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Léa Lorrain-Soligon, Frédéric Robin, Pierre Rousseau, Marko Jankovic, François
Brischoux

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

3 Léa Lorrain-Soligon¹, Frédéric Robin^{2,3,4}, Pierre Rousseau³, Marko Jankovic⁴, François
4 Brischoux¹

5 **Institutional affiliations**

6 1. Centre d'Etudes Biologiques de Chizé, CEBC UMR 7372 CNRS – La Rochelle
7 Université, 79360 Villiers en Bois, France
8 2. LPO France, Fonderies Royales, 17300 Rochefort, France
9 3. Réserve naturelle de Moëze-Oléron, LPO, Plaisance, 17 780 Saint-Froult, France
10 4. Réserve naturelle du marais d'Yves LPO, Ferme de la belle espérance, 17340 Yves,
11 France
12

13 **Corresponding author:**

14 lea.lorrain-soligon@cebc.cnrs.fr
15 ID ORCID: 0000-0002-8723-7478
16 + 33 (0) 5 49 09 35 14

17 Full postal address : Centre d'Etudes Biologiques de Chizé, CEBC UMR 7372 CNRS –
18 405 route de Prissé la Charrière, 79360 Villiers en Bois, France
19
20
21
22

23 **Contact information for all authors:**

24 **FR:** frederic.robin@lpo.fr
25 **PR:** pierre.rousseau@lpo.fr
26 **MJ :** marko.jankovic@lpo.fr
27 **FB:** francois.brischoux@cebc.cnrs.fr
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 m² to 156 824 m². These ponds are situated at an average distance of 556 m (± 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 m²
163 to 70 m². Their position relative to the ocean is 429m (± 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 (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 (5g.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⁻¹ for *P. punctatus*, 13.7 g.l⁻¹ for *H. meridionalis* and 17.1 g.l⁻¹ 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), where 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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443 anuran amphibians. *Front. Zool.* 14:1–16
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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.

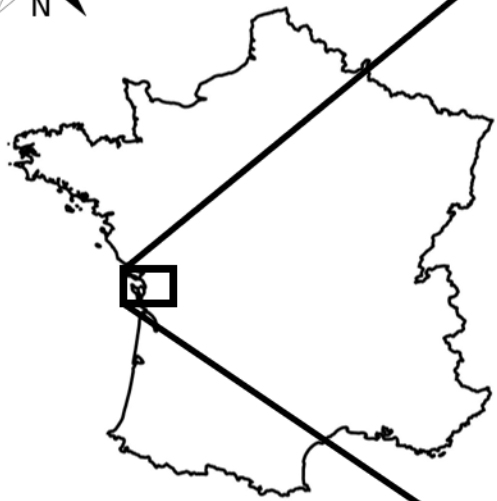
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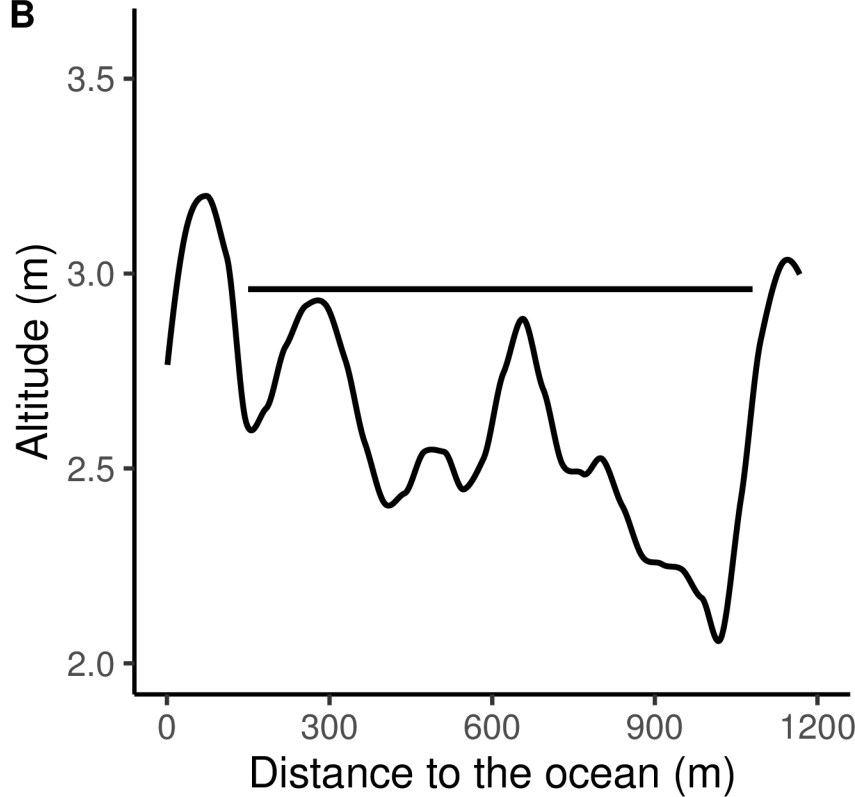
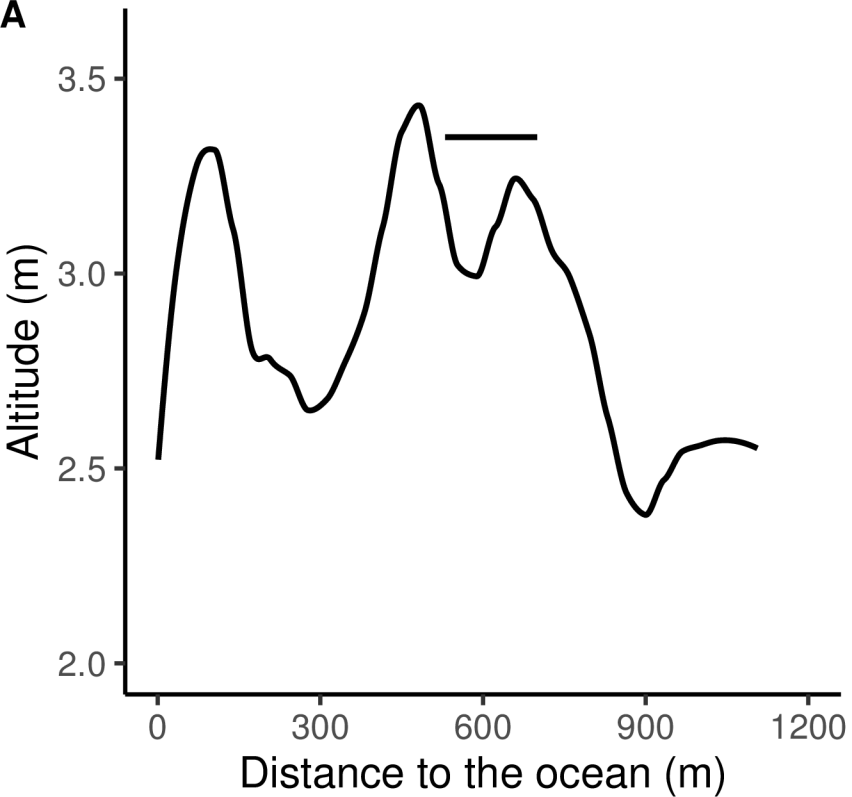
586 **Figure 3.** Mean (\pm SE) salinity measured for the four time periods of our surveys at
587 MY (A) and MO (B). The vertical dashed line represents the year of storm Xynthia
588 (2010). Different letters represent a significant difference at $\alpha = 0.05$.

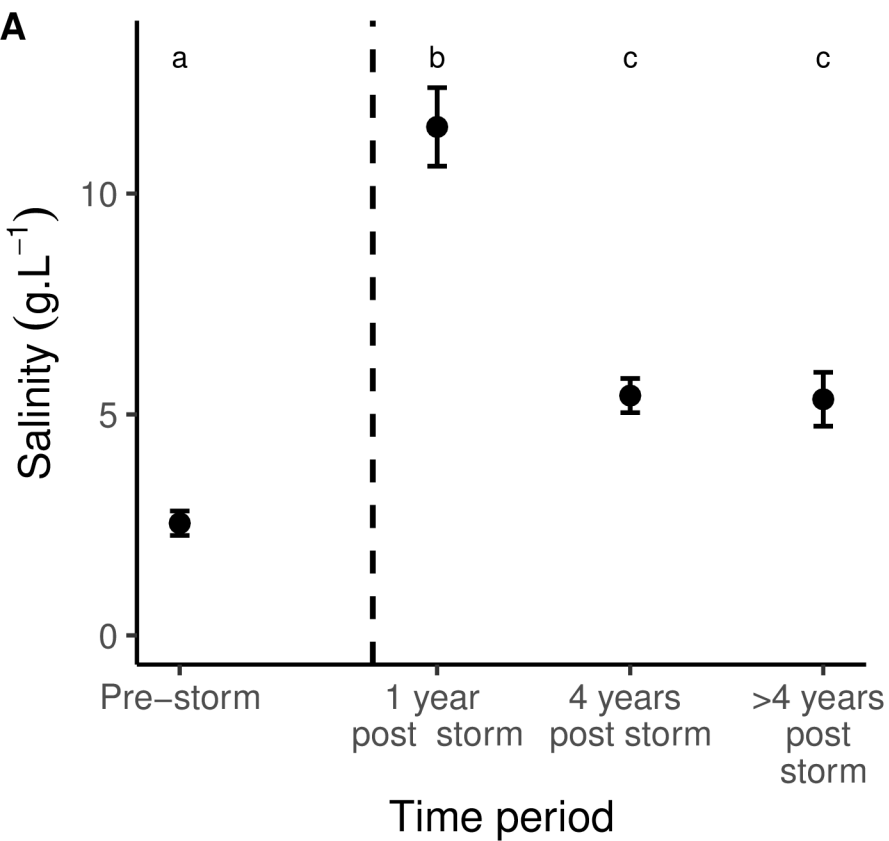
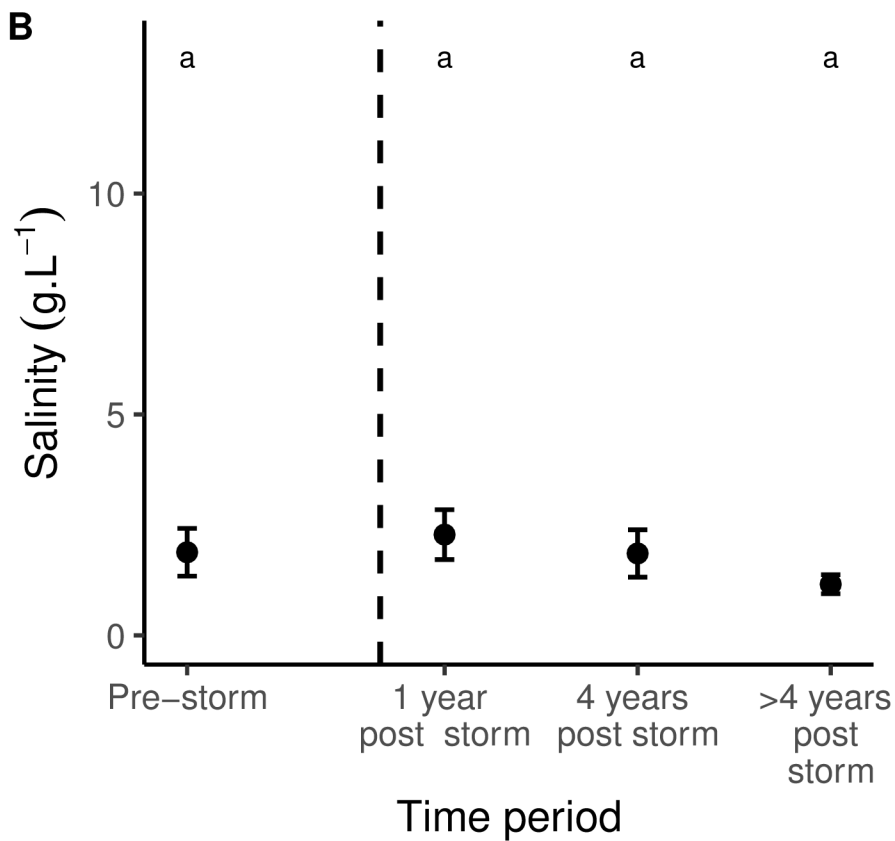
589 **Figure 4.** Mean (\pm SE) amphibian diversity measured for the four time periods of our
590 surveys at MY (A) and MO (B). The vertical dashed line represents the year of storm
591 Xynthia (2010). Different letters represent a significant difference at $\alpha = 0.05$.

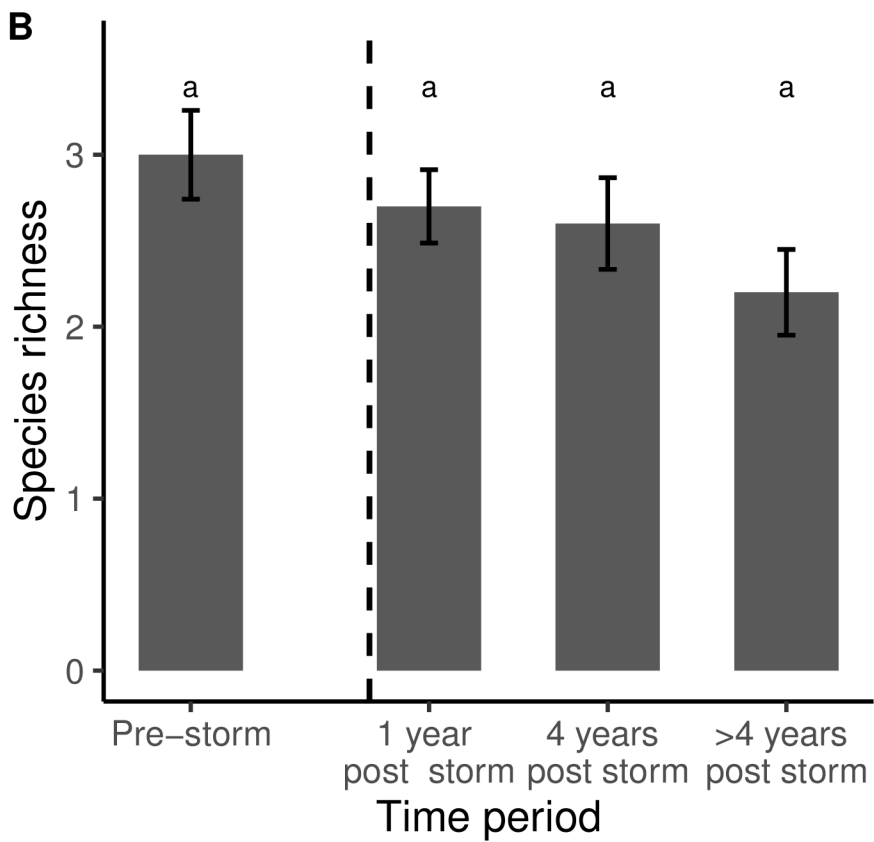
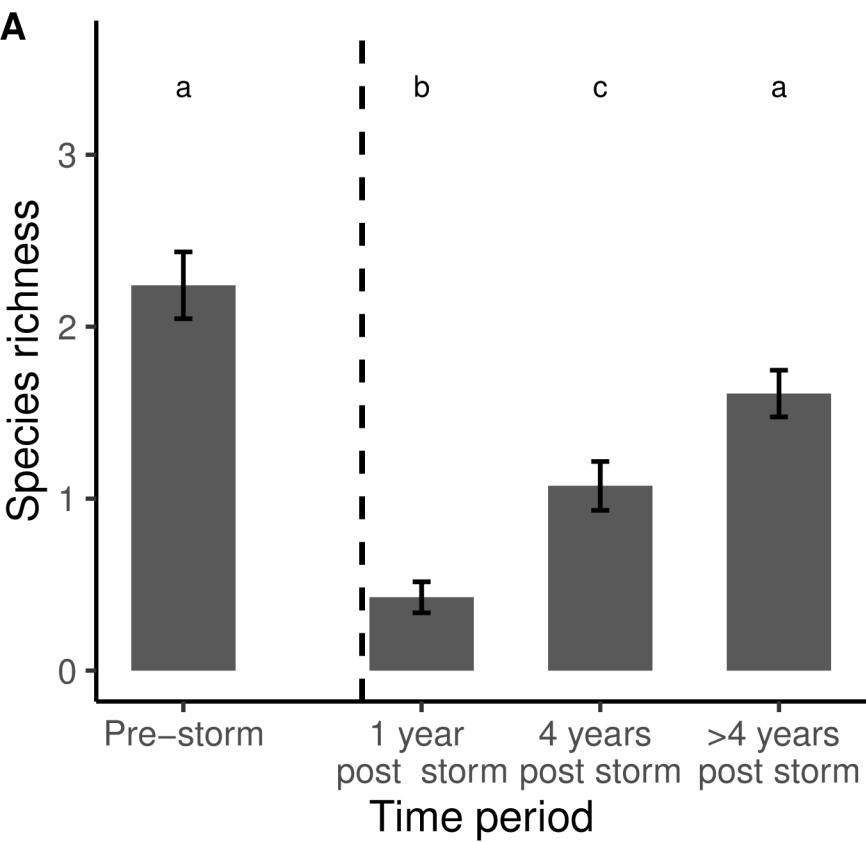
592

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**



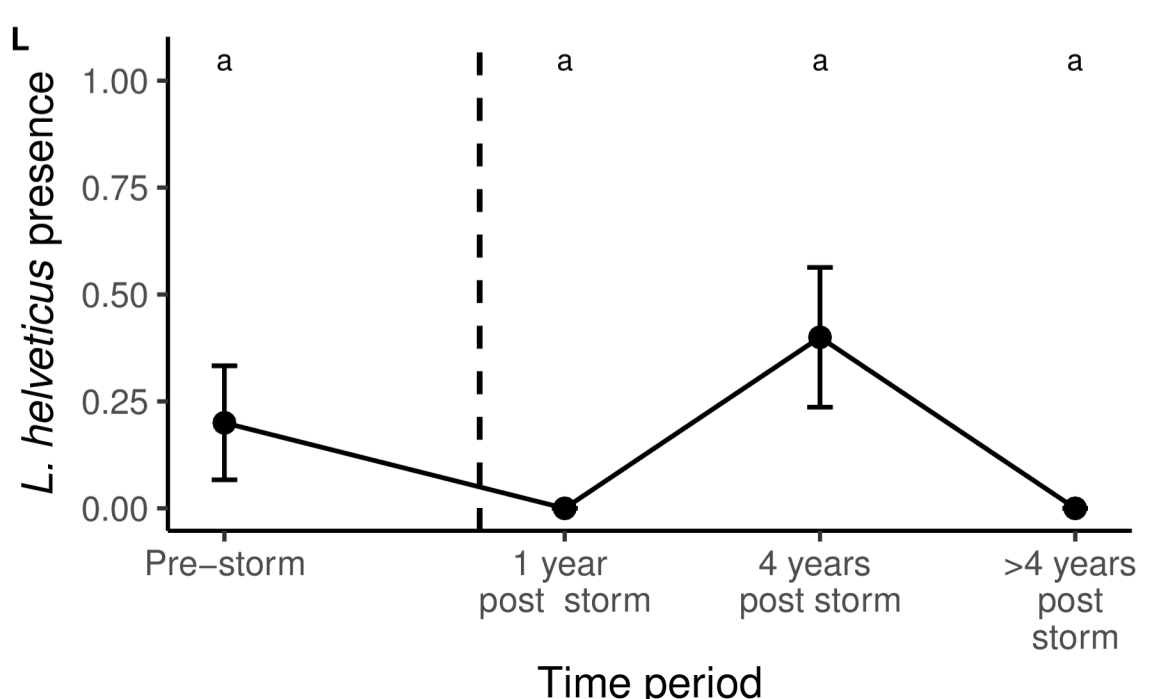
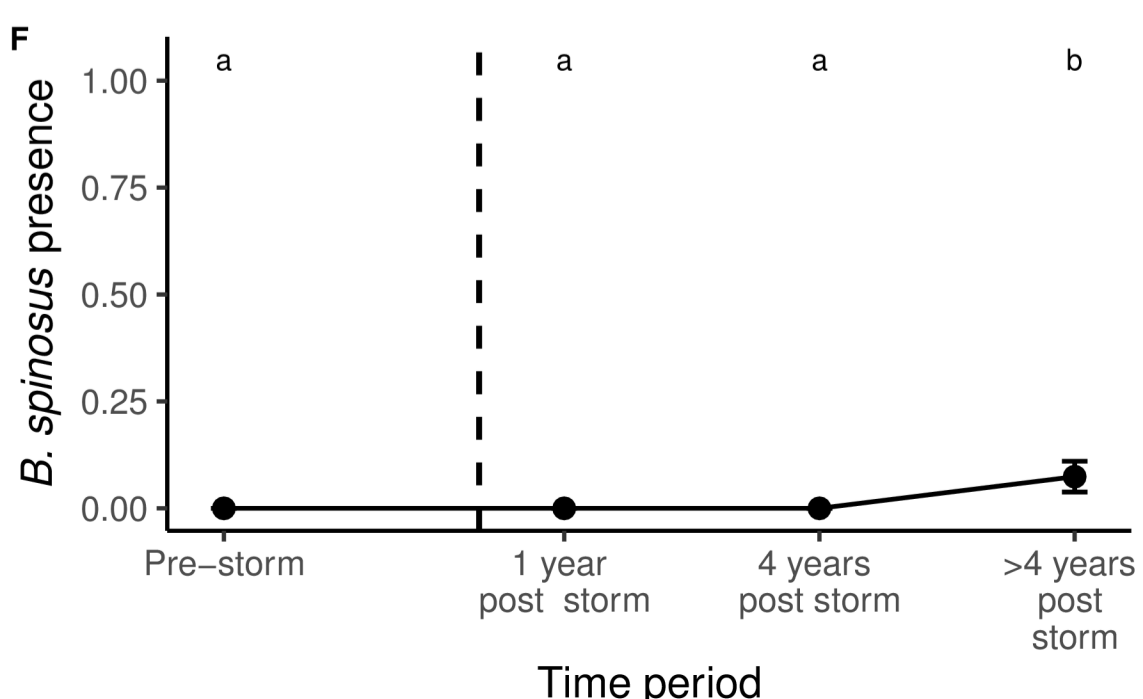
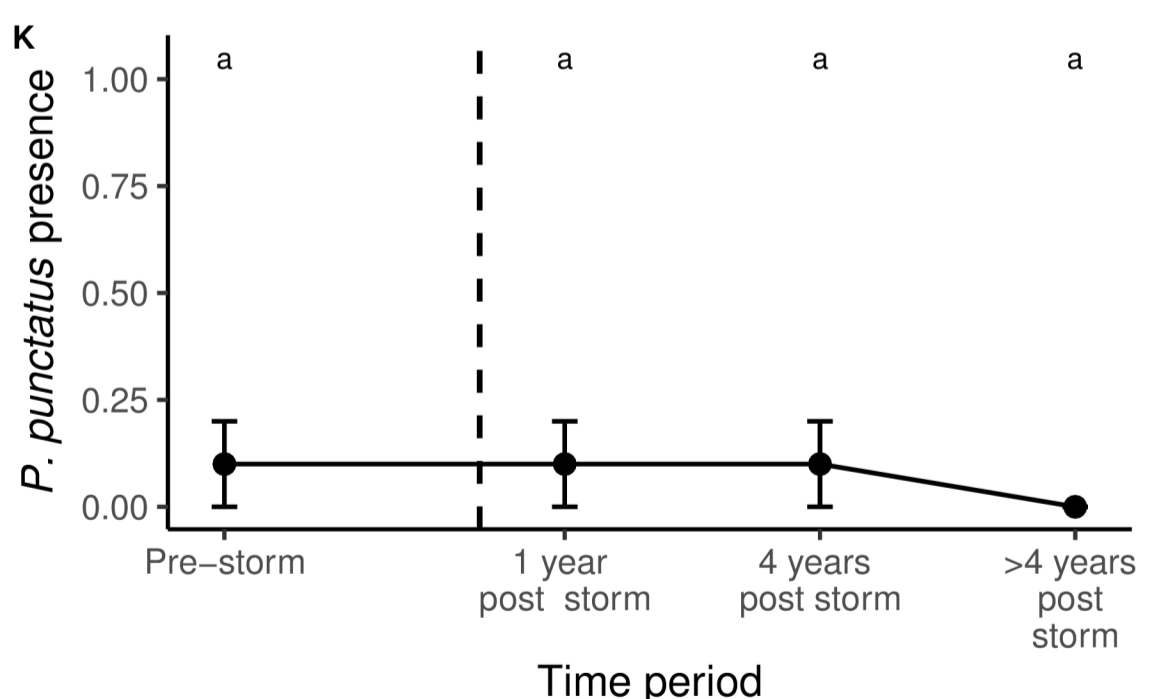
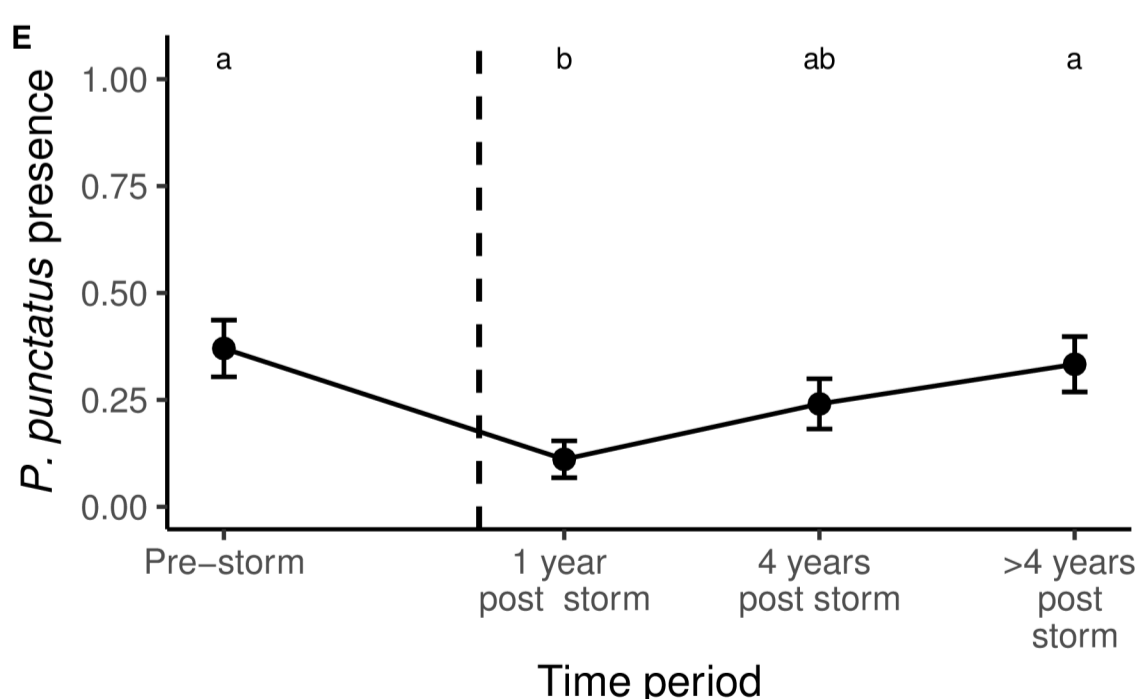
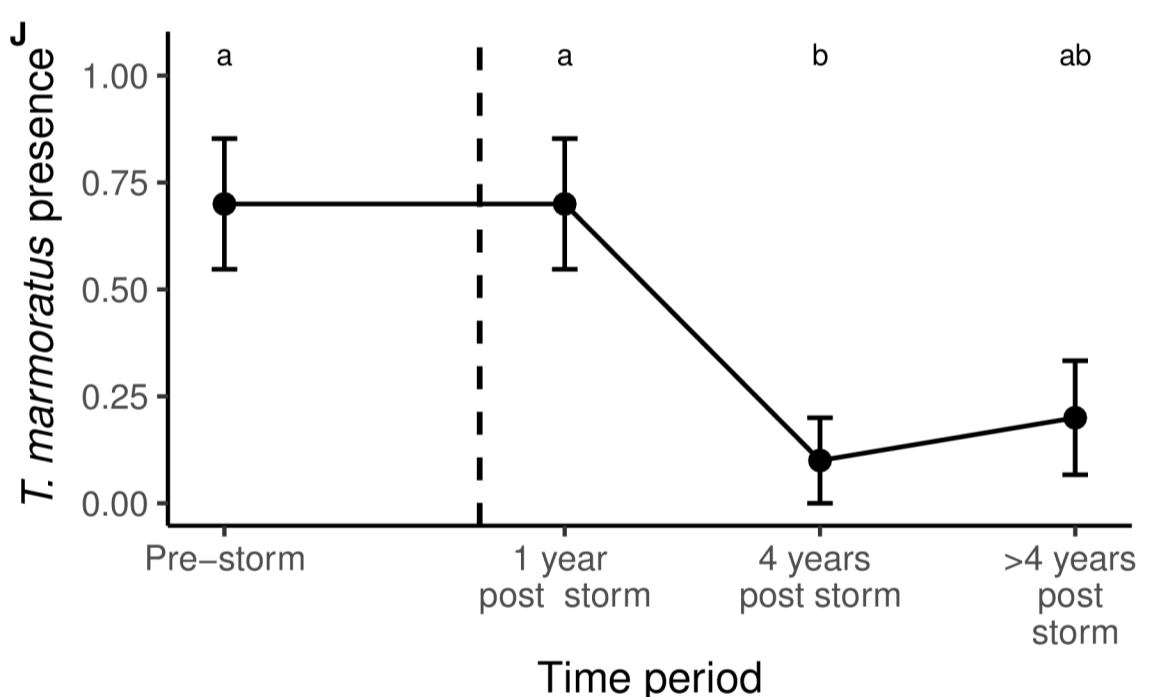
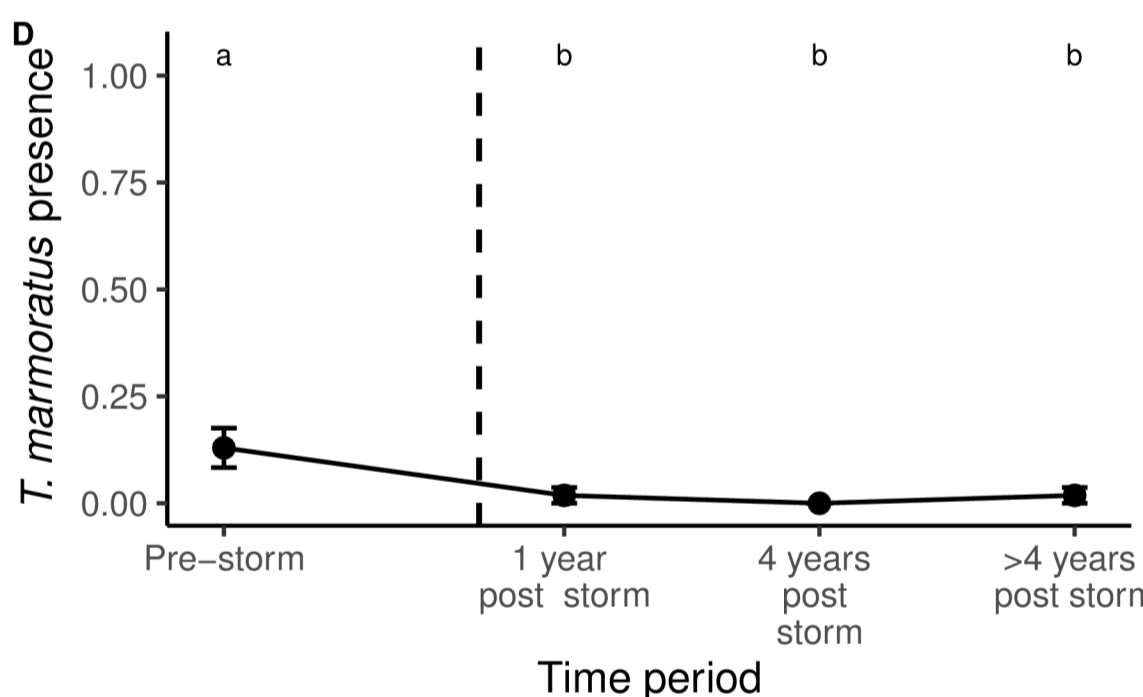
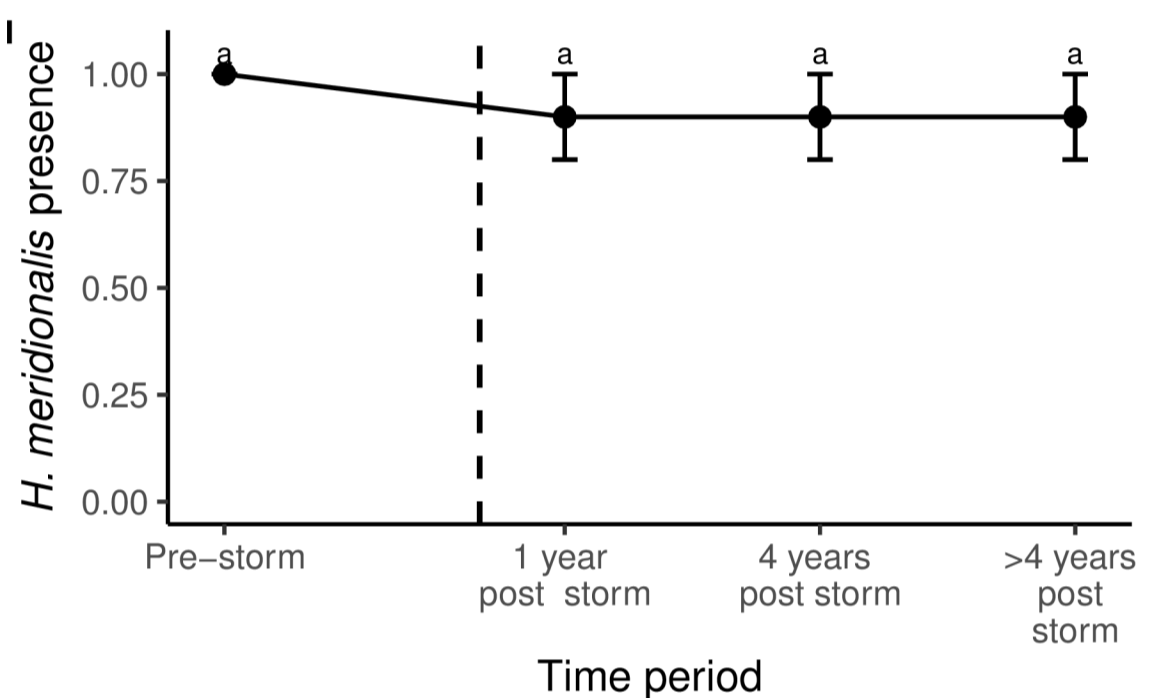
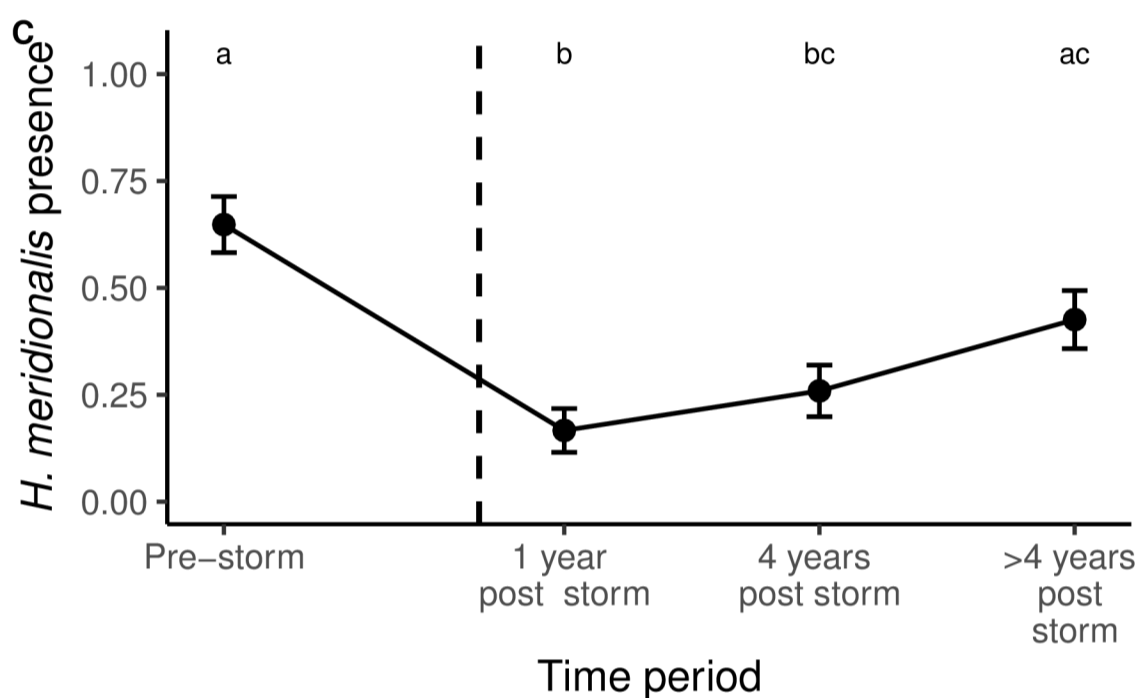
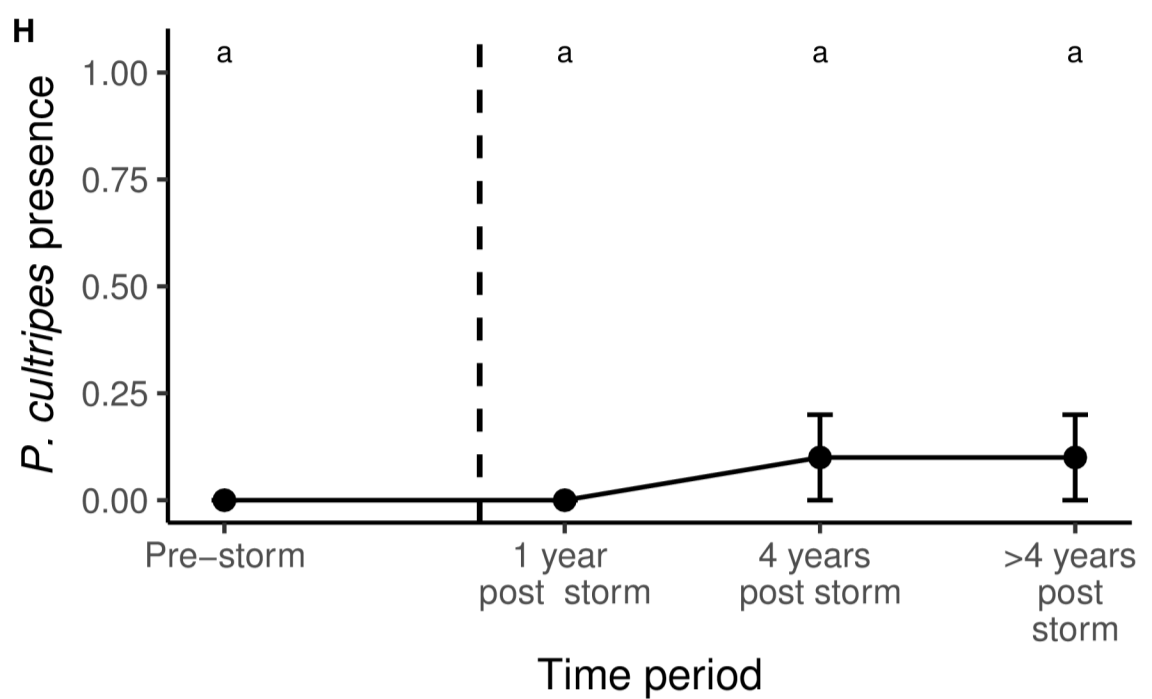
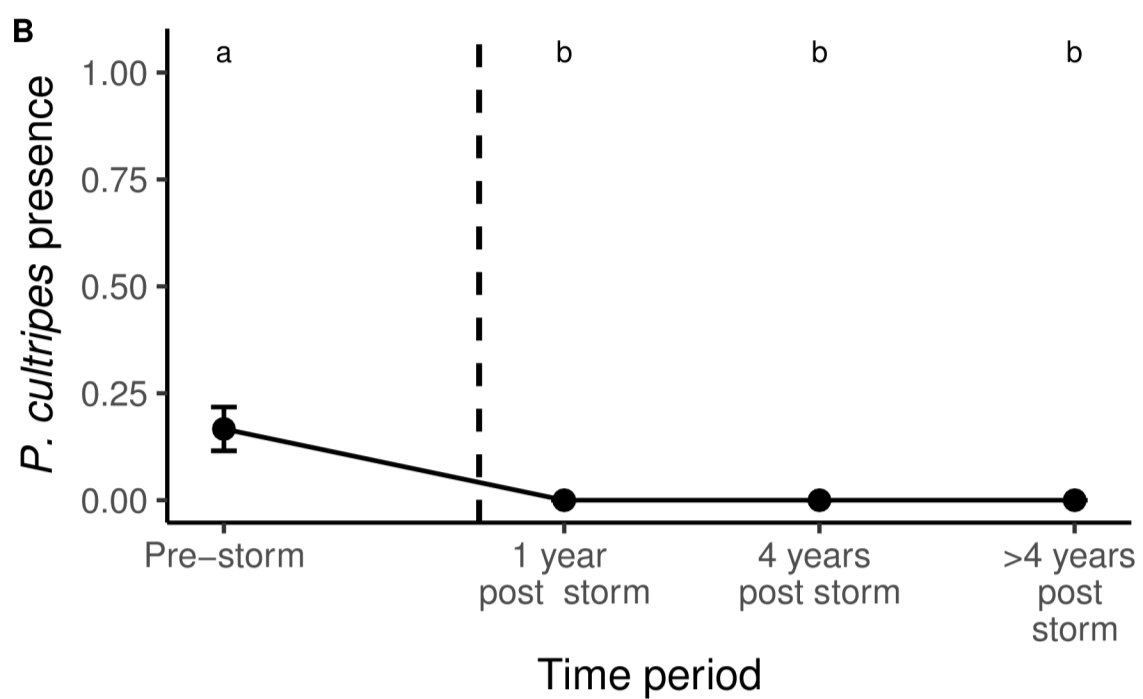
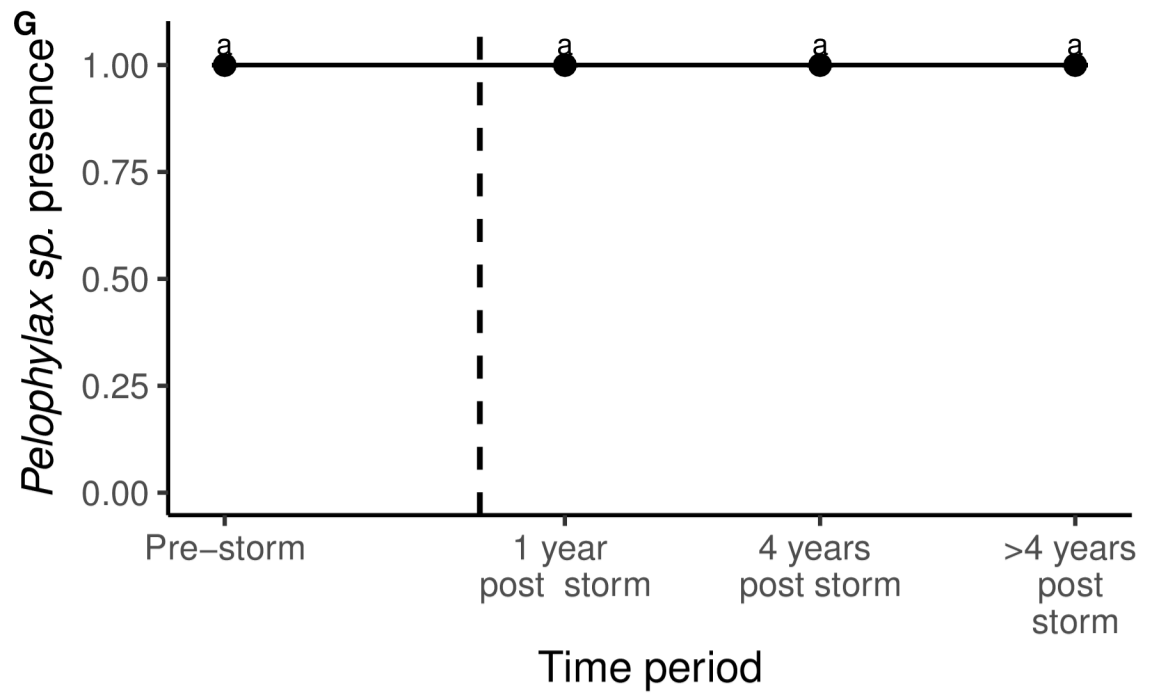
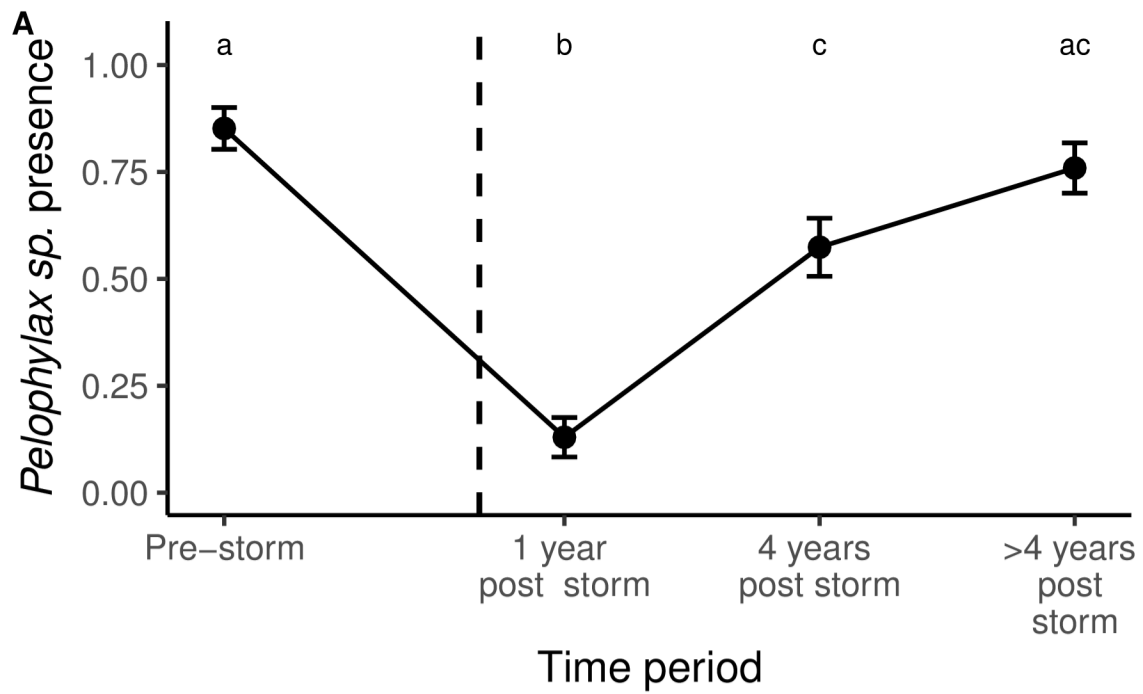


Table 1. Effect of the site, time period, and their interaction on salinity.

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

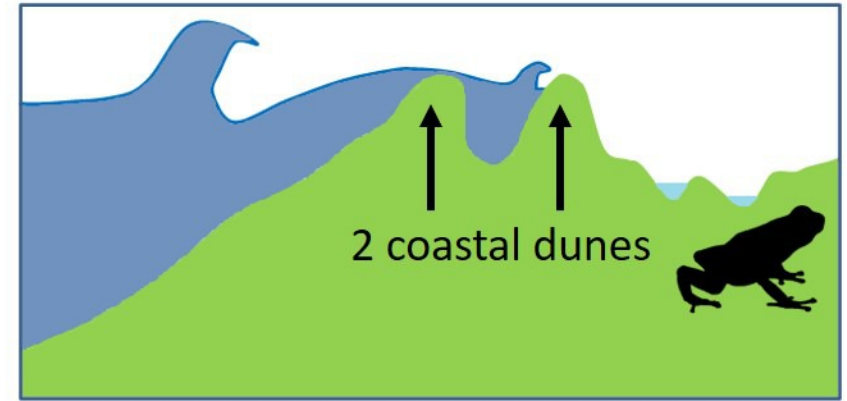
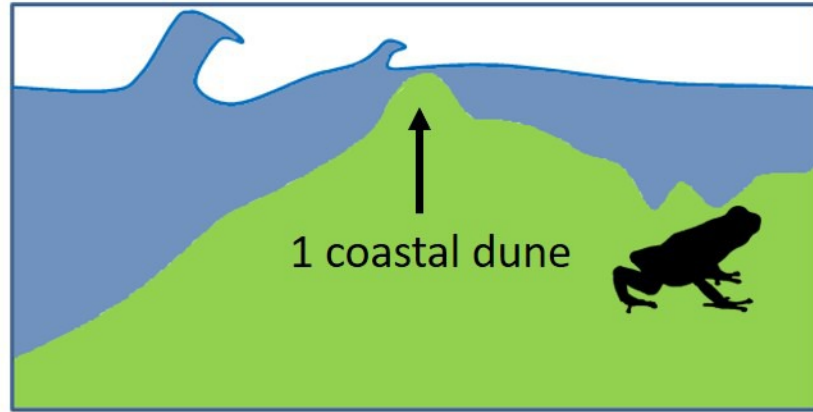
Table 2. Effect of the site, time period, and their interaction on species richness.

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

