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Abstract

In spite of their highly patchy distribution, the effects of landscape configuration on specialist biodiversity has been little studied in salt marshes. We investigated the impact of patch size on the abundance of specialist arthropods in two contrasted salt-marsh environments. Dominant ground-active species were sampled by pitfall traps in increasing areas of natural vegetation (dominated by *Atriplex portulacoides*) along two transects surrounded by either grazed (dominated by *Puccinellia maritima*) or invasive (dominated by *Elymus athericus*) vegetation. Spatially- and temporally-replicated sampling took place in the Mont Saint-Michel Bay (Western France) during 2012. Three dominant species, the wolf spider *Pardosa purbeckensis* (Araneae, Lycosidae), the ground beetle *Pogonus chalceus* (Coleoptera, Carabidae) and the beach-hopper *Orchestia gammarellus* (Amphipoda, Talitridrae), constituted 96% of all arthropods caught (N=66,299). Patch size only had an effect on the carabid and on the amphipod, with large patches more populous than small ones, reinforcing the idea that the effects of fragmentation are stronger for species with limited mobility. Environment had a significant effect on the population density of all species, with systematically more individuals in patches surrounded by invaded than by grazed salt marshes, which confirms the particularly negative impact of over-grazing on salt-marsh biodiversity. This study finally suggests that both invasive species and grazing impact salt-marsh biodiversity also at a landscape scale.

Key-words: fragmentation; Araneae; Carabidae; Amphipoda; pitfall traps; grazing.

Regional Terms: Western Europe, France, Normandy, Mont Saint-Michel Bay.

1. Introduction

Salt marshes play important roles in terms of environmental functionality and conservation. Their primary productivity is one of the highest in the world (up to 3900 g C m^{-2} yr^{-1}: Lefeuvre et al., 2000). As other estuarine and coastal ecosystems such as mangroves or dunes, salt marshes provide many environmental and economical benefits. Indeed they act like a physical barrier against erosion, protecting lands against waves and storm events (Adam, 2002). They also provide a useful shelter for growth and survival of young fishes, act like natural filter to purify water and are used by humans for fisheries, harvesting or pasture (Garbutt et al., 2017). They are yet submitted to several human threats: climate change, sea level rise, increasing sea and air temperature, pollution, vegetation disturbance, biological invasion or eutrophication. The degradation of 50% of worldwide salt marshes that has been reported over the last three decades has become a conservation issue, especially in Western Europe (Dijkema et al., 1984). Salt marshes indeed host several specialist species (i.e. only found there), some of them being also rare with low abundances and/or restricted distribution (e.g. Irmler et al., 2002). They also constitute ideal systems to test for the effects of habitat fragmentation on biodiversity because they have a linear, highly patchy distribution along coasts (Desender and Maelfait, 1999). Their fragmented repartition severely limits exchanges between populations from different salt marshes. Locally, they are submitted to various human disturbances (grazing, mowing, invasive species) that created within-site heterogeneity, and therefore differences in habitat suitability (either at local or at landscape scales). In Western Europe, salt marshes are mainly covered by *Atriplex portulacoides*, but for the last thirty years this natural vegetation is more and more replaced by the invasive species *Elymus athericus*, which was at first limited to the upper part of the marsh (Valéry et al., 2004), leading to a patchy landscape (Veeneklaas et al., 2012). This invasion does not seem to have strong negative impacts on diversity, as it favors in fact the settlement of continental species, but it undoubtedly modifies the functioning of the salt-marsh ecosystem and fragments populations living in *A. portulacoides* (Pétillon et al., 2005). Sheep grazing also induces frequent changes in salt-marsh natural vegetation, *A. portulacoides* being replaced by the short grass *Puccinellia maritima*. If local effects of both invasions by *Elymus athericus* and grazing were quite studied in the past (e.g. Kiehl et al., 1996; Veeneklaas et al., 2012; Leroy et al., 2014), no study investigated how the fragmentation of natural landscape they induced affects dominant species of arthropods so far.

In this study, we wanted to assess the consequences of within-site fragmentation (occurring at a scale inferior to 1km²) on salt-marsh biodiversity. The effects of patch size was investigated on the dominant species of ground-active arthropods. We first expect the effect of patch size to be different among species, weaker of salt-marsh predators with a high mobility (Bonte et al., 2007; Van Belleghem et al., 2015) and stronger for salt-marsh decomposers with a low mobility (Mantzouki et al., 2012). Because patches were distributed along transects set in two contrasted environments, we then expect an especially negative effect of the grazed environment on their abundances (see e.g. Rickert et al., 2012; Ford et al., 2012; van Klink et al., 2013).

2. Material and Methods

2.1. Sampling design

Sampling took place in the eastern part of the Mont Saint-Michel Bay (48°38′10″N; 1°30′41″W). To assess if there was an effect of patch size, three sizes of relictual patches of *A. portulacoides* were sampled: small (area<0.1ha), medium (0.1ha<area<1ha), and large (area>1ha). For each patch size, three replicates were sampling in both environments. Thus, there were nine patches of *A. portulacoides* distributed along each of two transects (see the map in ESM: Fig. A.1). The impact of environment (i.e. surrounding vegetation of the patch) on abundances was also considered because transects were surrounded by either invaded or grazed vegetation (around 10 sheep per hectare, see Pétillon et al., 2007 for a more detailed description of the study site). In each patch, four pitfall traps were placed at 10 m from each other (to avoid interference between them). Pitfall traps were polypropylene cups (10 cm diameter, 17 cm deep) filled of ethylene-glycol. All 64 traps were visited weekly from April 27th to June 15th of 2012, except during one week, when salt marshes were inundated due to strong tides, for a total of 5 sampling weeks. Because catches in pitfall are both function of local densities and mobilities of arthropods, abundances of the dominant species (based on the 5 sampling weeks pooled together) will be referred to "activity-densities" further.

2.2. Data analyses

A total of 66,299 arthropods were sorted and identified to family or species level. Three species, the wolf spider *Pardosa purbeckensis* (Araneae, Lycosidae), the ground beetle *Pogonus chalceus* (Coleoptera, Carabidae) and the beach-hopper *Orchestia gammarellus* (Amphipoda, Talitridrae) were the dominant ground-dwelling macro-arthropods, representing 96% of all individuals caught, with 30584, 2055 and 30989 individuals respectively).

In order to assess differences in the activity-density of the three main species according to patch size and environment, quasi-Poisson Generalized Linear Models were performed with activity-density of the species as dependent variable, patch size and environment and their interaction as fixed factors. Post-hoc Tukey tests, with Bonferroni correction, were performed in case of patch size significant effect. All data analyses were performed using R software packages (R Development Core Team, 2013).

3. Results

Patch size had no effect on the activity-density of *P. purbeckensis* (Table 1, Fig. 1). It had a significant effect on the activity-density of *P. chalceus* and *O. gammarellus*, with more individuals in large patches than in small ones independent of the transect (Figs. 2 & 3, respectively).

Environment had a significant effect on the activity-density of *P. purbeckensis*, *P. chalceus,* and *O. gammarellus* (Table 1), with systematically more individuals in patches surrounded by an invaded than by a grazed environment (Figs 1, 2 & 3, respectively).

4. Discussion

The two predator species had very contrasted responses to changes in patch size. The latter had indeed no effect on the wolf spider *Pardosa purbeckensis*, and a significant effect on the ground beetle *Pogonus chalceus*, with higher abundances in larger patches. This result should certainly be related to the mobility of the two species, *P. purbeckensis* having high dispersal capacities (for both short- and long-distances, see Richter et al., 1971 and Puzin et al., 2018, respectively) and *P. chalceus* being mostly brachypterous in the Mont Saint-Michel Bay (Desender et al., 1998). Salt-marsh fragmentation has consequently more drastic effects for low-mobility species. The short-distance dispersal and ground-level movements of *P. chalceus* are still to be investigated, yet.

Although transect interacted with patch size for *Orchestia*, results are quite similar for both environments, i.e. more individuals in the largest patches of natural vegetation. The fact that there was no difference in activity-density for both the amphipod and the carabid species between small- and medium-sized patches might indicate that a minimum patch-size is needed for these two species. Dispersal of *Orchestia gammarellus* is probably water-mediated (see Fanini & Lowry, 2014 on closely related species) and the low mobility of this species probably explains the strong effect of patch size on population density. This result has strong consequences for salt-marsh functioning, *Orchestia* being indeed an important prey item for several fish species, including some of high commercial value like the sea bass (Laffaille et al., 2005). Interestingly, it may help understanding why relictual areas of natural vegetation (e.g. like along the creeks) do not host amphipods enough to fulfil the nursery function, especially reduced in a grazed salt marsh (Laffaille et al., 2000).

Transect had an important effect on the activity-density of all dominant species in natural patches, populations being less dense in a grazed environment than in an invaded salt marsh. Although our design did not allow for spatial replication and statistical inference, we assume that the differences found between transects can be related to the effects of invasion vs grazing. Differences in humidity and organic matter (both lowered in grazed salt marshes) can also explain the differences in activity-density between environments for the three model species. That would overall confirm at a broader (landscape) level what was previously reported at a local scale, i.e. over-grazing is actually more deleterious to salt-marsh specialist arthropods than invasions by *Elymus athericus* (with very few exceptions, like e.g. the aeronaut linyphiid spider *Erigone longipalpis*, found to be more abundant in heavily grazed salt marshes: Pétillon et al., 2007). Intensive grazing usually leads to extremely homogeneous habitats, and the low variance of data in the grazed environment for all three species also supports this statement. Our study finally shows that the impacts of both grazing and plant invasion are not only local, but also influence specialist biodiversity at a landscape scale though the fragmentation they induce, which was not previously reported in salt marshes.

The way fragmentation had such adverse effects on population size of salt-marsh specialist arthropods is still to be investigated, and can notably encompass changes in micro-climate and/or strong edge effects. We limited our sampling to spring because it is the best season for sampling the target species, but patterns are likely similar in autumn (see Pétillon et al. 2007). Yet, our results are based on one sampling during one year only, and thus need to be confirmed by a long-term monitoring. Further studies should also get interested in inter-specific dynamics in such patchy environments, and especially changes in predator-prey densities. Metacommunity theory was indeed mostly tested on assembly rules, and more rarely on interspecific relationships (Vanschoenwinkel et al., 2007). Salt marshes are thus ideal model systems for such studies because they experience a high level of stress due regular tides, and have a highly patchy structure, both between and within sites.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at

Fig. A.1. Map of the study site (Mont Saint-Michel Bay, France), showing the 18 sampled patches of natural vegetation surrounded by invaded or grazed vegetation, and of increasing area (circle diameter increases with patch size).

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Table 1. GLMs of patch size (small, medium or large) and environment (surrounded by invaded or grazed vegetation) effects on the activity-density of the dominant ground-dwelling arthropods in salt marshes (significant effects at α=0.05 are in bold). F-ratio and P-values of 1st order terms are those from the full model if the interaction was significant, and those from the additive model if the interaction was non-significant.

Arthropod species	Factor	F	*P*
Pardosa purbeckensis	Patch size	0.99	**0.378**
(spider)	Environment	10.33	0.002
	Size* Environment	2.82	0.067
Pogonus chalceus	Patch size	5.99	**0.004**
(carabid)	Environment	32.22	**<0.001**
	Size* Environment	1.27	0.288
Orchestia gammarellus	Patch size	13.23	**<0.001**
(amphipod)	Environment	30.06	**<0.001**
	Size* Environment	3.22	**<0.001**
	Patch size in invaded environment	4.29	**0.022**
	Patch size in grazed environment	36.15	**<0.001**

Figure captions

Fig. 1. Activity-density of *Pardosa purbeckensis* according to patch size and environment. Different successive letters indicate significant differences between means at α = 0.05 (Post-hoc Tukey tests with Bonferroni correction if patch size had a significant effect in GLM).

Fig. 2. Activity-density of *Pogonus chalceus* according to patch size and environment. Different successive letters indicate significant differences between means at α = 0.05 (Post-hoc Tukey tests with Bonferroni correction if patch size had a significant effect in GLM).

Fig. 3. Activity-density of *Orchestia gammarellus* according to according to environment and patch size in invaded (left) and grazed (right) environments. Different successive letters indicate significant differences between means at α = 0.05 (Post-hoc Tukey tests with Bonferroni correction if patch size had a significant effect in GLM).

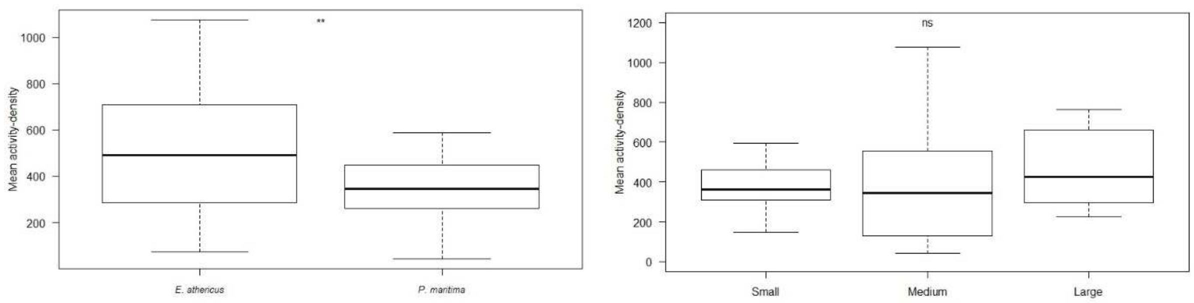
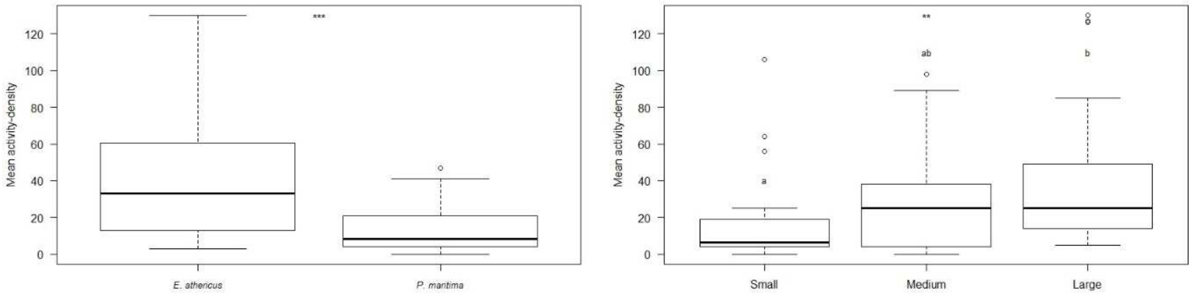


Figure 1. Puzin & Pétillon



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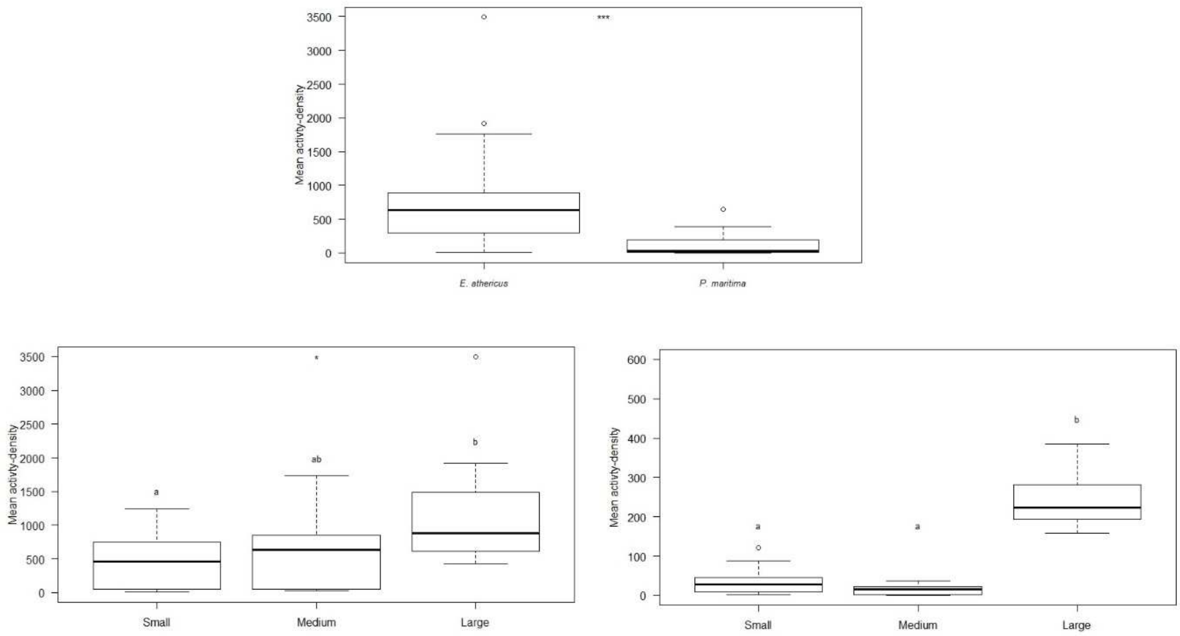

Figure 3. Puzin & Pétillon

- The effects of landscape on arthropods has been little studied in salt marshes
- The response of populations to fragmentation was assessed for 3 dominant species
- Patch size of natural vegetation had an effect on low-mobility species only
- More individuals were found in patches surrounded by invaded than by grazed marshes
- Results suggest that disturbances impact arthropods also at a landscape scale