones (Tukey post-hoc test following R-ANOVA: both comparisons at *p* < 0.001, df = 46).

Indicator species, salinity gradient and habitat type

A total of 5559 adult spiders belonging to 51 species (*see* Appendix) were caught during this experiment. At the first node, the hierarchical classification clustered sites according to salinity by contrasting dike *vs.* salt-marsh sites (Fig. 2). The second node separated high and low marshes. Finally, the discrimination according to habitat (vegetation type) was quite low. About 25% of the species caught (13) were identified as ecological indicators at various levels of the typology (Fig. 2). Three of them are considered ubiquitous since they were indicative for all the

samples irrespective of the habitat type. Three of four indicators of the dike were totally absent from the salt marsh and all indicative species of the salt marsh were absent from the dike. Within the salt marsh, some species were indicative either for high or low marsh habitats. Considering the type of vegetation, only one species was indicative for natural habitats in the low marsh.

Effects of tidal spring floods on spider communities

A total of 3026 adult spiders belonging to 37 species were caught (1573 by hand-collection and 1453 by pitfall traps); 17 species were exclusively caught by hand-collection but in fewer numbers (fewer than 5 individuals) and therefore omitted from analyses (*see* Appendix). Before the spring flood, species richness was 13 species at invaded sites and 12 species at natural ones (Fig. 3). Two species (*Mangora acalypha* and *Silometopus ambiguus*) were absent from natural sites, whereas only one species was exclusively found at natural sites (*Hypsosinga sanguinea*). Nine species were found before and after the spring flood at both natural and invaded sites. Invaded sites comprised more flood-resistant species than natural sites (Fig. 3). This can be explained by the disappearance of two species after the tidal flooding at natural sites (*Hyp-*
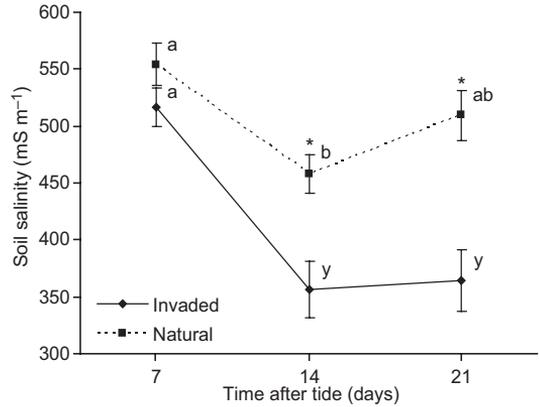
Fig. 1. Changes in mean soil salinities after salt-marsh immersion by the spring flood. Different letters and asterisks (*) indicate significant differences between time intervals and between habitats, respectively (mean ± SE; post-hoc Tukey-tests following R-ANOVA).

sosinga sanguinea and *Larinioides cornutus*). Yet, *L. cornutus* persisted at invaded sites after the flood. Only one species, *Stemonyphantes lineatus*, did not resist flooding, irrespective of the habitat. Species richness increased in both habitat types during the weeks following spring floods. At invaded sites, *Trochosa ruricola* appeared during the second week, followed by *Pardosa proxima* and *Pardosa pullata* at the following week. In natural habitats, *P. proxima* was the first to recolonize the salt marsh, whereas *P. pullata* and *Zelotes electus* were found from the

Fig. 2. Typology of dike and salt-marsh habitats based on spider abundances (hierarchical clustering using Ward's method) and significant indicator species (IndVal procedure and Monte-Carlo permutations, *p* < 0.05; species having their highest IndVal in a cluster are underlined). IndVal for each indicative species is presented between brackets.
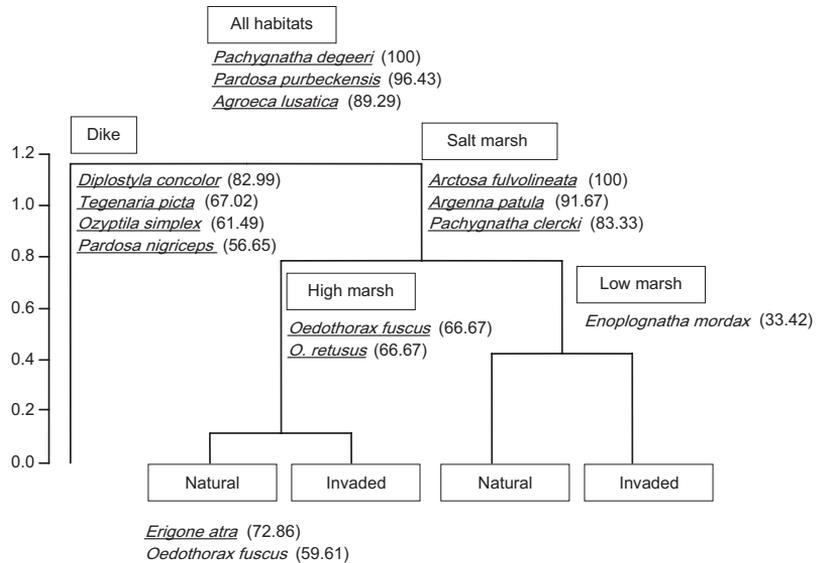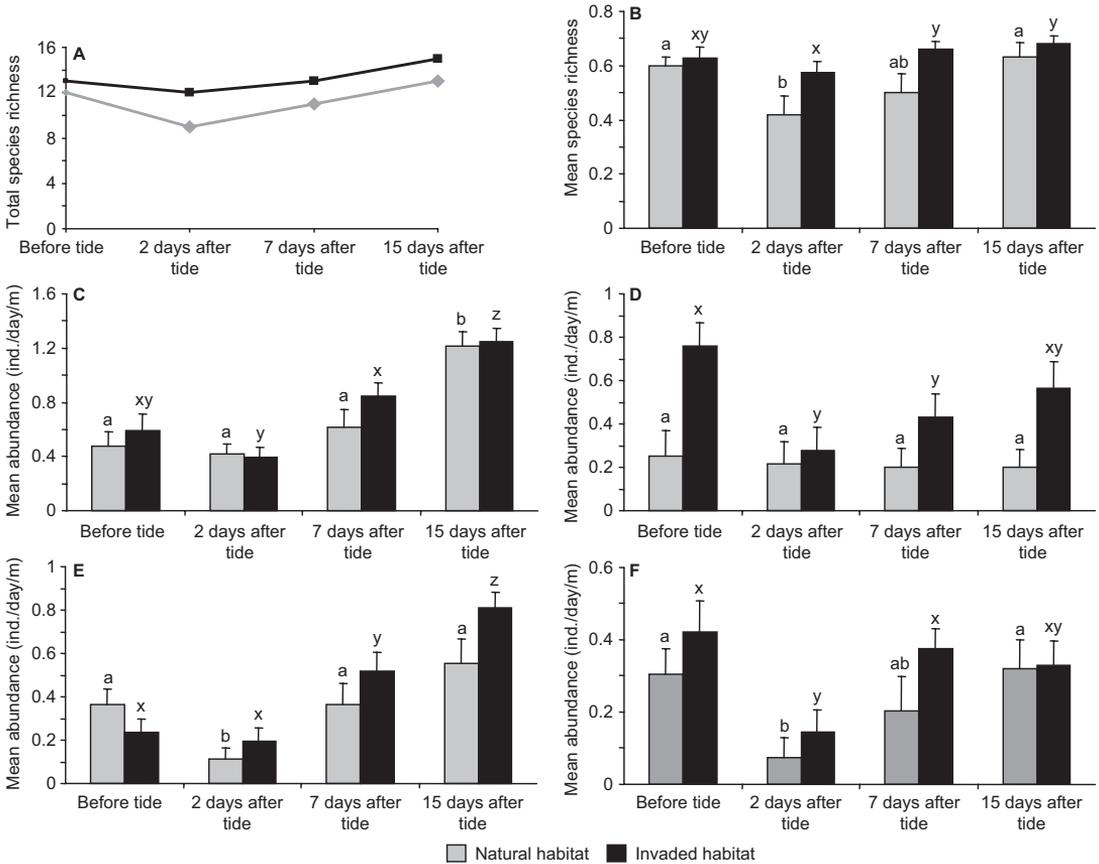
Fig. 3. Temporal changes (mean + SE) in (**A**) total species richness, (**B**) mean species richness and mean abundances (number of individuals/day/meter) of (**C**) *Pardosa purbeckensis*, (**D**) *Pachygnatha degeeri*, (**E**) *Arctosa fulvolineata* and (**F**) *Agroeca lusatica* in natural and invaded salt-marsh habitats. Different letters indicate significant differences in mean parameters between dates (*t*-test for dependent samples: $p < 0.05$), respectively for natural (a, b, c) and invaded (x, y, z) habitats.

third week onwards. *S. lineatus* recolonized the salt marsh two weeks after the flood, but only at natural sites.

Total and mean species richness decreased 3 days after the flood at natural sites (*t*-test for dependent samples: $t_{11} = 2.30$, $p = 0.042$) but remained unchanged in invaded areas (*t*-test for dependent samples: $t_{11} = 1.22$, $p = 0.246$). Mean species richness increased between the second and the seventh day after the flood at invaded sites (*t*-test for dependent samples: $t_{11} = -2.98$, $p = 0.013$) whereas it did not statistically change at natural sites (*t*-test for dependent samples: $t_{11} = -0.84$, $p = 0.420$). At the end of the experiment, species richness did not change in both types of habitat as compared with the previous date.

With the exception of *Agroeca lusatica* for

which abundances were reduced after the flood in both habitats (*t*-test for dependent samples: natural habitat: $t_{11} = 2.62$, $p = 0.024$; invaded habitat: $t_{11} = 2.37$, $p = 0.037$), dominant species displayed different temporal trends between habitat types (Fig. 3). Abundances of *Pachygnatha degeeri* decreased significantly after the flood at invaded sites (*t*-test for dependent samples: $t_{11} = 2.41$, $p = 0.034$), but remained constant at natural sites (*t*-test for dependent samples: $t_{11} = 0.20$, $p = 0.848$). Just after tidal flooding, abundances of *Arctosa fulvolineata* did not change at invaded sites (*t*-test for dependent samples: $t_{11} = -0.54$, $p = 0.603$) and decreased significantly at natural sites (*t*-test for dependent samples: $t_{11} = 4.56$, $p < 0.001$). Later, abundances of *Arctosa fulvolineata* did not show significant temporal pattern at

natural sites and gradually increased at invaded sites. Finally, abundances of *Pardosa purbeckensis* remained constant immediately after tidal flooding (*t*-test for dependent samples: natural habitat: t_{11} = 0.76, p = 0.462; invaded habitat: t_{11} = 1.68, p = 0.122) and even continued to increase at both sites afterwards (Fig. 3).

Discussion

Flooding and salinity shape spider communities. Irrespective of the vegetation type, salinity was found to be a major factor in determining spatial distribution of spiders whereas flooding affected their temporal distribution. Based on both temporal distribution patterns of spiders after the spring flood and their distribution along the salt marsh, we can define three guilds: (1) dike-restricted species i.e., species never found in the salt marsh and therefore not subjected to flooding; (2) stenotopic salt-marsh species i.e., species present before and after the flood; and (3) occasional salt-marsh species that disappear after tidal floods but (re)colonize the salt marsh thereafter.

Several behavioural or morphological features may explain species persistence in salt marshes. First, actively climbing vegetation before or during flooding may represent a way to resist flooding (study in floodplains: Adis 1997). Otherwise, webs may be situated above the maximum sea level (Cooke 1962). For instance, the flood-resistant *Clubiona stagnatilis* simply climbs surrounding vegetation (Canard 1981). Species living in the vegetation below the level of maximum high tides (mainly web-building species in low marshes) can resist tidal floods by retreating to web refuges (physical gills: Rovner 1987). This could be the case for *Larinioides cornutus*, which constructs a silken hideout at the top of high vegetation (e.g. Roberts 1995), as found at invaded sites. Alternatively, cursorial spiders may use large interstitial soil spaces as refuges, benefiting from the air caught in these pores. This way of resisting floods was suggested for Coleoptera and Homoptera by Foster and Treherne (1976), and for Collembola by Zinkler *et al*. (1999). In particular, we hypothesize that numerous small linyphiids as *Erigone* and *Oedothorax* spp. as well as the dictynid *Argenna patula* make use of soil interstices during short-lasting tidal floods (cf. Lambeets *et al*. 2008b).

Salinity was suggested as a selective factor for spiders occurring in littoral (Desender & Maelfait 1999) and in continental salt marshes (Hänggi *et al*. 1995). The observed species succession along the salinity gradient and the decrease of species richness as mean soil salinity increases (Pétillon *et al*. 2008) strongly support this hypothesis. Because we sampled up to five weeks after salt-marsh inundation, tidal floods and concordant fluctuations in the vegetation architecture alone cannot explain species' incidences along the salinity gradient during one year. Until now, arthropod responses to high salinity levels are poorly documented and mainly concern physiological mechanisms as a direct osmotic regulation, i.e. by producing osmo-protectors such as chloride and sodium ions (Moloney & Nicolson 1984, Heydemann 1970) or indirectly by the consumption of hypertonic preys or salt water (Bethge 1973).

Between two floods soil salinity decreases, which allows for the (re)colonization by halotolerant species from adjacent ecosystems. For instance, *Pardosa pullata* and *Zelotes electus*, appear in the salt marsh two or three weeks after the spring flood. Nevertheless, we suppose that recolonization may occur before soil salinity decreases, possibly by means of ballooning for aeronaut species (Bonte *et al*. 2007) or by cursorial dispersal for ground-living hunters (Morse 1997, 2002). Colonization by halotolerant species also strengthens the hypothesis that some species suffer from flooding disturbance. For instance, *Pardosa proxima* is absent when the seawater recedes, but appears with numbers increasing from two weeks after the spring flood onwards. Therefore, flood events may select for flood-resistant species, generally resident to salt marshes.

Impact of *Elymus athericus* on spider communities

We hypothesized that modified stand conditions could reduce the impact of salinity and tidal floods on spiders. Our results, however, did not

confirm that habitat modification by *E. athericus* affects the distribution of spiders along a land-sea transect, as spider assemblages were mainly structured by the salinity levels, at least for ground-living spiders. Consequently, spiders do not seem to be "isolated" from salinity effects by the presence of a deep litter layer (ground-dwellers) or by higher vegetation (web-builders). We showed that invaded habitats had lower soil salinities than natural habitats 2 and 3 weeks after tidal flooding, maybe due to better drainage of seawater (different structure of soil upper layer) or to a slightly higher elevation in invaded habitats (L. Valéry unpubl. data). Yet, mean salinities in stands of *E. athericus* when stabilized, do not differ from those at natural stands if measurements are made during a long period (including several weeks after the inundation: Pétillon *et al.* 2005). It is thus likely that lower salinities after the flood in invaded habitats act on the speed of recolonization process but not the species composition itself.

Elymus athericus is likely to provide important refuge microhabitats during tidal flood events, either due to its height rising above the sea level or by providing numerous interstices at the ground level. The higher ratio of flood-resistant species (12/13) at invaded sites therefore might be related to a modified habitat structure. Consequently, flood resistance, considered as a main characteristic of salt-marsh residents (Pétillon *et al.* 2004), might be enhanced, especially for non-coastal species. This confirms the increased terrestrialization process of salt marshes due to the invasion by *E. athericus*. Finally, if *E. athericus* favours the ability to resist tidal floods, typical salt-marsh species might react differently to flooding in this modified habitat (e.g. non-adaptive behaviour: Schlaepfer *et al.* 2002). For instance, habitat modification by *E. athericus* might favour litter-living species as *Arctosa fulvolineata* by increasing air stores within the litter, and associated withstanding behaviour (J. Pétillon & K. Lambeets unpubl. data).

With respect to nature conservation, the invasion by *E. athericus* might pose a threat for some halophilic residents, assumed to be adapted to local circumstances (e.g. *P. purbeckensis*: Pétillon *et al.* 2005b), but also provides an ideal opportunity to study the effects of such a harsh environment on newly colonizing, non-coastal species. Further investigations should concentrate on behavioural responses to flooding in relation to habitat structure, and particularly the presence of refuges. It remains unclear, however, whether changes in spider abundances can be attributed to sediment scouring or drowning. Previously, Pétillon *et al.* (2005a) demonstrated that invasions by *E. athericus* increase salt-marsh biodiversity by adding non-coastal taxa and reduce abundances of resident, halophilic spiders (Pétillon *et al.* 2005b).

Our results demonstrate the impact of habitat modification by an invasive grass on flood resistance of spider communities occurring in salt marshes, both in terms of presence/absence (newly flood-resistant species) as in abundances (for the dominant species), thereby changing the status of some salt-marsh resident species. *E. athericus* acts on spider assemblages via changes in habitat structure (by providing more refuges, both at low and high tide: respectively Pétillon *et al.* 2005, this study) and not via direct changes in salinity. In relation to the halotolerance of ground-living spiders, *E. athericus* is yet likely to modify (re)colonization processes by both reducing soil salinity and, hypothetically, isolating spiders from it during the first weeks after the spring flood.

Acknowledgements

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Appendix. Taxonomic list of spiders (nomenclature follows Canard 2005) caught in the salt marshes at the Mont Saint-Michel bay (France). [1]: species exclusively collected at 'Ferme Foucault'; [2]: species exclusively collected at 'Vivier-sur-Mer'; [1,2]: species collected at both sites; *: species exclusively collected by hand (only at 'Vivier-sur-Mer'). Typical salt-marsh species (designed by their high occurrence in salt marshes, based on Harvey *et al.* 2002) are underlined.

Agelenidae
Tegenaria picta [1]
Tegenaria silvestris [1]
Araneidae
Agalenatea redii [2]*
Hypsosinga sanguinea [2]*
Larinioides cornutus [2]*
Mangora acalypha [2]*
Clubionidae
Clubiona stagnatilis [1,2]
Dictynidae
Argenna patula [1, 2]
Dysderidae
Dysdera crocata [1]
Gnaphosidae
Trachyzelotes pedestris [1]
Zelotes electus [2]
Zelotes latreillei [1]
Drassyllus pusillus [1]
Linyphiidae
Agyneta conigera [1]
Bathyphantes gracilis [1,2]*
Centromerus sylvaticus [1]
Cnephalocotes obscurus [2]*
Diplostyla concolor [1]
Erigone atra [1,2]
Erigone dentipalpis [1,2]*

Erigone longipalpis [1,2]*
Gongylidiellum vivum [1]
Meioneta rurestris [2]*
Meioneta simplicitarsis [2]*
Microlinyphia pusilla [2]*
Oedothorax fuscus [1,2]
Oedothorax retusus [1,2]
Palliduphantes pallidus [1]
Silometopus ambiguus [1,2]
Stemonyphantes lineatus [1,2]
Tenuiphantes tenuis [1,2]
Tiso vagans [1]
Liocranidae
Agroeca inopina [1,2]*
Agroeca lusatica [1,2]
Scotina celans [1]
Lycosidae
Alopecosa accentuata [1]
Alopecosa pulverulenta [1,2]
Arctosa fulvolineata [1,2]
Arctosa leopardus [1]
Pardosa nigriceps [1,2]*
Pardosa prativaga [1]
Pardosa proxima [1,2]
Pardosa pullata [1,2]
Pardosa purbeckensis [1,2]
Pirata latitans [1]

Pirata piraticus [1]
Trochosa ruricola [1,2]
Mimetidae
Ero furcata [1,2]*
Philodromidae
Thanatus striatus [1]
Tibellus maritimus [1]
Salticidae
Talavera petrensis [1]
Tetragnathidae
Pachygnatha clercki [1,2]
Pachygnatha degeeri [1,2]
Tetragnatha extensa [2]
Theridiidae
Anelosimus vittatus [2]*
Crustulina sticta [1,2]
Enoplognatha latimana [1]
Enoplognatha mordax [1,2]*
Episinus truncatus [1]
Robertus lividus[1]
Thomisidae
Ozyptila simplex [1]
Zodariidae
Zodarion italicum [1]
Zoridae
Zora spinimana[2]*