



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

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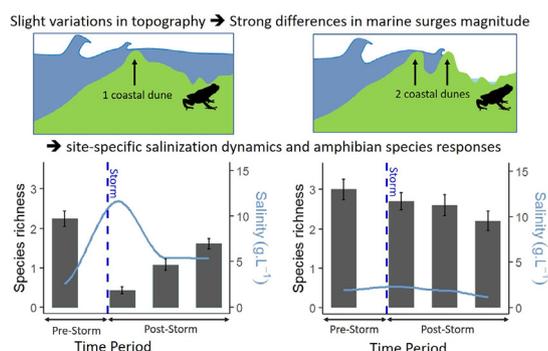
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HIGHLIGHTS

- Coastal marine submersions are expected to increase in frequency and intensity.
- Such extreme weather events threaten coastal wetlands.
- Long-term surveys pre/post marine submersion revealed site-specific responses.
- Variations in topography influenced salinization and associated wildlife responses.
- Topographical features can buffer consequences of such extreme weather events.

GRAPHICAL ABSTRACT



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ABSTRACT

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

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to elevated salinity), site-specific topography, and environmental parameters. Finally, our study emphasizes that relatively modest landscaping management may be critical to allow wildlife to successfully recover after a marine submersion.

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1. Introduction

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

Gradual changes of habitats linked to sea-level rise are expected to strongly affect coastal wetlands (Neubauer and Craft, 2009; Traill et al., 2011; Geselbracht et al., 2015). Yet, the relatively long temporal scale over which these changes are expected to occur may allow species to display adaptive responses. For instance, relatively mobile species could progressively adjust their coastal distribution, and thus gradually disperse to more suitable habitats (Convertino et al., 2012). Coastal wetland salinization is one of the main environmental changes linked to sea-level rise (Herbert et al., 2015), and associated osmoregulatory challenges are known to negatively affect wildlife (Greenberg et al., 2006; Pedersen et al., 2014; Gutiérrez, 2014; Rivera-Ingraham and Lignot, 2017). Nonetheless, progressive increases in salinity, such as those due to a gradual rise in sea levels, can allow species to display adaptive responses. Indeed, such responses have already been shown in various organisms such as fishes (Purcell et al., 2008), amphibians (Gomez-Mestre and Tejedo, 2003), aquatic snakes (Brischoux et al., 2017), waterbirds (Gutiérrez, 2014) and rodents (Getz, 1966).

In contrast, the sudden and unpredictable nature of marine submersions during extreme weather events can induce changes that may exceed the ability of species to disperse toward more suitable habitats and/or adapt to a new set of environmental conditions, especially when marine submersion events induce direct and brutal salinization of inland soil and water (Hopkins and Brodie, 2015; Wang et al., 2016). These short pulses of high salt concentrations may lead to extreme mortality events (Gunzburger et al., 2010; Herbert et al., 2015), in contrast to exposure to moderate salinity levels during a longer time period (Marshall and Bailey, 2004). Yet, to our knowledge, very few studies have examined the effects of extreme events, such as storm-induced marine submersions on wildlife from coastal areas (but see Greenberg et al. (2006); Ameica y Juárez et al. (2013)), especially in the context of the salinization induced by these marine submersions (but see Kokelj et al. (2012)).

Importantly, specific geographical features of coastal wetlands may dampen the expected effects of marine submersions on these ecosystems (Loder et al., 2009; Wamsley et al., 2010). For instance, low-lying coastal wetlands without relief should be particularly exposed to marine submersions (Eliot et al., 1999; Wang et al., 2012), while the presence of barriers may dampen the effects of extreme weather events (McLean et al., 2001). As a consequence, site-specific topographical features may buffer the expected detrimental effects of marine submersions on wildlife. Given the forecasted increase in the frequency and intensity of such extreme weather events (Dettinger, 2011), identifying such topographical features may prove useful for proposing landscaping solutions that aim to preserve these essential coastal ecosystems.

We examined the consequences of a major marine submersion (Xynthia) on Atlantic coastal wetlands in France. Xynthia was an exceptionally violent windstorm which crossed the Western European coast between 27 February and 1 March 2010, leading to the submersion of a large number of coastal sites for a few days to a few weeks (Durant et al., 2018). In order to identify the consequences of marine submersions linked to storm Xynthia, we investigated coastal amphibian communities, because these taxa display several traits that should increase their susceptibility to marine surges. For instance, amphibians are known to be highly sensitive to salinity levels because of their permeable skin and their comparatively low ability to osmoregulate in hyperosmotic environments (Shoemaker et al., 1992; Wells, 2007). Increasing salinity is known to decrease survival for amphibians across all life stages (Albecker and McCoy, 2017), but this is especially true for eggs and tadpoles that develop in aquatic environments (Hopkins and Brodie, 2015; Albecker and McCoy, 2017; Welch et al., 2019). In addition, they are characterized by low dispersal capacities (Wells, 2007), thereby affecting their ability to evade sudden detrimental conditions. Although several studies have assessed the effects of salinization on amphibians, particularly on tadpoles (Christy and Dickman, 2002; Smith et al., 2007; Hopkins and Brodie, 2015), less work has been performed on their long-term responses to marine submersions (but see Gunzburger et al., 2010), presumably because such an approach requires logistically complex surveys encompassing pre- and post-storm monitoring (Walls et al., 2019).

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

- ponds from the more protected site should be less affected by marine surge and, thus, should display relatively low and constant salinity levels across time, while ponds from the less protected site should be characterized by elevated salinity levels post-storm.
- amphibian richness should be negatively affected by salinity levels, and should decline post-storm in the less protected site.
- species more tolerant to salinity should recover rapidly following a marine surge while species more sensitive to osmotic stress may be extirpated.

2. Material and methods

2.1. Study sites

The study was carried out on two reserves in Western France: one in the "Réserve Naturelle Nationale de Moëze-Oléron" (45°53'33.36"N, 1°04'59.16"W, hereafter MO, Fig. 1), and one other in the "Réserve Naturelle Nationale du marais d'Yves" (46°2'40.735"N, 1°3'16.906"W, hereafter MY, Fig. 1). These two study sites, separated by ~15 km straight line, are situated on the Atlantic coast of France (Département de la Charente-Maritime), and cover a similar surface area (218 ha for

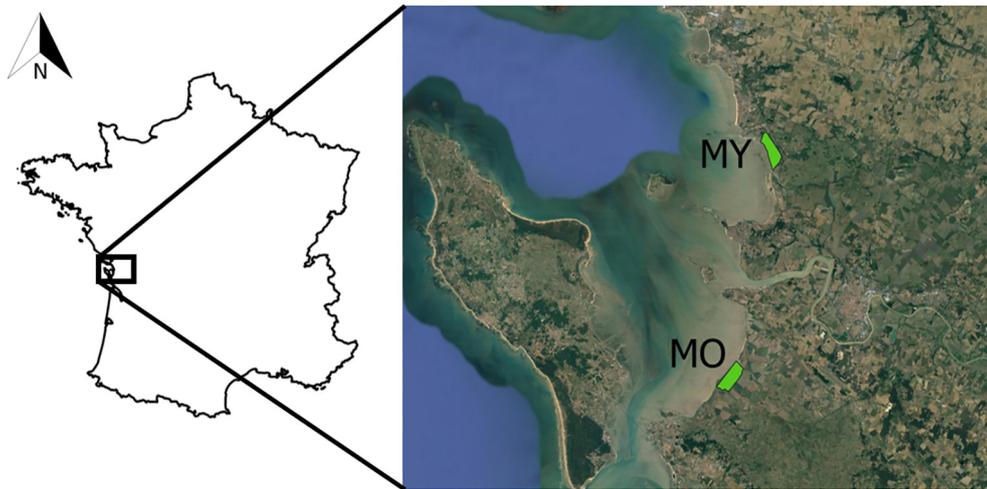


Fig. 1. Map of the study area relative to Western France illustrating the two study sites, using an OpenStreetMap basemap. Green areas represent the two study sites (MY and MO). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

MO and 204 ha for MY, Fig. 1). The two reserves were hit by Xynthia on 27 February 2010, with the same intensity (maximum wind intensity of 130–140 km/h, see Météo France (<http://tempetes.meteo.fr/spip.php?article132>) and Appendix A).

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

2.2. Sampling

2.2.1. Periods of sampling

For each site, amphibian monitoring in breeding ponds was performed both before and after storm Xynthia. Specifically, sampling occurred a few years before Xynthia (in 2007 and 2008 for MY and MO, respectively; hereafter “pre-storm”), the year after Xynthia (in 2011 for both sites, hereafter “1 year post-storm”), 4 years after Xynthia (in 2014 for both sites, hereafter “4 years post-storm”) and again a few

years later (in 2017 and 2019 for MY and MO respectively; hereafter “more than 4 years post-storm”).

2.2.2. Sampling ponds

For each site, amphibian presence was monitored in natural breeding ponds during the spring (see Section 2.2.3). At MY, 54 ponds were monitored during the 4 time periods mentioned above. These breeding sites vary in their size, ranging from <36 m² to 156,824 m². These ponds are situated at an average distance of 556 m (\pm 24 m SE) from the ocean, ranging from 27 to 832 m. At MO, 10 ponds were monitored during the 4 time periods mentioned above. The size of these sites ranges from 20 m² to 70 m². Their position relative to the ocean is 429 m (\pm 36 m SE), ranging from 262 m to 637 m. The positions of the ponds relative to site-specific topography are represented in Fig. 2.

2.2.3. Monitoring of amphibian presence

In order to take differences in phenology and detectability of the amphibian species occurring at each breeding pond into account, we performed three successive monitoring sessions for each pond, according to Petitot et al. (2014). These surveys occurred in the spring during the breeding period of amphibians in Western France (Miaud and Muratet, 2018). In March and April, surveys were conducted at night (2 h after sunset) during the activity peak of breeding amphibians; while for the last session (May), surveys occurred during daytime in

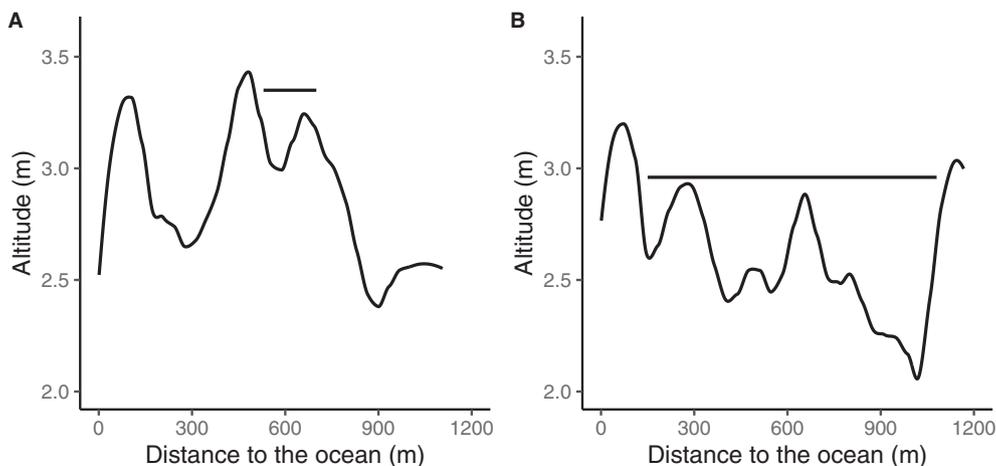


Fig. 2. Coastline topographic profile of MO (A) and MY (B) highlighting the presence of the additional small dune in MO. The relative position of the pond surveyed is indicated by a horizontal line and shows that ponds in MO were all situated behind the additional sand dune.

order to visually assess indices of effective reproduction (i.e., egg and tadpole presence).

At each site, two complementary survey methods were performed successively at each session. First, an acoustic survey was performed for 5 min at a distance of four meters from the pond edges. This method allowed us to assess species presence based on mating or territorial calls. Second, a visual survey was performed during another 5 min by slowly walking around the pond edge with a headlamp to detect individuals present nearby the pond edge (on land or in water). These two methods were occasionally (in order to limit the destruction of aquatic vegetation) complemented by the use of a net in order to assess the presence of the most secretive species, but it did not yield additional species that were not detected by the two methods described above.

2.2.4. Environmental parameters

For each pond, we recorded 9 environmental parameters: Water salinity, type of habitats, habitat permanence, area of the pond, shortest distance to the ocean, surrounding vegetation, aquatic vegetation, number of other species found, and water depth (see below). These parameters were chosen because of their possible impact on amphibian presence and diversity (Başkale and Kaya, 2009; Shulze et al., 2012; Hopkins and Brodie, 2015). Each parameter was recorded each year of survey, allowing to determine differences between years, and differences pre- and post-submersion. Water salinity (g.l^{-1}) of the breeding ponds was recorded in May using a Multi 340i multimeter (WTW, Xylem analytics). At MY, salinity was measured at 53 out of the 54 ponds monitored, while at MO, salinity was measured at 5 out of the 10 ponds surveyed. For each pond, we also characterized the type of habitat (pond or ditch), the habitat permanence (temporary or permanent water body), the area of the pond and the shortest distance to the ocean (both evaluated using QGIS 3.4.7), the surrounding vegetation (expressed in percentage cover), the aquatic vegetation (with a score ranging from 0 to 3, adapted from Lachavanne et al. (1995) and corresponding to diversity, i.e. number of species which can be differentiated, and water surface occupied by aquatic vegetation, evaluated visually, in April), the number of other species found in the pond (fishes, insect larvae, and crayfish), and the water depth (measured with a ruler in April).

2.3. Data analysis

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

To determine whether there were differences in the number of species between sites and time period, and variations of salinity between sites and time periods, we ran GLMs (General Linear Models) with site, time period, and their interaction as predictors. We computed GLMs on the total number of species present at each site and on salinity, using a Poisson and a Gaussian distribution, respectively. These distributions were chosen based on the fit to our data, and by checking overdispersion of residuals, and effects were assessed with a backward model selection using chi-squared tests. We computed Dunnett post-hoc tests on our GLMs using the “multcomp” package in order to assess within and across site and time period differences. These models could not be computed for each species separately, and species responses were investigated using Kruskal Wallis and Dunn post hoc test (package “PMCMR”). Multiplicity of responses (as the analyses included only 0 and 1) were corrected for multiplicity with the Holm correction, to account for ex aequo.

In addition, to determine whether environmental parameters affected amphibian presence at each site, we also tested the effects of our 9 environmental variables (see Section 2.2.2) on species presence (except for type of pond and permanence in MO, because ponds are all temporary and pond stricto sensu), using GLMs with a Poisson

regression. In these models, we first implemented the whole set of environmental parameters, for which correlations were tested with a Pearson correlation test. Variables were standardized before analyses. Beginning from a model with 9 parameters, we then carried out a backward model selection using Chi-square tests (Bolker et al., 2009).

All data analyses were performed using R 3.6.3 (R Core Team, 2020) and Rstudio v1.1.419.

3. Results

3.1. Salinity

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

3.2. Species richness

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

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

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

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

3.3. Species responses

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

In MO, most species did not seem to be directly impacted by storm Xynthia (Fig. 5). More specifically, *Pelophylax* sp., *Hyla meridionalis*, *Pelodytes punctatus*, *Pelobates cultripes* and *Triturus marmoratus* showed stable trends over time (Fig. 5GHJ). Interestingly, the two urodele

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 |

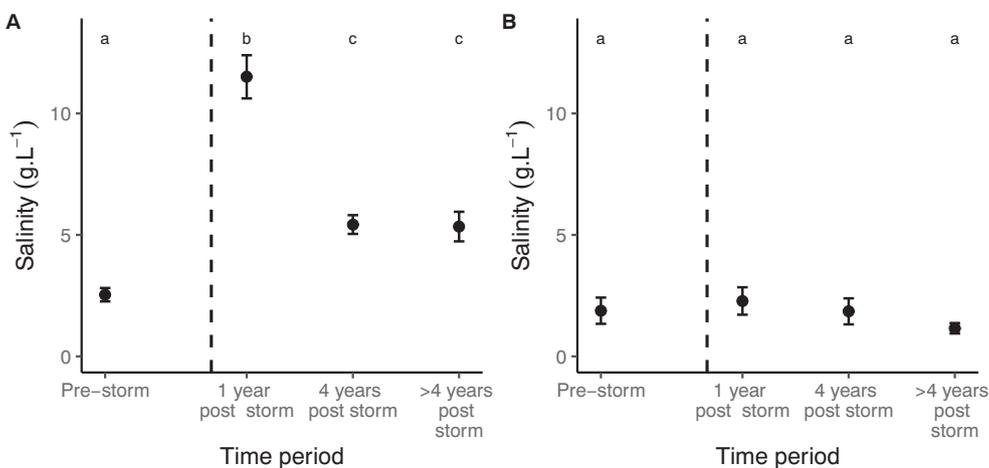


Fig. 3. Mean (\pm SE) salinity measured for the four time periods of our surveys at MY (A) and MO (B). The vertical dashed line represents the year of storm Xynthia (2010). Different letters represent a significant difference at $\alpha = 0.05$.

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 |

species displayed change over time, but these changes did not seem to be related to storm Xynthia (Fig. 5KL).

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

3.4. Environmental parameters influencing diversity

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

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

4. Discussion

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

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

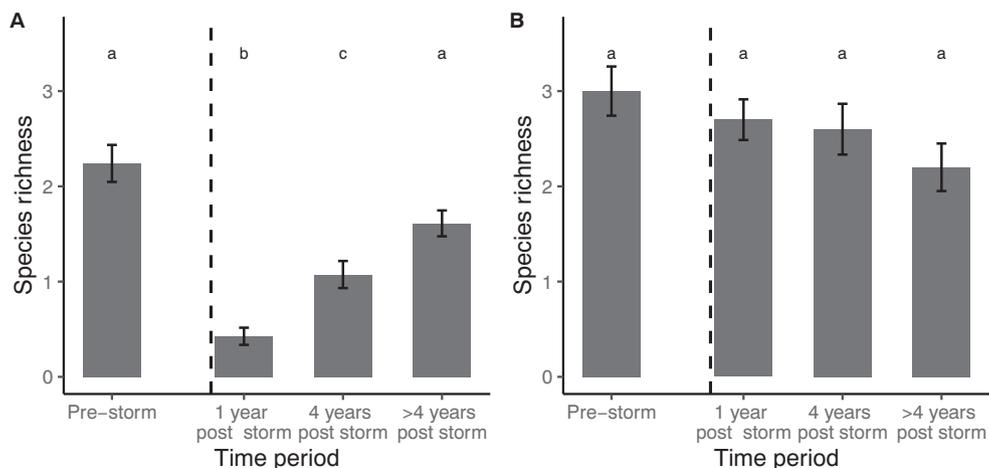


Fig. 4. Mean (\pm SE) amphibian diversity measured for the four time periods of our surveys at MY (A) and MO (B). The vertical dashed line represents the year of storm Xynthia (2010). Different letters represent a significant difference at $\alpha = 0.05$.

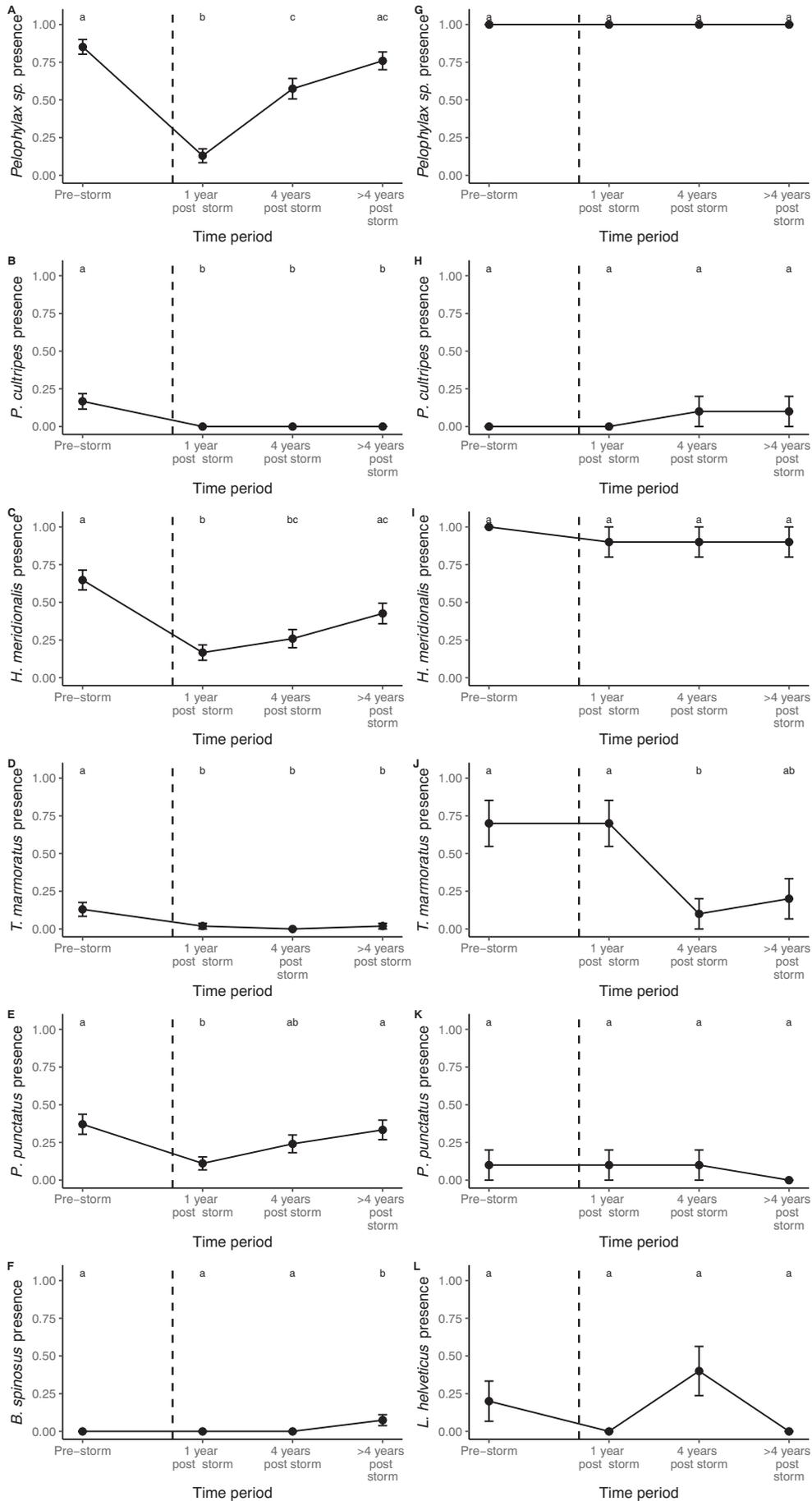


Table 3

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.

| Site | 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 |

low and similar to MO, the landward marine surge induced a massive increase in salinity, reaching a value of $\sim 11 \text{ g.l}^{-1}$ one year post-storm. These elevated salinity levels decreased post-storm (Fig. 3) but remained relatively high (5 g.l^{-1}) and did not decrease back to pre-storm conditions even 7 years post-storm. This result suggests potentially long-lasting influences of marine surges on coastal wetland salinity and contrasts with other studies showing rapid salinity decrease after storms (Frazer et al., 2006). Further studies are required in order to investigate the site-specific salinization dynamics linked to landward marine surges.

Similar to salinity, amphibian species richness responded differently at the two study sites. At MO, where the salinity of ponds remained low and constant, amphibian richness remained relatively constant across the study period for most species. Nevertheless, at this site, two urodele species displayed strong fluctuations over time (*T. marmoratus*, *L. helveticus*), but these fluctuations were not attributable to Xynthia, and may be linked to the increasing presence of non-native Louisiana crawfish, *Procambarus clarkii*, known to affect urodeles (Cruz et al., 2006). In addition, none of the pond characteristics we included in our analyses significantly explained the number of species observed, probably because most ponds are characterized by very similar features. In strong contrast, at MY, amphibian richness seems to have been affected by the change in salinity linked to Xynthia. Indeed, the mean number of species per pond showed a massive decrease following storm Xynthia, reaching the lowest values (~ 0.43 species per ponds) one year post-storm. Amphibian richness then progressively increased, attaining values similar to pre-storm conditions, 7 years after the storm. Importantly, salinity was a significant predictor of the number of species observed in ponds, suggesting that the increase in salinity due to storm Xynthia was responsible for the decrease in species richness found at MY. There are three different, but not mutually exclusive hypotheses to explain this result. First, the high salinities linked to storm Xynthia may have directly affected amphibians by inducing mortality of juvenile and adult individuals (Albecker and McCoy, 2017). Second, relatively high salinity values in breeding ponds may have inhibited the ability of surviving adults to reproduce (Albecker and McCoy, 2017). Third, reproduction may have occurred, but high salinity of breeding ponds may have induced direct mortality of developing embryos and/or larvae (Christy and Dickman, 2002; Kearney et al., 2014; Hopkins and Brodie, 2015). Indeed, some amphibian species are relatively tolerant to salinity and may be able to reproduce in brackish conditions (Hopkins et al., 2020). Yet, even in relatively salt-tolerant species, eggs and larvae have decreased survival linked to salinity (Natchev et al., 2011). These three hypotheses involve different processes with different consequences for population dynamics (e.g., affecting adult survival versus reproduction). Future studies should investigate the relative contributions of these different possible responses on the influence of marine submersions on coastal amphibian communities.

Despite the strong influence of storm Xynthia on amphibians at MY, some studies have highlighted that recovery can occur (Schriever et al., 2009; Gunzburger et al., 2010; Wang et al., 2016; Maxwell et al., 2019; Chen et al., 2020), and it is noteworthy in our study that the amphibian community did recover to pre-storm conditions 7 years after the submersion. Yet, different species diverged strongly in their ability to recover from the negative impact of storm Xynthia (Fig. 5). Most notably, three species were clear drivers of the increase in amphibian richness back to pre-storm conditions. These species were *Pelophylax* spp., *H. meridionalis* and *P. punctatus*, and have all been described as salt tolerant (Sillero and Ribeiro, 2010; Natchev et al., 2011; Thirion, 2014; Hopkins and Brodie, 2015). In our study sites, these species can be found in water bodies with markedly elevated salinities (i.e., maximum salinity of 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 contrast, two species were lost, or almost lost, after storm Xynthia (i.e., *P. cultripes*, *T. marmoratus*). *T. marmoratus* is a newt, that is characterized by comparatively lower mobility (Wells, 2007). Such a trait may have prevented adult individuals from evading detrimental conditions during storm Xynthia, or may have impeded other individuals from less impacted nearby areas to recolonize our study sites in MY. The reasons for the disappearance of *P. cultripes* are less clear, because this species is known to be relatively tolerant to salinity (Stănescu et al., 2013; Thirion, 2014). Because *P. cultripes* is a burying species which shelters in sandy soils, it is possible that sheltered individuals may have died during the submersion. Finally, it is noteworthy that a new species, the Spined toad (*Bufo spinosus*), appeared for the first time more than 4 years after submersion, highlighting that the colonization of some individuals from new species can occur following environmental perturbations (pattern also shown in Gunzburger et al. (2010), were some species are only present in overwashed wetlands post-storm).

These different species-specific responses highlight that, although amphibian richness could recover to that of pre-storm conditions, the composition of the community can change (Marroquín-Páramo et al., 2020; Stockwell et al., 2020), with one third of the species being lost at MY after Xynthia. Interestingly, because several pond characteristics were shown to be positively related to amphibian diversity (e.g., pond type, aquatic vegetation), it is likely that such features may positively influence either species resilience to environmental perturbations (Bernhardt-Römermann et al., 2011; Suazo-Ortuño et al., 2018; Marroquín-Páramo et al., 2020) or to favor recolonization from nearby and less impacted sites [i.e. shelters (Walsh, 1983)]. This may be the case for *P. cultripes*, which appeared in MO post-storm, while it was the first to disappear in MY, suggesting that MO could be one of these shelters for surrounding sites. Future studies should investigate the interactions between salt-tolerance and ecological characteristics (e.g., micro-habitat use, mobility) in order to understand the drivers of the species-specific responses that we have highlighted.

5. Conclusions

Our study is, to our knowledge, the first multi-species long term survey of the consequences of marine submersion induced salinization on coastal amphibians (but see Gunzburger et al. (2010)). Most notably, we highlight that the presence of amphibians in coastal wetlands post-submersion results from an interaction between species-specific traits (tolerance to elevated salinity, ecology) and site-specific characteristics (topography). This latter category is especially interesting to take into account at a time when the frequency and intensity of extreme weather events, such as marine submersion, are expected to increase (Dettinger, 2011). Habitats management can promote adaptation to

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

extreme climatic events (Maxwell et al., 2019) and, in this respect, our study shows that relatively modest landscaping management (i.e., the creation of additional barriers similar to the small sand dune found at MO) may be critical to allow amphibians to successfully recover after a marine submersion, either by providing a barrier to marine surge and/or by increasing the surface area of land that remains unsubmerged, providing an elevated refuge. Clearly, it is plausible that such a refuge may also provide protection for other wildlife susceptible to marine submersion and may, thus, offer a cost-effective solution to buffer the detrimental consequences of marine submersion on coastal wetlands.

CRedit authorship contribution statement

FB & FR: Conceptualization; PR & MJ: Data collection; FR: Data curation; LLS, FR, FB: Formal analysis; FR & FB: Funding acquisition; LLS, FB, FR: Writing - original draft; LLS, FB, FR, PR & MJ: Writing - review & editing. All authors have reviewed and edited the manuscript and approved the final version.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

Data will be made available upon reasonable request.

Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.145382>.

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