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1 **Contrasted responses of dominant ground-dwelling arthropods**
2 **to landscape salt-marsh fragmentation**

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13

14

15 **Abstract**

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

34

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

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

37

38 1. Introduction

39 Salt marshes play important roles in terms of environmental functionality and conservation.
40 Their primary productivity is one of the highest in the world (up to $3900 \text{ g C m}^{-2} \text{ yr}^{-1}$:
41 Lefeuvre et al., 2000). As other estuarine and coastal ecosystems such as mangroves or dunes,
42 salt marshes provide many environmental and economical benefits. Indeed they act like a
43 physical barrier against erosion, protecting lands against waves and storm events (Adam,
44 2002). They also provide a useful shelter for growth and survival of young fishes, act like
45 natural filter to purify water and are used by humans for fisheries, harvesting or pasture
46 (Garbutt et al., 2017). They are yet submitted to several human threats: climate change, sea
47 level rise, increasing sea and air temperature, pollution, vegetation disturbance, biological
48 invasion or eutrophication. The degradation of 50% of worldwide salt marshes that has been
49 reported over the last three decades has become a conservation issue, especially in Western
50 Europe (Dijkema et al., 1984). Salt marshes indeed host several specialist species (i.e. only
51 found there), some of them being also rare with low abundances and/or restricted distribution
52 (e.g. Irmiler et al., 2002). They also constitute ideal systems to test for the effects of habitat
53 fragmentation on biodiversity because they have a linear, highly patchy distribution along
54 coasts (Desender and Maelfait, 1999). Their fragmented repartition severely limits exchanges
55 between populations from different salt marshes. Locally, they are submitted to various
56 human disturbances (grazing, mowing, invasive species) that created within-site
57 heterogeneity, and therefore differences in habitat suitability (either at local or at landscape
58 scales). In Western Europe, salt marshes are mainly covered by *Atriplex portulacoides*, but for
59 the last thirty years this natural vegetation is more and more replaced by the invasive species
60 *Elymus athericus*, which was at first limited to the upper part of the marsh (Valéry et al.,
61 2004), leading to a patchy landscape (Veeneklaas et al., 2012). This invasion does not seem to
62 have strong negative impacts on diversity, as it favors in fact the settlement of continental

63 species, but it undoubtedly modifies the functioning of the salt-marsh ecosystem and
64 fragments populations living in *A. portulacoides* (Pétillon et al., 2005). Sheep grazing also
65 induces frequent changes in salt-marsh natural vegetation, *A. portulacoides* being replaced by
66 the short grass *Puccinellia maritima*. If local effects of both invasions by *Elymus athericus*
67 and grazing were quite studied in the past (e.g. Kiehl et al., 1996; Veeneklaas et al., 2012;
68 Leroy et al., 2014), no study investigated how the fragmentation of natural landscape they
69 induced affects dominant species of arthropods so far.

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

80 **2. Material and Methods**

81 **2.1. Sampling design**

82 Sampling took place in the eastern part of the Mont Saint-Michel Bay (48°38'10"N;
83 1°30'41"W). To assess if there was an effect of patch size, three sizes of relictual patches of *A.*
84 *portulacoides* were sampled: small (area<0.1ha), medium (0.1ha<area<1ha), and large
85 (area>1ha). For each patch size, three replicates were sampling in both environments. Thus,
86 there were nine patches of *A. portulacoides* distributed along each of two transects (see the

87 map in ESM: Fig. A.1). The impact of environment (i.e. surrounding vegetation of the patch)
88 on abundances was also considered because transects were surrounded by either invaded or
89 grazed vegetation (around 10 sheep per hectare, see Pétillon et al., 2007 for a more detailed
90 description of the study site). In each patch, four pitfall traps were placed at 10 m from each
91 other (to avoid interference between them). Pitfall traps were polypropylene cups (10 cm
92 diameter, 17 cm deep) filled of ethylene-glycol. All 64 traps were visited weekly from April
93 27th to June 15th of 2012, except during one week, when salt marshes were inundated due to
94 strong tides, for a total of 5 sampling weeks. Because catches in pitfall are both function of
95 local densities and mobilities of arthropods, abundances of the dominant species (based on the
96 5 sampling weeks pooled together) will be referred to “activity-densities” further.

97 **2.2. Data analyses**

98 A total of 66,299 arthropods were sorted and identified to family or species level. Three
99 species, the wolf spider *Pardosa purbeckensis* (Araneae, Lycosidae), the ground beetle
100 *Pogonus chalceus* (Coleoptera, Carabidae) and the beach-hopper *Orchestia gammarellus*
101 (Amphipoda, Talitridae) were the dominant ground-dwelling macro-arthropods, representing
102 96% of all individuals caught, with 30584, 2055 and 30989 individuals respectively).

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

109

110 3. Results

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

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

118

119 4. Discussion

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

129 Although transect interacted with patch size for *Orchestia*, results are quite similar for both
130 environments, i.e. more individuals in the largest patches of natural vegetation. The fact that
131 there was no difference in activity-density for both the amphipod and the carabid species
132 between small- and medium-sized patches might indicate that a minimum patch-size is

133 needed for these two species. Dispersal of *Orchestia gammarellus* is probably water-mediated
134 (see Fanini & Lowry, 2014 on closely related species) and the low mobility of this species
135 probably explains the strong effect of patch size on population density. This result has strong
136 consequences for salt-marsh functioning, *Orchestia* being indeed an important prey item for
137 several fish species, including some of high commercial value like the sea bass (Laffaille et
138 al., 2005). Interestingly, it may help understanding why relictual areas of natural vegetation
139 (e.g. like along the creeks) do not host amphipods enough to fulfil the nursery function,
140 especially reduced in a grazed salt marsh (Laffaille et al., 2000).

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

156 The way fragmentation had such adverse effects on population size of salt-marsh specialist
157 arthropods is still to be investigated, and can notably encompass changes in micro-climate

158 and/or strong edge effects. We limited our sampling to spring because it is the best season for
159 sampling the target species, but patterns are likely similar in autumn (see Pétilion et al. 2007).
160 Yet, our results are based on one sampling during one year only, and thus need to be
161 confirmed by a long-term monitoring. Further studies should also get interested in inter-
162 specific dynamics in such patchy environments, and especially changes in predator-prey
163 densities. Metacommunity theory was indeed mostly tested on assembly rules, and more
164 rarely on interspecific relationships (Vanschoenwinkel et al., 2007). Salt marshes are thus
165 ideal model systems for such studies because they experience a high level of stress due
166 regular tides, and have a highly patchy structure, both between and within sites.

167

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172 Bretagne ("PEPS" project).

173

174 **Appendix A. Supplementary data**

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

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

179

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251

252 **Table 1.** GLMs of patch size (small, medium or large) and environment (surrounded by
 253 invaded or grazed vegetation) effects on the activity-density of the dominant ground-dwelling
 254 arthropods in salt marshes (significant effects at $\alpha=0.05$ are in bold). F-ratio and P-values of
 255 1st order terms are those from the full model if the interaction was significant, and those from
 256 the additive model if the interaction was non-significant.

Arthropod species	Factor	F	P
<i>Pardosa purbeckensis</i> (spider)	Patch size	0.99	0.378
	Environment	10.33	0.002
	Size* Environment	2.82	0.067
<i>Pogonus chalceus</i> (carabid)	Patch size	5.99	0.004
	Environment	32.22	<0.001
	Size* Environment	1.27	0.288
<i>Orchestia gammarellus</i> (amphipod)	Patch size	13.23	<0.001
	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

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259 **Figure captions**

260 **Fig. 1.** Activity-density of *Pardosa purbeckensis* according to patch size and environment.

261 Different successive letters indicate significant differences between means at $\alpha = 0.05$ (Post-
262 hoc Tukey tests with Bonferroni correction if patch size had a significant effect in GLM).

263 **Fig. 2.** Activity-density of *Pogonus chalceus* according to patch size and environment.

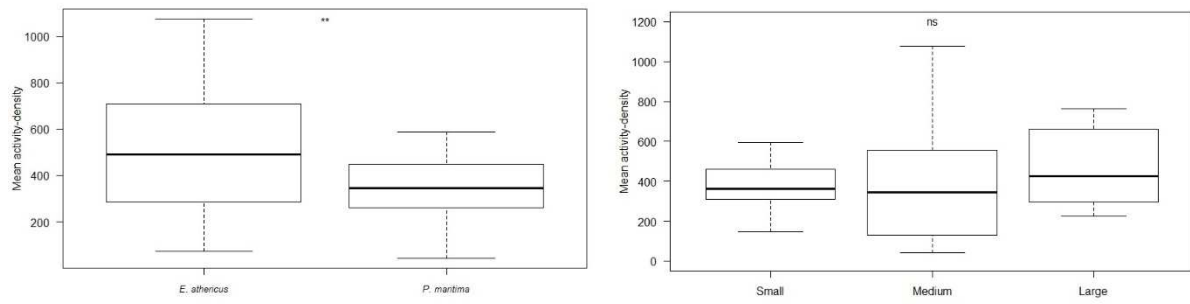
264 Different successive letters indicate significant differences between means at $\alpha = 0.05$ (Post-
265 hoc Tukey tests with Bonferroni correction if patch size had a significant effect in GLM).

266 **Fig. 3.** Activity-density of *Orchestia gammarellus* according to environment and

267 patch size in invaded (left) and grazed (right) environments. Different successive letters
268 indicate significant differences between means at $\alpha = 0.05$ (Post-hoc Tukey tests with
269 Bonferroni correction if patch size had a significant effect in GLM).

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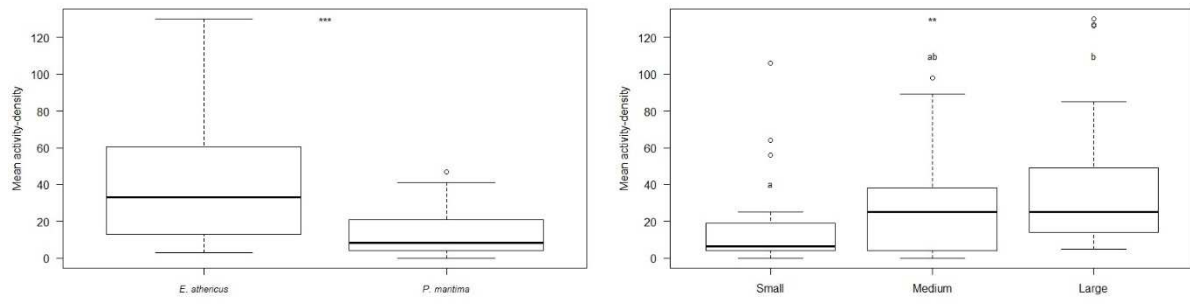


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Figure 1. Puzin & Pétilion



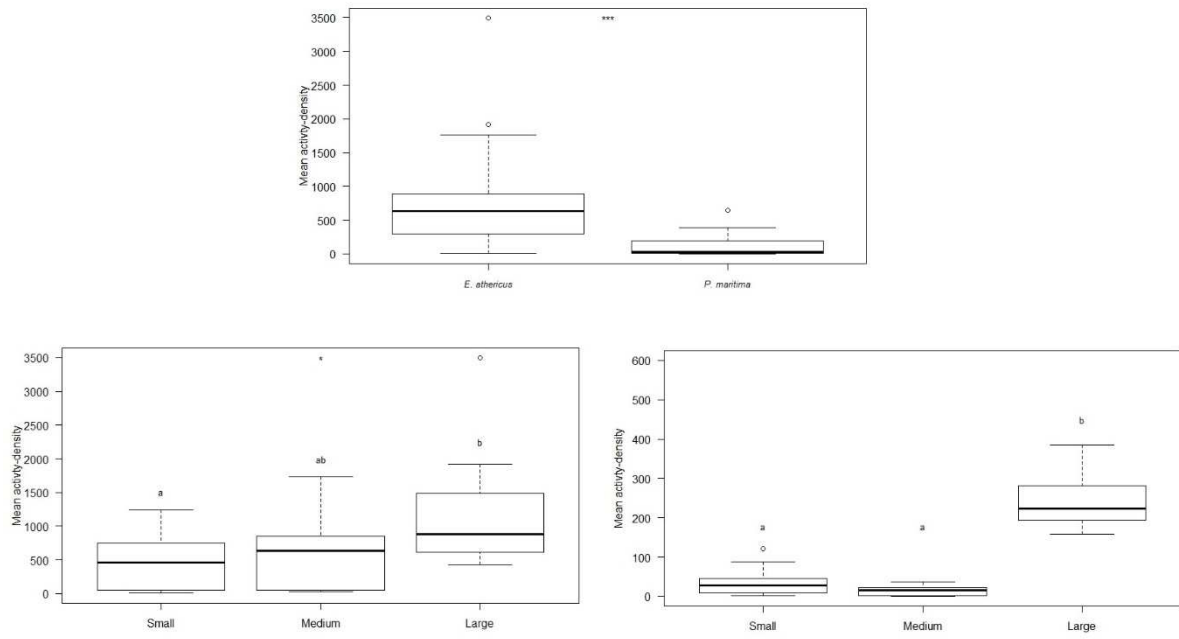
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Figure 2. Puzin & Pétilion



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Figure 3. Puzin & Pétilon

- 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