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1 **Slight variations in coastal topography mitigate the consequence of**  
2 **storm-induced marine submersion on amphibian communities**

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28

1 **Abstract.**

2 The rise in sea-level and the increase in frequency and intensity of extreme weather  
3 events (i.e., storms and associated surges) are expected to strongly impact coastal  
4 areas. The gradual impacts of sea-level rise may allow species to display adaptive  
5 responses to overcome environmental changes. In contrast, the abruptness of marine  
6 submersions during extreme weather events can induce changes that may exceed the  
7 ability of species to respond to brutally changing environments. Yet, site-specific  
8 topographical features may buffer the expected detrimental effects of marine  
9 submersions on wildlife. In order to test such topographical effects, we examined the  
10 long-term consequences of a major marine submersion (storm Xynthia) on the  
11 amphibian communities of two French Atlantic coastal wetlands that slightly differ  
12 in their topography and, thus, their susceptibility to marine submersion.  
13 Amphibians were monitored on 64 ponds for up to 13 years, using acoustic and  
14 visual methods, in conjunction with environmental parameters (e.g., pond topology,  
15 vegetation, salinity). We found that the amphibian communities at the two  
16 neighboring sites displayed different responses to the marine submersion linked to  
17 storm Xynthia. As predicted, slight differences in local topography induced strong  
18 differences in local magnitude of the landward marine surge, influencing salinization  
19 dynamics and associated consequences on wildlife (amphibians). The different  
20 species responses show that amphibian richness can recover to that of pre-storm  
21 conditions, but with significant changes in the composition of the community. Our  
22 results suggest that amphibian presence post-submersion in coastal wetlands results  
23 from an interaction between species traits (e.g., tolerance to elevated salinity), site-  
24 specific topography, and environmental parameters. Finally, our study emphasizes

25 that relatively modest landscaping management may be critical to allow wildlife to  
26 successfully recover after a marine submersion.

27

28 **Keywords:**

29 Coastal wetlands, extreme weather event, marine surge, salinity, topography,

30 Xynthia

31

32        **1. Introduction**

33

34 Anthropogenic activities have led to unprecedented rates of global climate change  
35 (Vitousek et al. 1997). Among the multiple consequences of climate change, the  
36 progressive rise in sea-level, as well as the increase in frequency and intensity of  
37 extreme weather events (i.e., storms and associated surge), are expected to strongly  
38 impact biodiversity and particularly in coastal areas (McLean et al. 2001; Herbert et  
39 al. 2015; Wang et al. 2016; Maxwell et al. 2019; Chen et al. 2020). Although coastal  
40 wetlands are recognized as some of the most diverse and productive habitats on  
41 earth (Denny 1994; McLean et al. 2001), they are currently particularly vulnerable  
42 because of several interacting threats (i.e., agriculture, land use, urbanization, sea  
43 level rise) (McLean et al. 2001).

44

45 Gradual changes of habitats linked to sea-level rise are expected to strongly affect  
46 coastal wetlands (Neubauer and Craft 2009; Traill et al. 2011; Geselbracht et al. 2015).  
47 Yet, the relatively long temporal scale over which these changes are expected to  
48 occur may allow species to display adaptive responses. For instance, relatively  
49 mobile species could progressively adjust their coastal distribution, and thus  
50 gradually disperse to more suitable habitats (Convertino et al. 2012). Coastal  
51 wetland salinization is one of the main environmental changes linked to sea-level rise  
52 (Herbert et al. 2015), and associated osmoregulatory challenges are known to  
53 negatively affect wildlife (Greenberg et al. 2006; Pedersen et al. 2014; Gutiérrez 2014;  
54 Rivera-Ingraham and Lignot 2017). Nonetheless, progressive increases in salinity,  
55 such as those due to a gradual rise in sea levels, can allow species to display adaptive

56 responses. Indeed, such responses have already been shown in various organisms  
57 such as fishes (Purcell et al. 2008), amphibians (Gomez-Mestre and Tejado 2003),  
58 aquatic snakes (Brischoux et al. 2017), waterbirds (Gutiérrez 2014) and rodents (Getz  
59 1966).

60

61 In contrast, the sudden and unpredictable nature of marine submersions during  
62 extreme weather events can induce changes that may exceed the ability of species to  
63 disperse toward more suitable habitats and/or adapt to a new set of environmental  
64 conditions, especially when marine submersion events induce direct and brutal  
65 salinization of inland soil and water (Hopkins and Brodie 2015; Wang et al. 2016).

66 These short pulse of high salt concentrations may lead to extreme mortality events  
67 (Gunzburger et al. 2010; Herbert et al. 2015), in contrast to exposure to moderate  
68 salinity levels during a longer time period (Marshall and Bailey 2004). Yet, to our  
69 knowledge, very few studies have examined the effects of extreme events, such as  
70 storm-induced marine submersions on wildlife from coastal areas (but see Greenberg  
71 et al. (2006); Ameca y Juárez et al. (2013)), especially in the context of the salinization  
72 induced by these marine submersions (but see Kokelj et al. (2012)).

73

74 Importantly, specific geographical features of coastal wetlands may dampen the  
75 expected effects of marine submersions on these ecosystems (Loder et al. 2009;  
76 Wamsley et al. 2010). For instance, low-lying coastal wetlands without relief should  
77 be particularly exposed to marine submersions (Eliot et al. 1999; Wang et al. 2012),  
78 while the presence of barriers may dampen the effects of extreme weather events

79 (McLean et al. 2001). As a consequence, site-specific topographical features may  
80 buffer the expected detrimental effects of marine submersions on wildlife. Given the  
81 forecasted increase in the frequency and intensity of such extreme weather events  
82 (Dettinger 2011), identifying such topographical features may prove useful for  
83 proposing landscaping solutions that aim to preserve these essential coastal  
84 ecosystems.

85  
86 We examined the consequences of a major marine submersion (Xynthia) on Atlantic  
87 coastal wetlands in France. Xynthia was an exceptionally violent windstorm which  
88 crossed the Western European coast between 27 February and 1 March 2010, leading  
89 to the submersion of a large number of coastal sites for a few days to a few weeks  
90 (Durant et al. 2018). In order to identify the consequences of marine submersions  
91 linked to storm Xynthia, we investigated coastal amphibian communities, because  
92 these taxa display several traits that should increase their susceptibility to marine  
93 surges. For instance, amphibians are known to be highly sensitive to salinity levels  
94 because of their permeable skin and their comparatively low ability to osmoregulate  
95 in hyperosmotic environments (Shoemaker et al. 1992; Wells 2007). Increasing  
96 salinity is known to decrease survival for amphibians across all life stages (Albecker  
97 and McCoy 2017), but this is especially true for eggs and tadpoles that develop in  
98 aquatic environments (Hopkins and Brodie 2015; Albecker and McCoy 2017; Welch  
99 et al. 2019). In addition, they are characterized by low dispersal capacities (Wells  
100 2007), thereby affecting their ability to evade sudden detrimental conditions.

101 Although several studies have assessed the effects of salinization on amphibians,

102 particularly on tadpoles (Christy and Dickman 2002; Smith et al. 2007; Hopkins and  
103 Brodie 2015), less work has been performed on their long-term responses to marine  
104 submersions (but see Gunzburger et al. 2010), presumably because such an approach  
105 requires logistically complex surveys encompassing pre- and post-storm monitoring  
106 (Walls et al. 2019).

107

108 In this study, we monitored the amphibian community during a time period (13  
109 years) that surrounded storm Xynthia, in the ponds of two neighboring natural  
110 reserves on the Western Atlantic coast of France. Both sites are relatively low coastal  
111 wetlands displaying a coastal sand dune close to the sea limit. Importantly, these two  
112 neighboring coastal sites display slightly different topographies with one of them  
113 having an additional sand barrier. We posited that these small differences in  
114 topography should influence the magnitude of landward marine surge and  
115 determine the responses of amphibians. We specifically predicted that:

116 - ponds from the more protected site should be less affected by marine surge and,  
117 thus, should display relatively low and constant salinity levels across time, while  
118 ponds from the less protected site should be characterized by elevated salinity levels  
119 post-storm.

120 - amphibian richness should be negatively affected by salinity levels, and should  
121 decline post-storm in the less protected site.

122 - species more tolerant to salinity should recover rapidly following a marine surge  
123 while species more sensitive to osmotic stress may be extirpated.



## 124 2. Material and Methods

125

### 126 2.1. Study sites

127 The study was carried out on two reserves in Western France: one in the « Réserve  
128 Naturelle Nationale de Moëze-Oléron » (45°53'33.36"N, 1°04'59.16"W, hereafter MO,  
129 Fig. 1), and one other in the « Réserve Naturelle Nationale du marais d'Yves »  
130 (46°2'40.735"N, 1°3'16.906"W, hereafter MY, Fig. 1). These two study sites, separated  
131 by ~15km straight line, are situated on the Atlantic coast of France (Département de  
132 la Charente-Maritime), and cover a similar surface area (218ha for MO and 204ha for  
133 MY, Fig. 1). The two reserves were hit by Xynthia on 27 February 2010, with the same  
134 intensity (maximum wind intensity of 130-140 km/h, see MeteoFrance  
135 (<http://tempetes.meteo.fr/spip.php?article132>) and Appendix A).

136

137 Both sites are relatively low (mean elevation: MY= 2.64 m ± 0.02 SE ; MO=2.90 m ±  
138 0.01 SE) coastal wetlands displaying a coastal sand dune (3.30 m high both in MY  
139 and MO) situated nearby the high sea limit (Fig. 2), which is followed by typical  
140 coastal wetlands composed of a matrix of salt marsh, meadows, and freshwater  
141 ponds. Importantly, these two neighboring coastal sites display slightly different  
142 topographies with MO having an additional barrier (a fossil sand dune) running  
143 parallel to the shore and situated ~500 m inland (Fig. 2). The two sites are exposed to  
144 an oceanic climate (Cfb according to Köppen classification).

145

### 146 2.2. Sampling

#### 147 2.2.1. Periods of sampling

148 For each site, amphibian monitoring in breeding ponds was performed both before  
149 and after storm Xynthia. Specifically, sampling occurred a few years before Xynthia  
150 (in 2007 and 2008 for MY and MO, respectively; hereafter “pre-storm”), the year after  
151 Xynthia (in 2011 for both sites, hereafter “1 year post-storm”), 4 years after Xynthia  
152 (in 2014 for both sites, hereafter “4 years post-storm”) and again a few years later (in  
153 2017 and 2019 for MY and MO respectively; hereafter “more than 4 years post-  
154 storm”).

155

### 156 2.2.2. *Sampling ponds*

157 For each site, amphibian presence was monitored in natural breeding ponds during  
158 the spring (see section 2.2.3.). At MY, 54 ponds were monitored during the 4 time  
159 periods mentioned above. These breeding sites vary in their size, ranging from < 36  
160 m<sup>2</sup> to 156 824 m<sup>2</sup>. These ponds are situated at an average distance of 556 m ( $\pm 24$  m  
161 SE) from the ocean, ranging from 27 to 832 m. At MO, 10 ponds were monitored  
162 during the 4 time periods mentioned above. The size of these sites ranges from 20 m<sup>2</sup>  
163 to 70 m<sup>2</sup>. Their position relative to the ocean is 429m ( $\pm 36$  m SE), ranging from 262 m  
164 to 637 m. The positions of the ponds relative to site-specific topography are  
165 represented in Fig.2.

166

### 167 2.2.3. *Monitoring of amphibian presence*

168 In order to take differences in phenology and detectability of the amphibian species  
169 occurring at each breeding pond into account, we performed three successive  
170 monitoring sessions for each pond, according to Petitot et al. (2014). These surveys  
171 occurred in the spring during the breeding period of amphibians in Western France

172 (Miaud and Muratet 2018). In March and April, surveys were conducted at night  
173 (two hours after sunset) during the activity peak of breeding amphibians; while for  
174 the last session (May), surveys occurred during daytime in order to visually assess  
175 indices of effective reproduction (i.e., egg and tadpole presence).

176 At each site, two complementary survey methods were performed successively at  
177 each session. First, an acoustic survey was performed for five minutes at a distance  
178 of four meters from the pond edges. This method allowed us to assess species  
179 presence based on mating or territorial calls. Second, a visual survey was performed  
180 during another five minutes by slowly walking around the pond edge with a  
181 headlamp to detect individuals present nearby the pond edge (on land or in water).  
182 These two methods were occasionally (in order to limit the destruction of aquatic  
183 vegetation) complemented by the use of a net in order to assess the presence of the  
184 most secretive species, but it did not yielded additional species that were not  
185 detected by the two methods described above.

186

#### 187 *2.2.4. Environmental parameters*

188 For each pond, we recorded 9 environmental parameters: Water salinity, type of  
189 habitats, habitat permanence, area of the pond, shortest distance to the ocean,  
190 surrounding vegetation, aquatic vegetation, number of other species found, and  
191 water depth (see below). These parameters were chosen because of their possible  
192 impact on amphibian presence and diversity (Başkale and Kaya 2009; Shulse et al.  
193 2012; Hopkins and Brodie 2015). Each parameter was recorded each year of survey,  
194 allowing to determine differences between years, and differences pre- and post-  
195 submersion. Water salinity ( $\text{g.l}^{-1}$ ) of the breeding ponds was recorded in May using a

196 Multi 340i multimeter (WTW, Xylem analytics). At MY, salinity was measured at 53  
197 out of the 54 ponds monitored, while at MO, salinity was measured at 5 out of the 10  
198 ponds surveyed. For each pond, we also characterized the type of habitat (pond or  
199 ditch), the habitat permanence (temporary or permanent water body), the area of the  
200 pond and the shortest distance to the ocean (both evaluated using QGIS 3.4.7), the  
201 surrounding vegetation (expressed in percentage cover), the aquatic vegetation (with  
202 a score ranging from 0 to 3, adapted from Lachavanne et al. (1995) and  
203 corresponding to diversity, i.e. number of species which can be differentiated, and  
204 water surface occupied by aquatic vegetation, evaluated visually, in April), the  
205 number of other species found in the pond (fishes, insect larvae, and crayfish), and  
206 the water depth (measured with a ruler in April).

207

### 208 **2.3. Data analysis**

209 For species presence, we used presence/absence data (coded as 1 and 0 respectively),  
210 and considered a species to be present for a given year in a given pond if we had  
211 detected the presence of adults (either visually or acoustically), eggs, or larvae during  
212 at least one of the surveys.

213 To determine whether there were differences in the number of species between sites  
214 and time period, and variations of salinity between sites and time periods, we ran  
215 GLMs (General Linear Models) with site, time period, and their interaction as  
216 predictors. We computed GLMs on the total number of species present at each site  
217 and on salinity, using a Poisson and a Gaussian distribution, respectively. These  
218 distributions were chosen based on the fit to our data, and by checking

219 overdispersion of residuals, and effects were assessed with a backward model  
220 selection using chi-squared tests. We computed Dunnett post-hoc tests on our GLMs  
221 using the “*multcomp*” package in order to assess within and across site and time  
222 period differences. These models could not be computed for each species separately,  
223 and species responses were investigated using Kruskal Wallis and Dunn post hoc  
224 test (package “*PMCMR*”). Multiplicity of responses (as the analyses included only 0  
225 and 1) were corrected for multiplicity with the Holm correction, to account for ex  
226 æquo.

227

228 In addition, to determine whether environmental parameters affected amphibian  
229 presence at each site, we also tested the effects of our 9 environmental variables (see  
230 2.2.2.) on species presence (except for type of pond and permanence in MO, because  
231 ponds are all temporary and pond *sticto sensu*), using GLMs with a Poisson  
232 regression. In these models, we first implemented the whole set of environmental  
233 parameters, for which correlations were tested with a Pearson correlation test.  
234 Variables were standardized before analyses. Beginning from a model with 9  
235 parameters, we then carried out a backward model selection using Chi-square tests  
236 (Bolker et al. 2009).

237

238 All data analysis were performed using R 3.6.3 (R Core Team 2020) and Rstudio  
239 v1.1.419.

## 240 3. Results

### 241 3.1. Salinity

242 We found an effect of the site, time period, and their interaction on salinity (Table 1,  
243 Fig. 3). More specifically, pre-storm salinity was similar between MO and MY (Fig.  
244 3). Salinity was significantly higher at MY 1 year post-storm than either pre-storm  
245 values at MY or 1 year post-storm at MO (Fig. 3). Salinity at MY significantly  
246 decreased 4 years post-storm and more than 4 years post-storm but remained higher  
247 than pre-storm values and salinity measured at MO for the same periods (Fig. 3). In  
248 contrast, salinity at MO remained steady across time periods (Fig. 3).

249

### 250 3.2. Species richness

251 At MY, these surveys led to the detection of 6 different species composed of 5  
252 anurans (*Pelophylax* sp. [Green frogs], *Hyla meridionalis* [Mediterranean tree frog],  
253 *Pelodytes punctatus* [Common parsley frog], *Bufo spinosus* [Spined toad] and *Pelobates*  
254 *cultripes* [Western spadefoot toad]) and 1 urodel (*Triturus marmoratus* [Marbled  
255 newt]).

256 At MO, surveys allowed to detect 6 species composed of 4 anurans (*Pelophylax* sp.  
257 [Green frogs], *Hyla meridionalis* [Mediterranean tree frog], *Pelodytes punctatus*  
258 [Common parsley frog] and *Pelobates cultripes* [Western spadefoot toad]) and 2  
259 urodeles (*Lissotriton helveticus* [Palmate newt] and *Triturus marmoratus* [Marbled  
260 newt]).

261 Interestingly, 5 of these species were found at both of our study sites.

262

263 We found an effect of the site, time period, and their interaction on species richness  
264 (Table 2, Fig. 4). More specifically, pre-storm species richness was similar between  
265 MO and MY (Fig. 4). Species richness was significantly lower at MY 1 year post-  
266 storm than either pre-storm values at MY or 1 year post-storm at MO (Fig. 4).  
267 Species richness at MY increased post-storm progressively attaining similar values  
268 than MO more than 4 years post-storm, and regaining pre-submersion levels (Fig. 4).  
269 At MO, we observed a slight but not significant decrease of species richness across  
270 time periods (Fig. 4).

271

### 272 3.3. Species responses

273 In MY, the presence of all species strongly decreased post-storm (Fig. 5). Some  
274 species (*Pelophylax sp.*, *Hyla meridionalis*, *Pelodytes punctatus*) recovered pre-storm  
275 level 4 years post-storm or more than 4 years post-storm (Fig. 5ABC). Two species  
276 (*Pelobates cultripes*, *Triturus marmoratus*) disappeared (Fig. 5DE), and one species (*Bufo*  
277 *spinosus*) appeared for the first time more than 4 years post-storm (Fig. 5F).

278 In MO, most species did not seem to be directly impacted by storm Xynthia (Fig. 5).

279 More specifically, *Pelophylax sp.*, *Hyla meridionalis*, *Pelodytes punctatus*, *Pelobates*  
280 *cultripes* and *Triturus marmoratus* showed stable trends over time (Fig. 5GHIJ).

281 Interestingly, the two urodele species displayed change over time, but these changes  
282 did not seem to be related to storm Xynthia (Fig. 5KL).

283

284 Detailed statistical analyses can be found in appendices B and C.

285

286

287        **3.4. Environmental parameters influencing diversity**

288    In MY, 4 parameters out of the 9 tested were found to be significant, with higher  
289    amphibian diversity found in ponds (rather than ditches) with low salinity levels,  
290    low levels of surrounding vegetation, and high aquatic vegetation (Table 3). All  
291    other tested parameters (pond permanence, pond area, distance to the ocean, depth,  
292    or presence of other species) were not retained during the selection procedure.

293    In MO, we did not observe an effect of any of the 9 tested parameters (Table 3, only  
294    the results for the same parameters that were significant for MY are presented for the  
295    sake of comparison).

296

297



#### 298 4. Discussion

299

300 Overall, we found that two neighboring coastal wetlands displayed different  
301 responses to the marine submersion linked to storm Xynthia. As predicted, slight  
302 differences in local topography (i.e., an additional sand dune at MO, Fig. 2) induced  
303 strong differences in the local magnitude of landward marine surge, influencing  
304 salinization dynamics and associated consequences for wildlife (amphibians).

305

306 The protective aspect of the additional sand dune at MO (Fig. 2) is exemplified by the  
307 salinity levels measured before and after storm Xynthia. Indeed, at this site, mean  
308 salinity remained steady across a relatively long time period (11 years), with no  
309 increase in salinity one year post-storm, suggesting that the marine surge did not  
310 reach the studied ponds. The constant salinity measured at this site further suggests  
311 that salinization of nearby land has not induced progressive salt percolation across  
312 soil layers (i.e. salt infiltration in groundwater, Gunzburger et al., 2010). In contrast,  
313 at MY (the less protected site displaying a single coastal sand dune), salinity  
314 measured at the studied ponds drastically changed following storm Xynthia.

315 Although pre-storm salinity was low and similar to MO, the landward marine surge  
316 induced a massive increase in salinity, reaching a value of  $\sim 11 \text{g.l}^{-1}$  one year post-  
317 storm. These elevated salinity levels decreased post-storm (Fig. 3) but remained  
318 relatively high ( $5 \text{g.l}^{-1}$ ) and did not decrease back to pre-storm conditions even 7 years  
319 post-storm. This result suggests potentially long-lasting influences of marine surges  
320 on coastal wetland salinity and contrasts with other studies showing rapid salinity

321 decrease after storms (Frazer et al. 2006). Further studies are required in order to  
322 investigate the site-specific salinization dynamics linked to landward marine surges.  
323  
324 Similar to salinity, amphibian species richness responded differently at the two study  
325 sites. At MO, where the salinity of ponds remained low and constant, amphibian  
326 richness remained relatively constant across the study period for most species.  
327 Nevertheless, at this site, two urodele species displayed strong fluctuations over time  
328 (*T. marmoratus*, *L. helveticus*), but these fluctuations were not attributable to Xynthia,  
329 and may be linked to the increasing presence of non-native Louisiana crawfish,  
330 *Procambarus clarkii*, known to affect urodeles (Cruz et al. 2006). In addition, none of  
331 the pond characteristics we included in our analyses significantly explained the  
332 number of species observed, probably because most ponds are characterized by very  
333 similar features. In strong contrast, at MY, amphibian richness seems to have been  
334 affected by the change in salinity linked to Xynthia. Indeed, the mean number of  
335 species per pond showed a massive decrease following storm Xynthia, reaching the  
336 lowest values (~0.43 species per ponds) one year post-storm. Amphibian richness  
337 then progressively increased, attaining values similar to pre-storm conditions, 7  
338 years after the storm. Importantly, salinity was a significant predictor of the number  
339 of species observed in ponds, suggesting that the increase in salinity due to storm  
340 Xynthia was responsible for the decrease in species richness found at MY. There are  
341 three different, but not mutually exclusive hypotheses to explain this result. First, the  
342 high salinities linked to storm Xynthia may have directly affected amphibians by  
343 inducing mortality of juvenile and adult individuals (Albecker and McCoy 2017).

344 Second, relatively high salinity values in breeding ponds may have inhibited the  
345 ability of surviving adults to reproduce (Albecker and McCoy 2017). Third,  
346 reproduction may have occurred, but high salinity of breeding ponds may have  
347 induced direct mortality of developing embryos and/or larvae (Christy and  
348 Dickman 2002; Kearney et al. 2014; Hopkins and Brodie 2015). Indeed, some  
349 amphibian species are relatively tolerant to salinity and may be able to reproduce in  
350 brackish conditions (Hopkins et al. 2020). Yet, even in relatively salt-tolerant species,  
351 eggs and larvae have decreased survival linked to salinity (Natchev et al. 2011).  
352 These three hypotheses involve different processes with different consequences for  
353 population dynamics (e.g., affecting adult survival *versus* reproduction). Future  
354 studies should investigate the relative contributions of these different possible  
355 responses on the influence of marine submersions on coastal amphibian  
356 communities.

357

358 Despite the strong influence of storm Xynthia on amphibians at MY, some studies  
359 have highlighted that recovery can occur (Schriever et al. 2009; Gunzburger et al.  
360 2010; Wang et al. 2016; Maxwell et al. 2019; Chen et al. 2020), and it is noteworthy in  
361 our study that the amphibian community did recover to pre-storm conditions 7 years  
362 after the submersion. Yet, different species diverged strongly in their ability to  
363 recover from the negative impact of storm Xynthia (Fig. 5). Most notably, three  
364 species were clear drivers of the increase in amphibian richness back to pre-storm  
365 conditions. These species were *Pelophylax* spp., *H. meridionalis* and *P. punctatus*, and  
366 have all been described as salt tolerant (Sillero and Ribeiro 2010; Natchev et al. 2011;

367 Thirion 2014; Hopkins and Brodie 2015). In our study sites, these species can be  
368 found in water bodies with markedly elevated salinities (i.e., maximum salinity of  
369 11.8 g.l<sup>-1</sup> for *P. punctatus*, 13.7 g.l<sup>-1</sup> for *H. meridionalis* and 17.1 g.l<sup>-1</sup> for *Pelophylax sp.*). In  
370 contrast, two species were lost, or almost lost, after storm Xynthia (i.e., *P. cultripes*, *T.*  
371 *marmoratus*). *T. marmoratus* is a newt, that are characterized by comparatively lower  
372 mobility (Wells 2007). Such a trait may have prevented adult individuals from  
373 evading detrimental conditions during storm Xynthia, or may have impeded other  
374 individuals from less impacted nearby areas to recolonize our study sites in MY. The  
375 reasons for the disappearance of *P. cultripes* are less clear, because this species is  
376 known to be relatively tolerant to salinity (Stănescu et al. 2013, Thirion 2014). Because  
377 *P. cultripes* is a burying species which shelters in sandy soils, it is possible that  
378 sheltered individuals may have died during the submersion. Finally, it is  
379 noteworthy that a new species, the Spined toad (*Bufo spinosus*), appeared for the first  
380 time more than 4 years after submersion, highlighting that the colonization of some  
381 individuals from new species can occur following environmental perturbations  
382 (pattern also shown in Gunzburger et al. (2010), were some species are only present  
383 in overwashed wetlands post-storm).

384

385 These different species-specific responses highlight that, although amphibian  
386 richness could recover to that of pre-storm conditions, the composition of the  
387 community can change (Marroquín-Páramo et al. 2020; Stockwell et al. 2020), with  
388 one third of the species being lost at MY after Xynthia. Interestingly, because several  
389 pond characteristics were shown to be positively related to amphibian diversity (e.g.,

390 pond type, aquatic vegetation), it is likely that such features may positively influence  
391 either species resilience to environmental perturbations (Bernhardt & Römermann et  
392 al. 2011; Suazo & Ortuño et al. 2018; Marroquín-Páramo et al. 2020) or to favor  
393 recolonization from nearby and less impacted sites [i.e. shelters (Walsh 1983)]. This  
394 may be the case for *P. cultripes*, which appeared in MO post-storm, while it was the  
395 first to disappear in MY, suggesting that MO could be one of these shelters for  
396 surrounding sites. Future studies should investigate the interactions between salt-  
397 tolerance and ecological characteristics (e.g., micro-habitat use, mobility) in order to  
398 understand the drivers of the species-specific responses that we have highlighted.

399

## 400 5. Conclusions

401 Our study is, to our knowledge, the first multi-species long term survey of the  
402 consequences of marine submersion induced salinization on coastal amphibians (but  
403 see Gunzburger et al. (2010)). Most notably, we highlight that the presence of  
404 amphibians in coastal wetlands post-submersion results from an interaction between  
405 species-specific traits (tolerance to elevated salinity, ecology) and site-specific  
406 characteristics (topography). This latter category is especially interesting to take into  
407 account at a time when the frequency and intensity of extreme weather events, such  
408 as marine submersion, are expected to increase (Dettinger 2011). Habitats  
409 management can promote adaptation to extreme climatic events (Maxwell et al. 2019)  
410 and, in this respect, our study shows that relatively modest landscaping management  
411 (i.e., the creation of additional barriers similar to the small sand dune found at MO)  
412 may be critical to allow amphibians to successfully recover after a marine  
413 submersion, either by providing a barrier to marine surge and/or by increasing the

414 surface area of land that remains unsubmerged, providing an elevated refuge.  
415 Clearly, it is plausible that such a refuge may also provide protection for other  
416 wildlife susceptible to marine submersion and may, thus, offer a cost-effective  
417 solution to buffer the detrimental consequences of marine submersion on coastal  
418 wetlands.

419

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427

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433

#### 434 **Conflict of Interest Statement**

435 The authors declare that they have no conflict of interest.

436

437

438 **Data availability statement**

439 Data will be made available upon reasonable request.

440

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- 575

576 **Caption to figures**

577 **Figure 1:** Map of the study area relative to Western France illustrating the two study  
578 sites, using an OpenStreetMap basemap. Green areas represent the two study sites  
579 (MY and MO).

580

581 **Figure 2.** Coastline topographic profile of MO (A) and MY (B) highlighting the  
582 presence of the additional small dune in MO. The relative position of the pond  
583 surveyed is indicated by a horizontal line and shows that ponds in MO were all  
584 situated behind the additional sand dune.

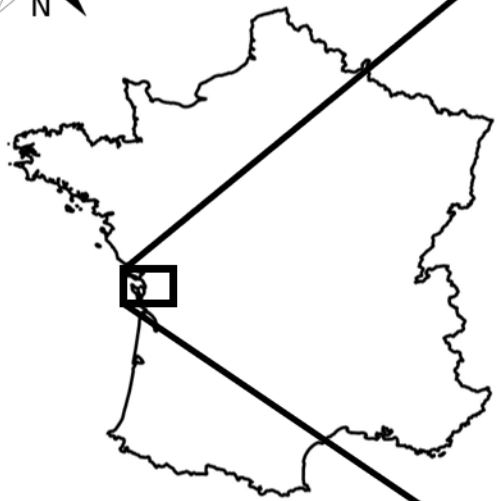
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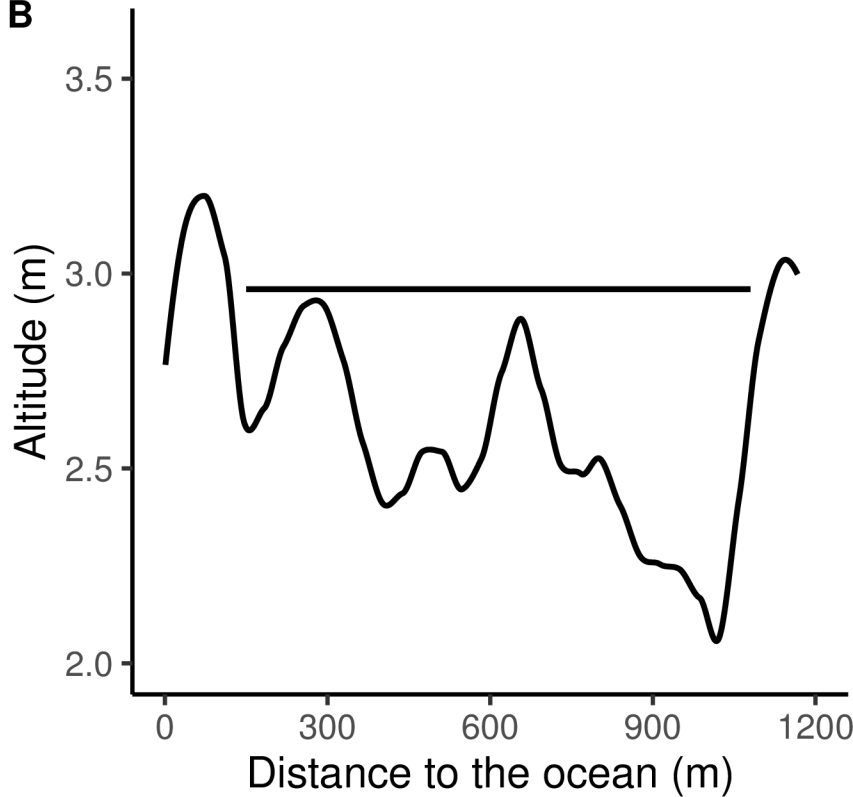
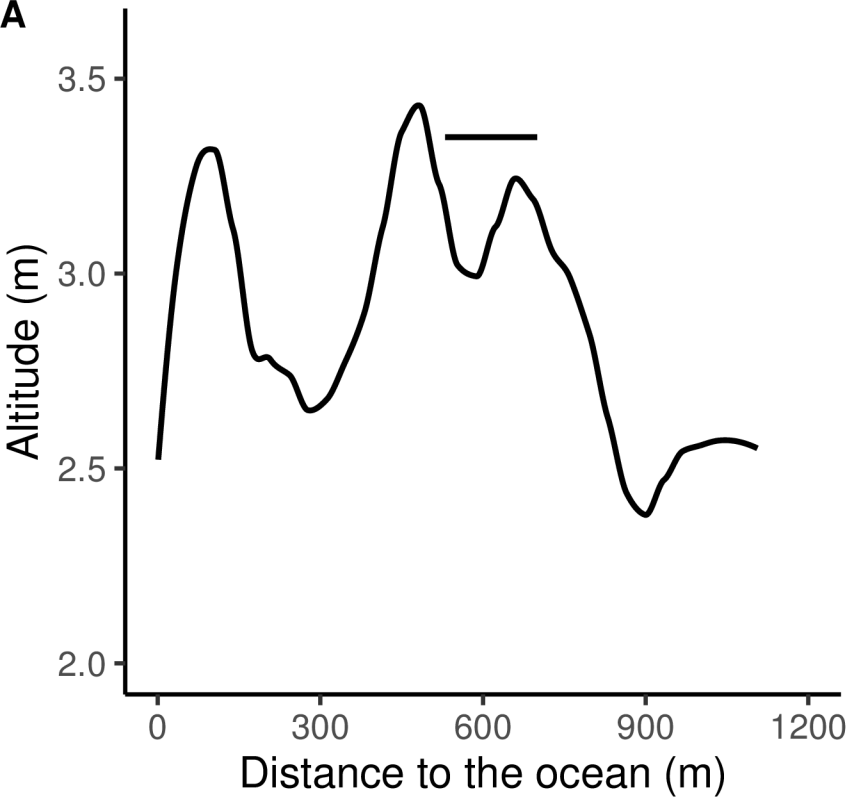
586 **Figure 3.** Mean ( $\pm$ SE) salinity measured for the four time periods of our surveys at  
587 MY (A) and MO (B). The vertical dashed line represents the year of storm Xynthia  
588 (2010). Different letters represent a significant difference at  $\alpha = 0.05$ .

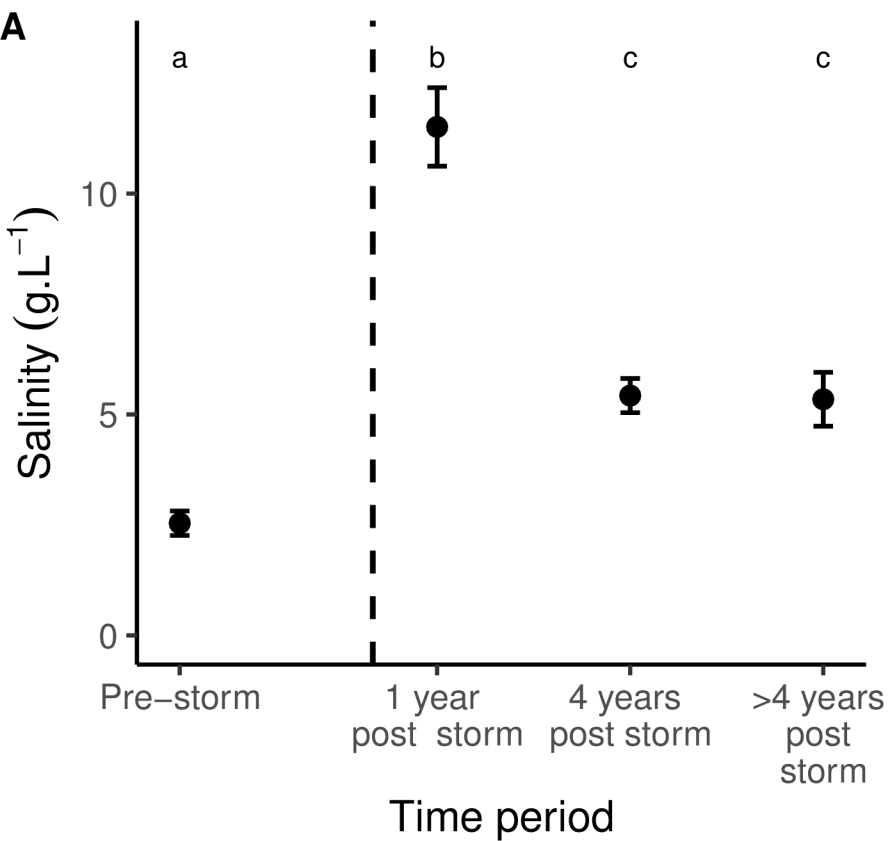
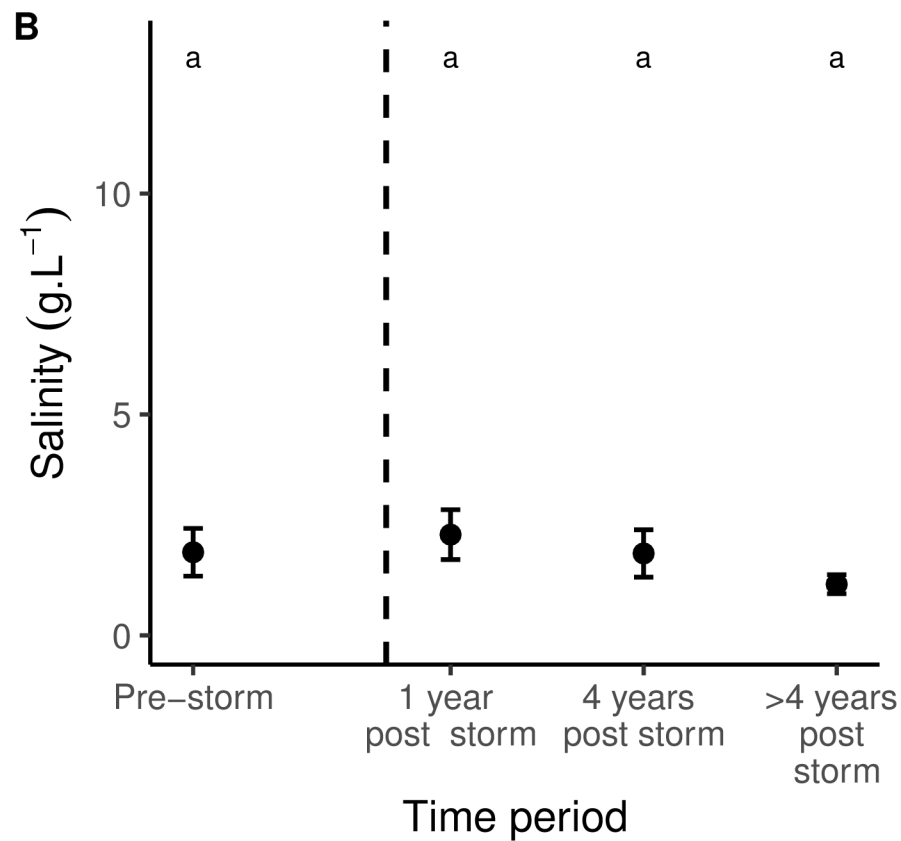
589 **Figure 4.** Mean ( $\pm$ SE) amphibian diversity measured for the four time periods of our  
590 surveys at MY (A) and MO (B). The vertical dashed line represents the year of storm  
591 Xynthia (2010). Different letters represent a significant difference at  $\alpha = 0.05$ .

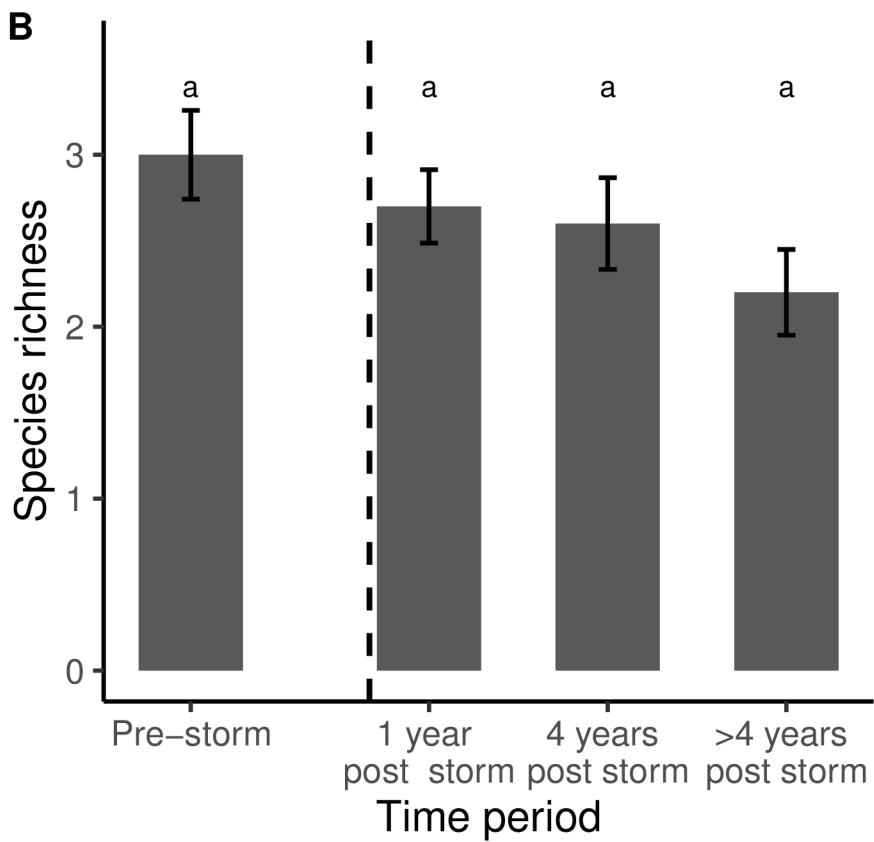
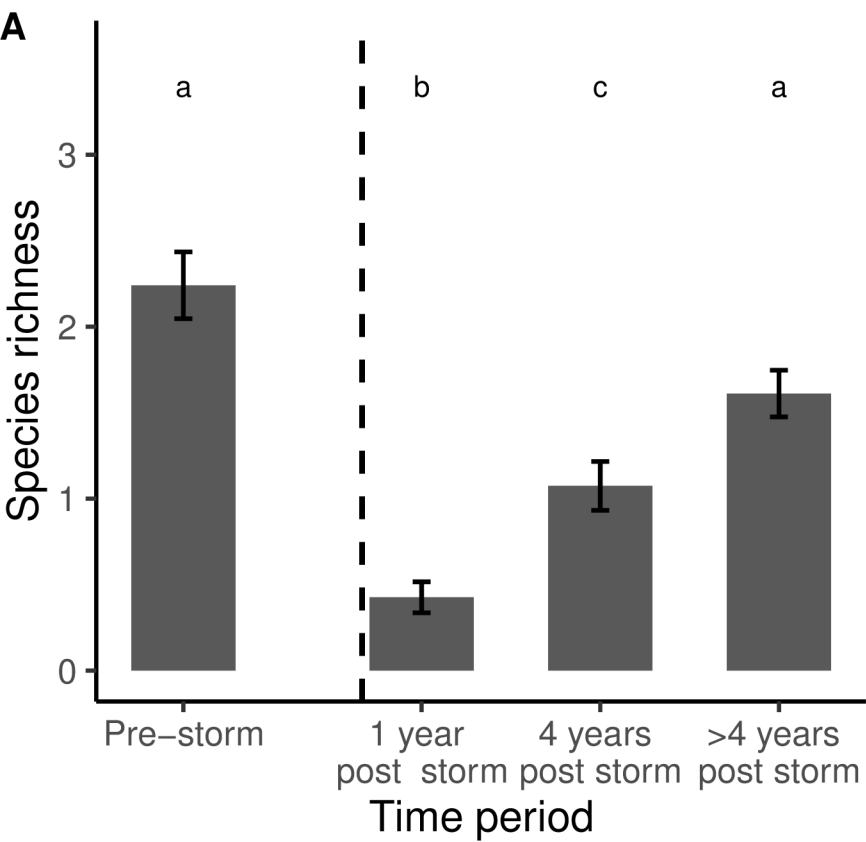
592

593 **Figure 5.** Mean ( $\pm$ SE) species presence measured for the four time periods of our  
594 surveys at MY (left panels) and MO (right panels). A, G: *Pelophylax sp.*, B, H: *Hyla*  
595 *meridionalis*, C, I: *Pelodytes punctatus*, D, J: *Pelobates cultripes*, E, K: *Triturus marmoratus*,  
596 F: *Bufo spinosus* and L: *Lissotriton helveticus*. The vertical dashed line represents the  
597 year of storm Xynthia (2010). Different letters represent a significant difference at  
598  $\alpha = 0.05$ .





**A****B**



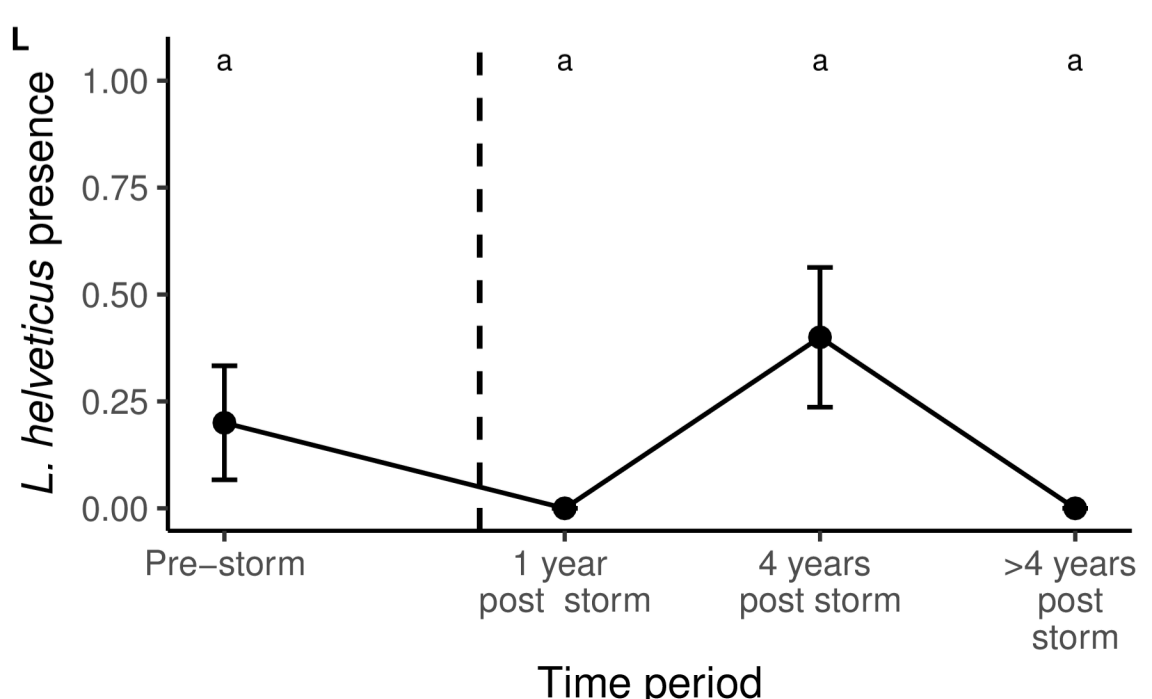
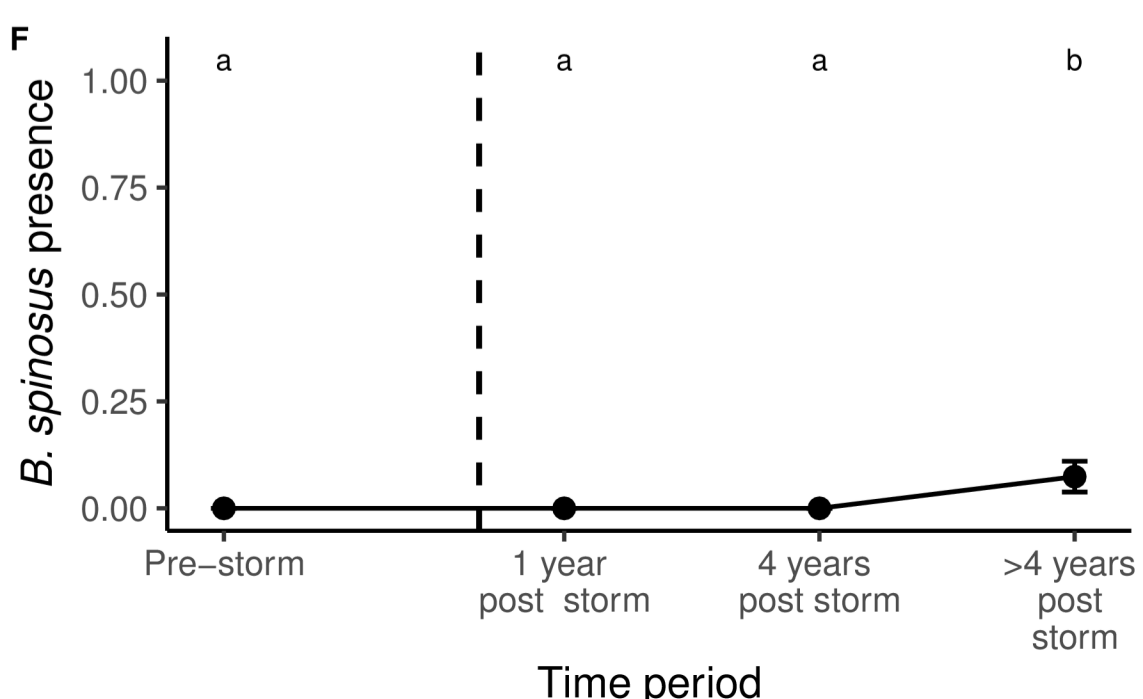
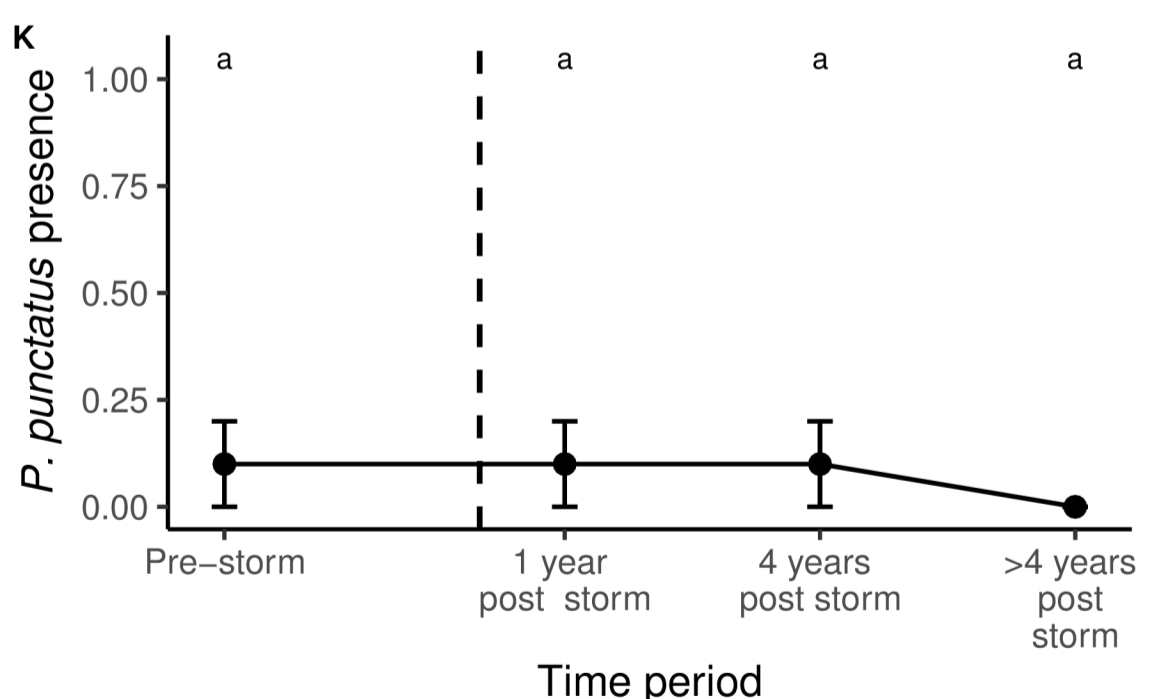
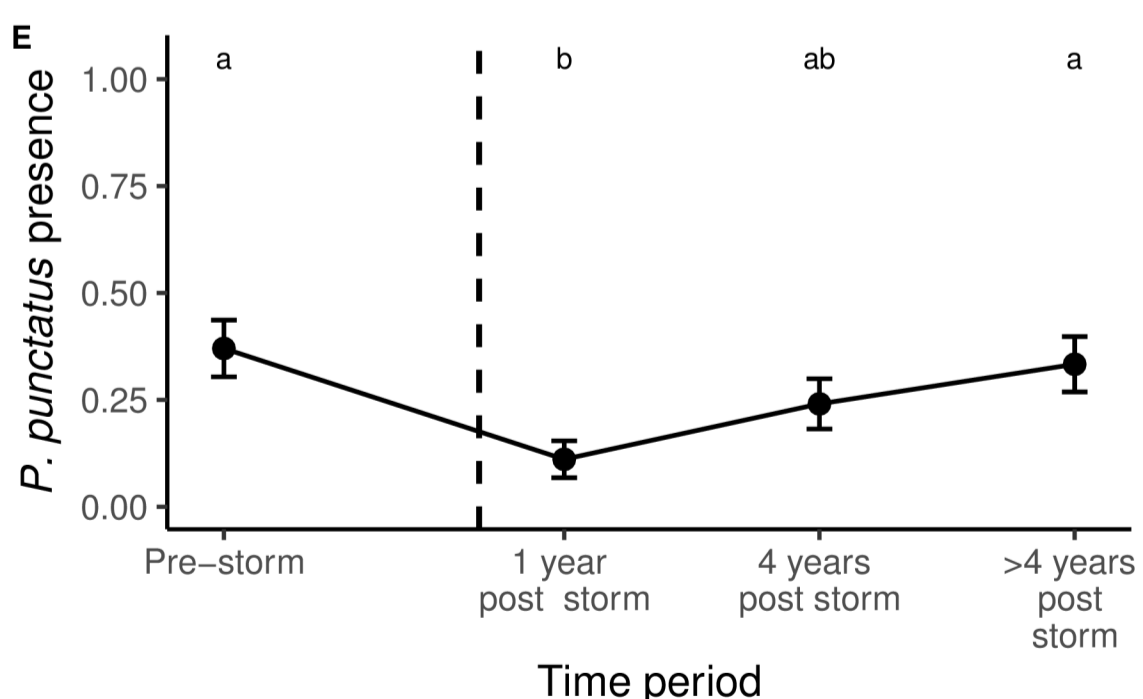
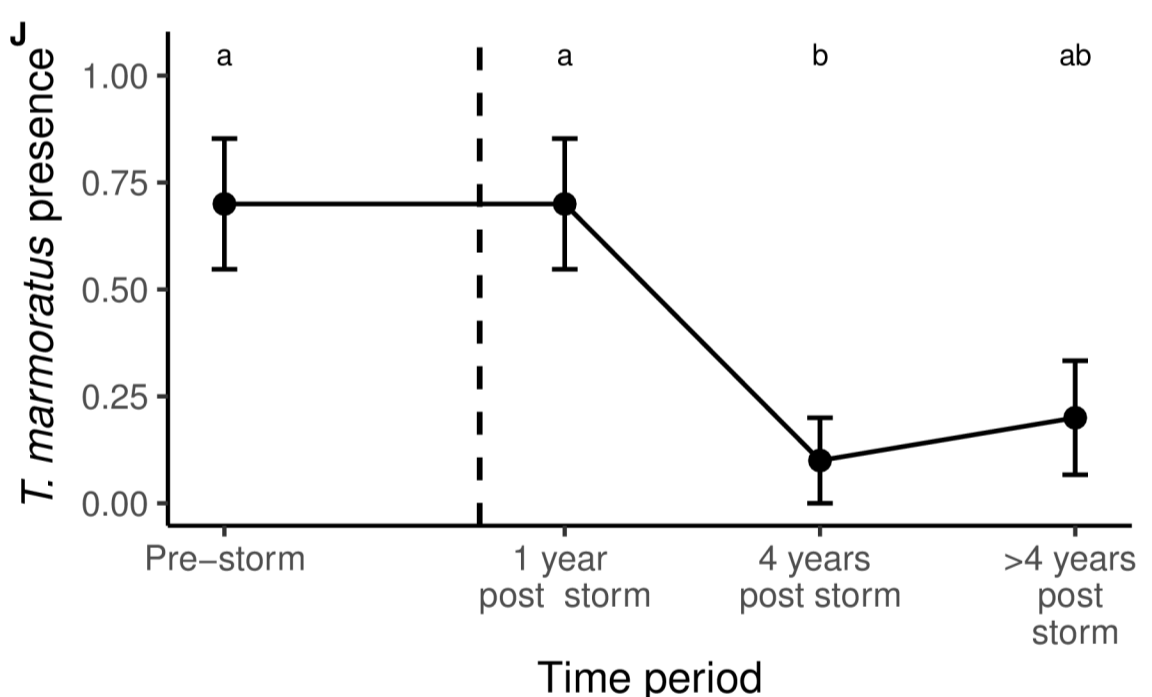
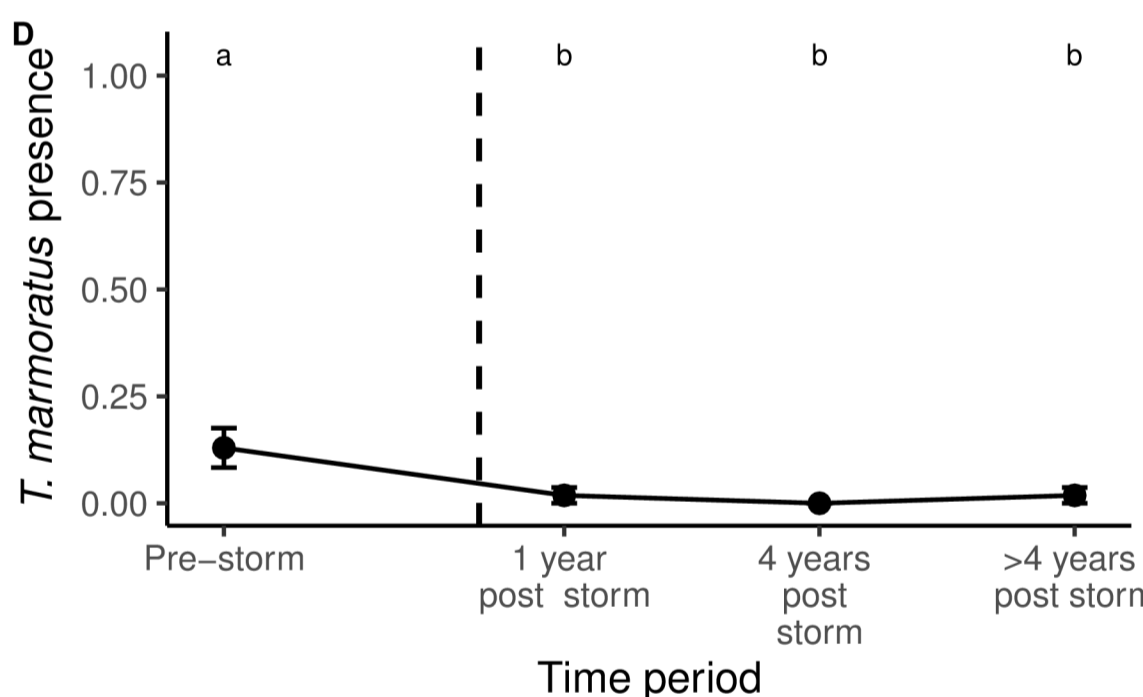
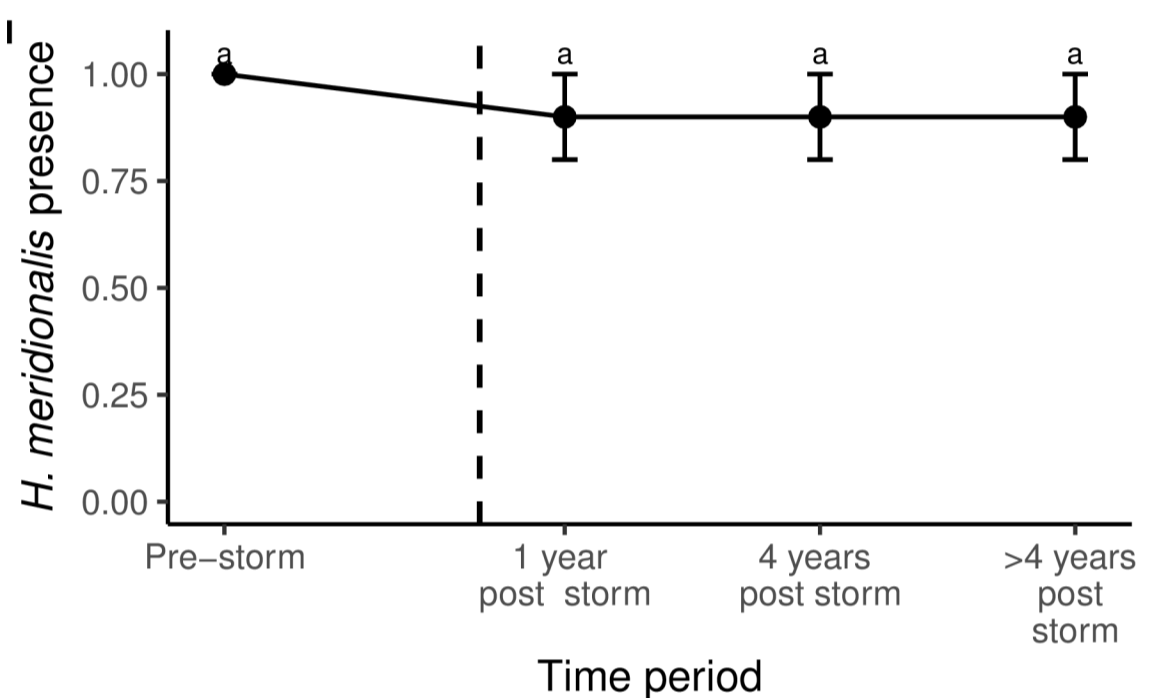
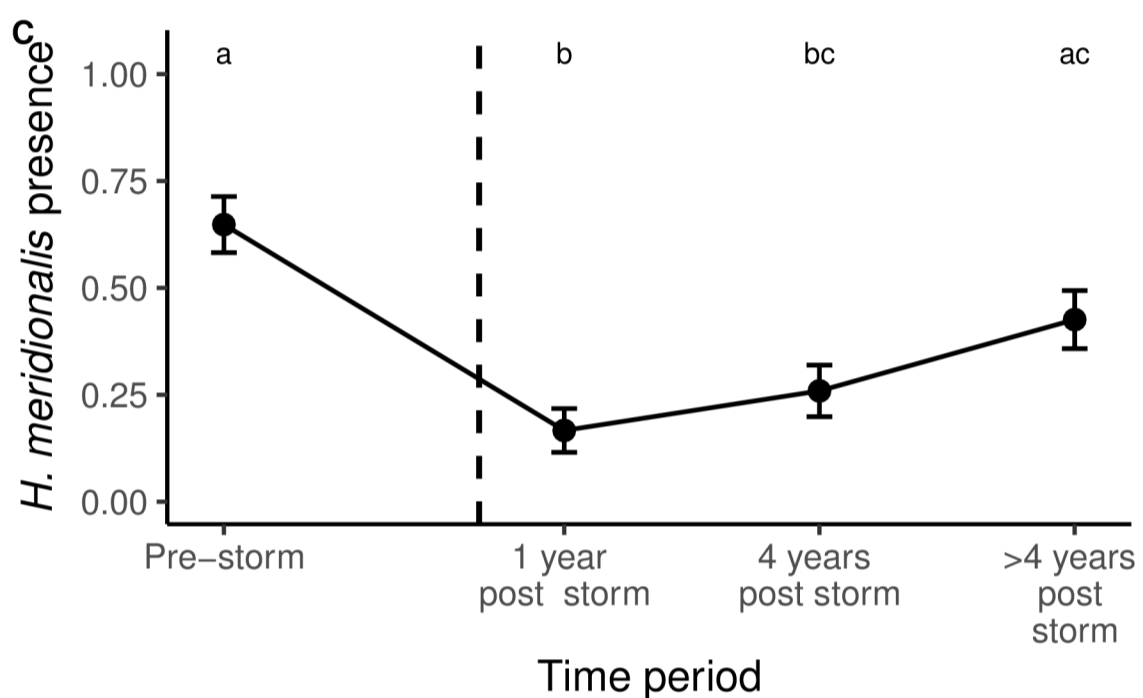
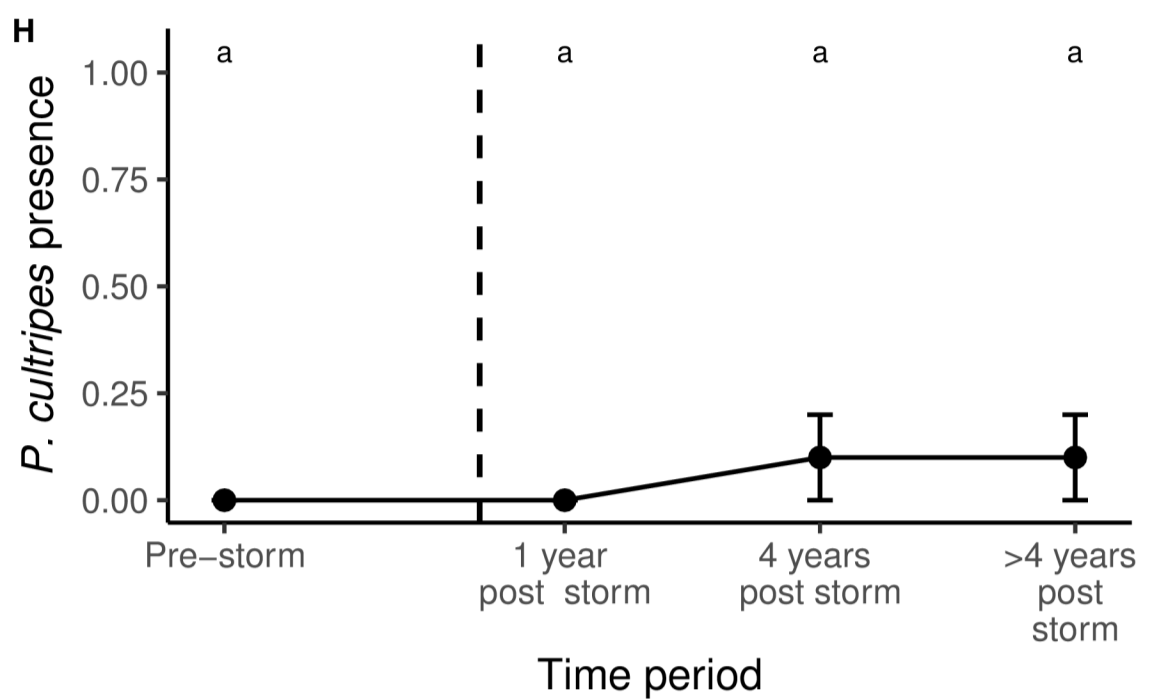
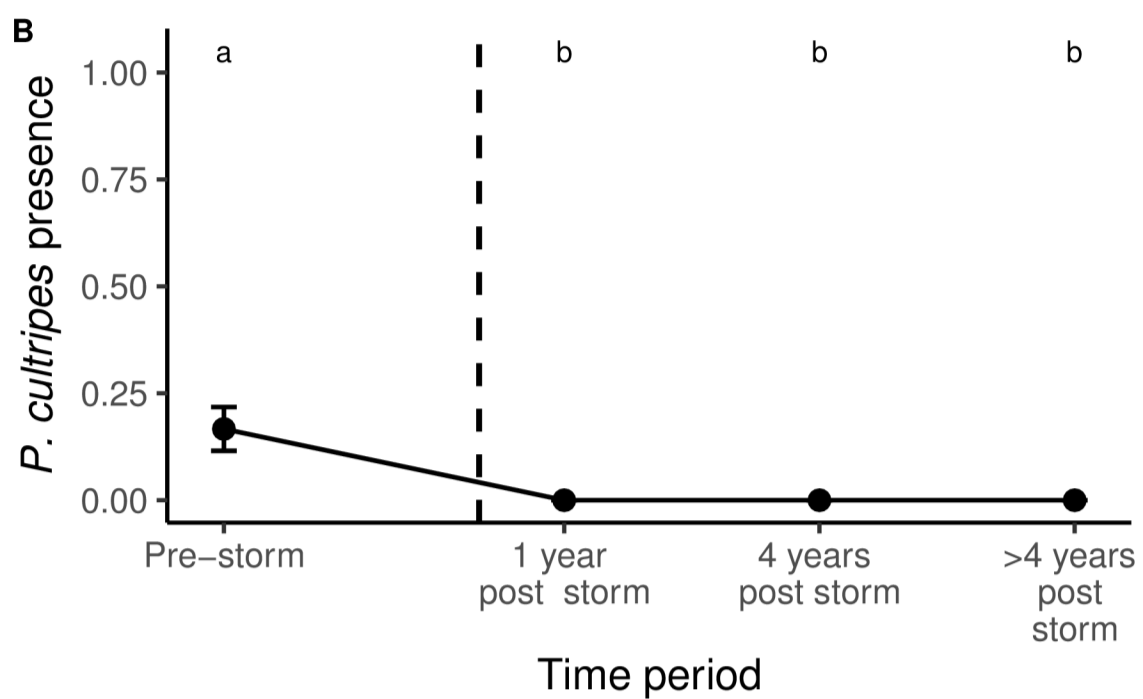
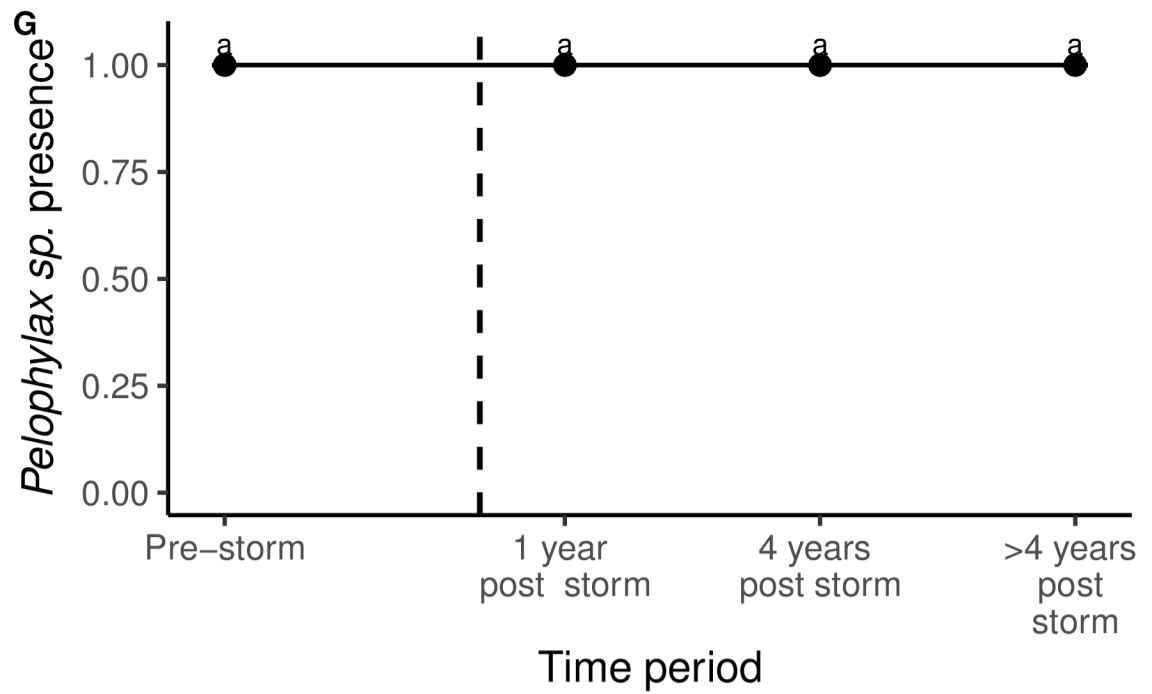
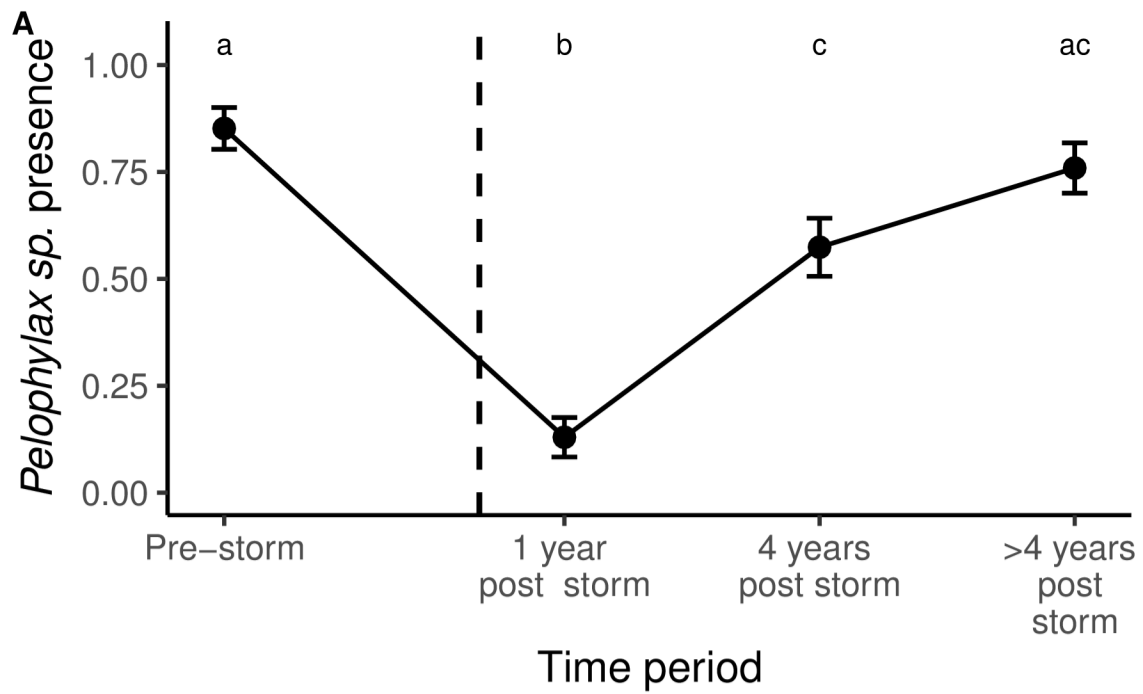




Table 1. Effect of the site, time period, and their interaction on salinity.

Tested variable	Parameters	Df	Deviance	AIC	scaled deviance/LRT	p-value
Salinity	Time period	3	4265.6	1180.7	99.748	<0.001
	Site	1	2928.8	1109.7	24.925	<0.001
	Time period:Site	7	4565.4	1192.2	122.54	<0.001

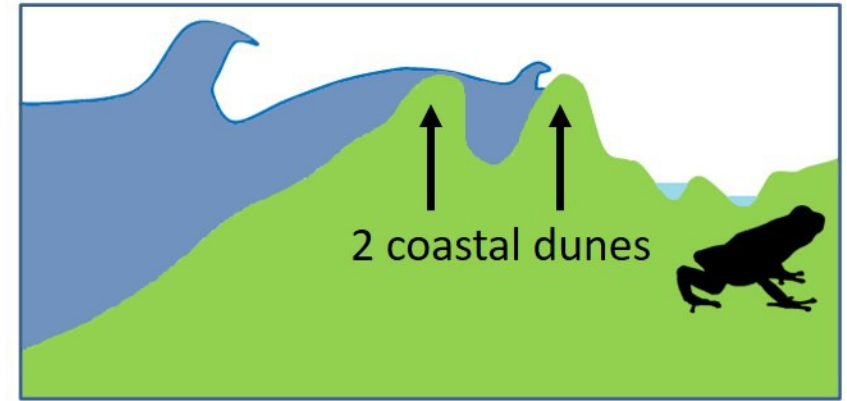
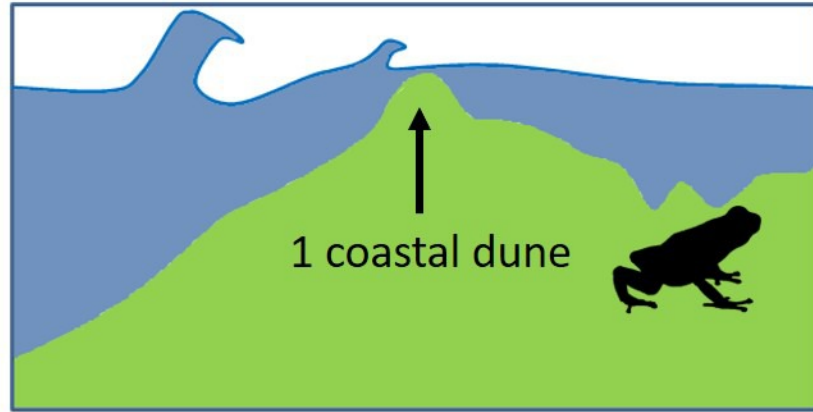
Table 2. Effect of the site, time period, and their interaction on species richness.

Tested variable	Parameters	Df	Deviance	AIC	scaled deviance/LRT	p-value
Species richness	Time period	3	295.36	784.92	56.547	<0.001
	Site	1	270	763.55	31.186	<0.001
	Time period :Site	7	326.55	814.1	111.43	<0.001

Table 3. Influence of habitat characteristics on species presence. Only significant factors are shown for MY. The same factors (although not significant) are shown for MO for comparison.

Reseve	Parameters	Estimate	SE	z	p
Marais d'Yves	Typology (pond)	0.68	0.159	4.269	<0.001
	Surrounding				
	vegetation	-0.226	0.099	-2.269	0.023
	Aquatic vegetation	0.273	0.082	3.311	<0.001
	Salinity	-0.147	0.073	-2.025	0.042
Moëze-Oléron	Typology (pond)	-	-	-	-
	Surrounding				
	vegetation	0.057	0.17	0.337	0.736
	Aquatic vegetation	0.118	0.303	0.388	0.698
	Salinity	0.072	0.178	0.405	0.686

Slight variations in topography → Strong differences in marine surges magnitude



→ site-specific salinization dynamics and amphibian species responses

