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1 **The interactive effects of salt and heat on coastal ectotherms**

2 Léa Lorrain-Soligon^{1,2#}, François Brischoux^{1*}, Julien Pétillon^{3,4*}

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4
5 **Institutional affiliations**

6 ¹ Centre d'Etudes Biologiques de Chizé, CEBC UMR 7372 CNRS - La Rochelle Université, 79360

7 Villiers en Bois, France

8 ² UMR 7619 METIS, Sorbonne Université- CNRS-EPHE, Paris, France

9 ³ UMR CNRS 6553 ECOBIO, Université de Rennes, Rennes, France.

10 ⁴ Institute for Coastal and Marine Research, Nelson Mandela University, Port Elizabeth, South Africa.

11
12 LLS: ORCID: 0000-0002-8723-7478; twitter: @LSoligon

13 FB: ORCID: 0000-0002-5788-1326; twitter: @Ecophy_CEBC

14 JP: ORCID: 0000-0002-7611-5133; twitter: @ECOBIO_Rennes

15
16 **#Correspondence:** llorrain.lea@gmail.com

17 ID ORCID: 0000-0002-8723-7478

18 Full postal address : Sorbonne Université, UMR 7619 METIS EPHE/SU/CNRS, 4 place

19 Jussieu 75252 PARIS

20
21
22 ***both authors contributed equally and should be considered co-last authors.**

23

24 **Abstract**

25 Coastal ecosystems face salinization and rising temperatures. In coastal ectotherms,
26 salinity and temperature affect metabolism, tolerance, infections, growth, behavior
27 and survival. Overall, the combined effects of salinity and temperature on species
28 distribution, community structure, invasive species and ecosystem functioning need
29 to be fully assessed to understand impacts from these stressors.

30 **Key-words:** Life History Traits, Salinization, Survival, Warming

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33

34 **Coastal ecosystems and global changes**

35 Located at the boundary between terrestrial and oceanic environments, coastal
36 habitats (both terrestrial and aquatic, influenced by their proximity to the sea) are
37 considered to be keystone habitats playing major roles at the global scale [1].
38 However, being at the interface between the land and the sea, and being exposed to
39 human pressure due to coastal urbanization, create specific risks, and coastal
40 environments are affected by a wide variety of interacting global changes, among
41 which increasing salinity (salinization) and increasing temperatures (global
42 warming) appear to be of main importance [1] (Box 1).

43

44 **Why do temperature and salinity matter in coastal areas?**

45 Temperatures are predicted to rapidly increase along with the frequency, duration,
46 and intensity of extreme thermal events. Importantly, environmental temperature
47 can critically influence the physiological processes of ectothermic organisms [2] (Box
48 1).

49

50 Concomitantly, salinization – an overlooked consequence of global change – is
51 currently occurring at unprecedented rates worldwide [3], due to primary (linked to
52 natural processes, e.g. sea-spray) or secondary (linked to the consequences of human
53 activity, either direct [e.g. freshwater pumping] or indirect [e.g. sea-level rise])
54 processes (Figure 1). Salinization can induce strong physiological costs and
55 ultimately provoke mortality [4]. Salt-sensitive species display a narrow peak within
56 their optimal low salinity range [5]. On the contrary, salt-tolerant and eurhaline

57 species (i.e. those adapted to variable salt concentrations) typically have a broader
58 curve, with lower survival at low and high salinities [5] (Box 1).

59

60 Notably, both salinity and temperature are expected to strongly interact,
61 exerting significant abiotic pressures on coastal ecosystems. Higher temperatures and
62 the increased frequency, duration, and intensity of extreme thermal events are
63 anticipated to disrupt the balance between evaporation and precipitation, thereby
64 intensifying salinization. This phenomenon is particularly relevant in coastal systems
65 already characterized by pronounced spatio-temporal heterogeneity of salinity [5].
66 Elevated salinity levels, exacerbated by rising temperatures, can directly affect the
67 physiology, behavior, and the distribution of many coastal species. Indirectly, these
68 changes can impact key habitat features and have cascading effects throughout
69 ecosystem-level processes.

70

71 **Interactions between temperature and salinity are largely overlooked in coastal** 72 **ectotherms**

73 Terrestrial ectothermic organisms are particularly interesting in this context because
74 of their strong dependency on thermal and hydric conditions which affect individual
75 performance. They are often small-sized, increasing the surface of exchange with the
76 external environment (e.g., salt and water fluxes). As temperatures rise, these
77 organisms must adjust their metabolic rates, behaviors, and physiological functions
78 to cope with warmer conditions, while increased temperatures can also exacerbate
79 dehydration, especially in habitats where freshwater availability is limited. Second,

80 increases in salt content affect osmoregulation, leading to altered hydration and
81 electrolyte levels.

82

83 Importantly, some species use diverse (micro-)habitat types according to their
84 life stage, and can encompass both terrestrial and aquatic habitats (e.g. arthropods,
85 reptiles and particularly amphibians), thus being subjected to constraints on both
86 habitat types. These particular groups are abundant and diversified in coastal
87 habitats, and encompass a diversity of trophic levels and phylogenetic lineages,
88 including both invertebrate and vertebrate species.

89

90 Given the responses found in ectotherms, it is expected that the performance
91 of coastal ectotherms should peak at intermediate temperatures and decreases at
92 both extremes [2]. In contrast, responses to increasing salinity are species-specific [4]
93 (Figure 1). Interestingly, the effects of these two stressors are rarely examined
94 together. Here we particularly focused on coastal wetlands *sensu lato* (i.e., including
95 both terrestrial and aquatic habitats that are directly influenced by their proximity to
96 the sea). These habitats include a continuum between intertidal sandy areas,
97 mudflats and seagrass beds; through salt and freshwater marshes or swamps; along
98 with increasing distance from the sea. We specifically searched studies investigating
99 combined effects of temperature and salinity in the main groups of terrestrial
100 ectotherms inhabiting these habitats. This investigation encompassed reptiles
101 (squamates, either terrestrial, semi-aquatic or aquatic; crocodylians, semi-aquatic, and
102 chelonians, either terrestrial or semi-aquatic), amphibians (anurans, caudates, and

103 gymnophiones, most of which have an aquatic larval stage and a terrestrial or semi-
104 aquatic adult stage) and terrestrial arthropods.

105 The only study we found investigating the interactive effects of temperature
106 and salinity in coastal reptiles considered physiological and metabolic parameters in
107 the estuarine diamondback terrapin (*Malaclemys terrapin*) which typically live in
108 coastal marshes, tidal creeks and estuaries along the East coast of the USA [6]. This
109 study found few interactions between these two parameters, with stronger effects of
110 temperature on metabolism than salinity [6]. There was more information available
111 in amphibians. Elevated temperature combined with increased salinity has been
112 linked to higher infection and pathogen risk, higher developmental deformities,
113 lower survival, and changes in larval development duration, growth rate, and
114 behavior [7,8] (Figure 1). The interaction induces complex responses, with higher
115 temperature increasing susceptibility to salinity while higher salinity influences
116 thermal tolerance [9]. This pattern was also demonstrated to occur in an insect
117 species (the invasive ground beetle, *Merizodus soledadinus*), for which, although
118 similar metabolic fingerprints can be expected in response to saline and thermal
119 stress, the expression of a heat shock protein decreased with increasing salinity [10].
120 However, in an amphibian species living in an arid environment (the Warty Toad,
121 *Rhinella spinulosa*, from Monte Desert, Argentina), elevated salinities increase heat
122 and cold tolerance [11], showing an inverse effect according to the typology of
123 Jackson et al. [12]. While it seems likely that the resistance to extreme temperatures
124 is a trait shared by many amphibians (particularly in tropical or desert regions), the
125 physiological adaptations of salinity tolerance are scarcer and probably slower to

126 respond. This could be due to the multifaceted challenges of adapting to salinity,
127 involving evolutionary history, physiological constraints, energy costs, and genetic
128 limitations. Importantly, while there are more studies examining these effects in
129 amphibians than in arthropods and reptiles, only amphibian larvae and
130 metamorphic individuals have been considered so far, highlighting the need to
131 consider other life stages.

132

133 More generally, it appears that the temperature*salinity interaction has been
134 solely tested in a handful of coastal ectotherms (mostly amphibians), while other taxa
135 remain understudied. Such taxonomic bias in research effort precludes to propose
136 global patterns to the temperature*salinity interaction. Yet, understanding how these
137 stressors interact is crucial for predicting how a wide diversity of organisms might
138 respond to environmental pressures.

139

140 **Large scale effects and perspectives**

141 Tolerance to high temperatures declines under stressful conditions, or when
142 individuals are subjected to other extremes environmental conditions, which could
143 include increased salinity [13]. Facing global warming, ectotherms are expected to
144 suffer a “metabolic meltdown”, linked to reduced activity, reduced energy intake
145 and accelerating metabolic costs at high temperatures [2]. Indeed, heat stress
146 increases energy requirements while impairing the ability to efficiently acquire
147 resources [13]. This metabolic meltdown can lead to altered predator-prey
148 relationships, shifts in species composition, and alterations in ecosystem processes
149 such as nutrient cycling. Additionally, salinity decreases food availability due to

150 reduced diversity in salinized habitats [3], and reduced activity [11]. As such, salinity
151 can reduce energy acquisition which could result in lowered optimal temperatures
152 and upper thermal limits [2]. All these responses can lead to reduced thermal
153 tolerance, but also to reduced tolerance to salinity, as exemplified in amphibians
154 (e.g., the Asian common toad [*Duttaphrynus melanostictus*], the Indian cricket frog
155 [*Fejervarya limnocharis*] and the East Asian ornate chorus frog [*Microhyla fissipes*]) [9].
156 There is, however, contrasting evidence with another amphibian species (*Rhinella*
157 *spinulosa*, living in an arid environment) showing higher temperature tolerance
158 under higher salinity [11], suggesting potential adaptive processes. Moreover, an
159 increase in temperature could potentially lead to decreased salinity tolerance; this
160 has not been tested in neither arthropods, amphibians nor reptiles to our knowledge.

161

162 The interactions between environmental stressors could be more prominent at
163 the limits of tolerance of organisms. For example, in the rough-skinned newt (*Taricha*
164 *granulosa*) the impacts of salinity were greater at temperature extremes (both low and
165 high), leading to decreased survival, delayed hatching, reduced length, and an
166 increased occurrence of developmental deformities [8]. This emphasizes the need to
167 consider not only the increase in temperature or salinity but, and perhaps more
168 especially, the impact of their extremes (both low and high temperature and salinity
169 outside the optimal range of the species) [2,8] (Figure 1).

170

171 If species are expected to migrate towards cooler regions when confronted to
172 increased temperatures, species experiencing higher salinity levels could survive by

173 migrating towards moderate or low salinity environments [13]. However, these types
174 of environments are not necessarily available for coastal populations for which
175 anthropogenic infrastructures can impede landward migration and human
176 development can reduce the presence of suitable habitats. In addition, the increase in
177 these two parameters are predicted to favor the invasion of alien species, [3,14] as
178 invasive species often have broader tolerance ranges and higher adaptability to
179 changing conditions compared to native species. As a result, the combined increases
180 in temperature and salinity can either physiologically benefit invasive species, or
181 create conditions that are more favorable for them, allowing them to outcompete and
182 displace native species.

183

184 Global warming and salinization can alter ecosystem dynamics, impacting not
185 only ectotherms but also the wider community. Shifts in species distributions,
186 changes in community composition, and disruptions to trophic interactions are all
187 possible consequences of these environmental stressors. Differences in sensitivity
188 might be species- as well as taxon-dependent (e.g. aquatic vs terrestrial
189 development), but also dependent on species plasticity and/or adaptability. For
190 instance, facing salinization and increased evaporation, species inhabiting freshwater
191 ponds may experience more dramatic shifts than euryhaline species adapted to
192 variable salinity in coastal lagoons. Yet, to our knowledge, sensitivity and
193 susceptibility to increased salinity has mainly been investigated in aquatic habitats
194 while such changes are also expected to occur in terrestrial habitats [15].
195 Additionally, depending on their habitat (i.e., terrestrial, aquatic or both),

196 ectothermic coastal species might display different salinity and temperature
197 tolerance. The effects of these changes need to be investigated. Investigating the
198 effects of combined salt and heat will allow us to understand how these patterns
199 impact understudied, keystone species, such as predatory arthropods and reptiles,
200 but also adult life stages in amphibians, which remain overlooked in salinization
201 studies. Future studies will need to consider both direct and indirect effects of
202 temperature and salinity changes. This includes a thorough examination of the
203 adaptive responses of coastal ectotherms, with a particular focus on those that are
204 especially sensitive to environmental changes. Overall, this interaction also needs to
205 be investigated on other ecosystems (e.g. high mountain streams, inland lakes),
206 where patterns of salinization and global warming are also expected to occur as a
207 result of similar processes, linked to human impacts (e.g. road deicing salts and
208 global warming) or natural processes (e.g. seasonal variations and patterns of
209 evaporation).

210

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250

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256

257 *Competing interest statement*

258 The authors declare no competing interests.

259

260 *Author contributions statement*

261 LLS, FB and JP conceived the ideas; all authors have participated in writing the
262 manuscript, they all contributed critically to the drafts and gave final approval for
263 publication. FB and JP contributed equally and should both be considered as co-last
264 authors.

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269

270

271

272 Box 1 – Variation of salinity and temperature on coastal ecosystems

273 Primary (linked to natural processes) and secondary (linked to the consequences of

274 human activity) salinization can be exacerbated by increasing temperatures and

275 drought, marine submersions and sea-water intrusions, sea-level rise, abstraction of

276 underground freshwater, and anthropogenic alteration of hydrological cycles [1,4]

277 (Figure I). In coastal areas, there is significant co-variation of salinity and

278 temperature. We expect that coastal ectotherms will show distinct performance

279 responses to increasing temperature or increasing salinity. These responses are

280 expected to vary according to the sensitivity of the species (thermal generalist or

281 thermal specialist, salt-sensitive or salt-tolerant) (Figure I). However, the combined

282 effects of both increasing temperature and salinity on these organisms are not well

283 understood, highlighting the need for theoretical or experimental studies predicting

284 performance variations to these combined constraints. Such studies should consider

285 the species-specific sensitivities and the potential for additive synergistic,

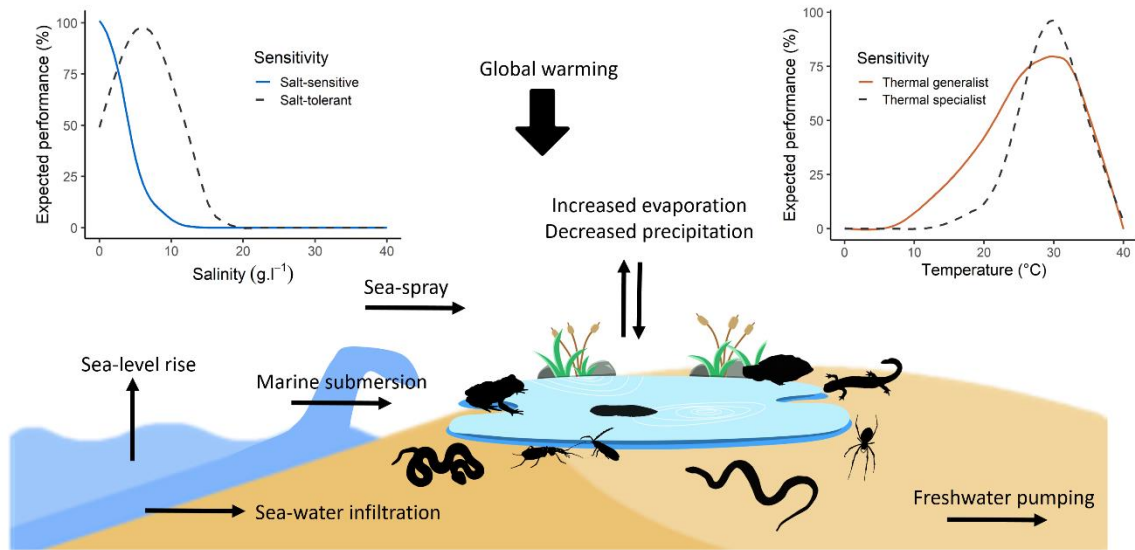
286 antagonistic, effects of temperature and salinity. Understanding these dynamics is

287 crucial for predicting the resilience of coastal ectotherms to changing environmental

288 conditions driven by various processes linked to climate change and anthropogenic

289 activities.

290

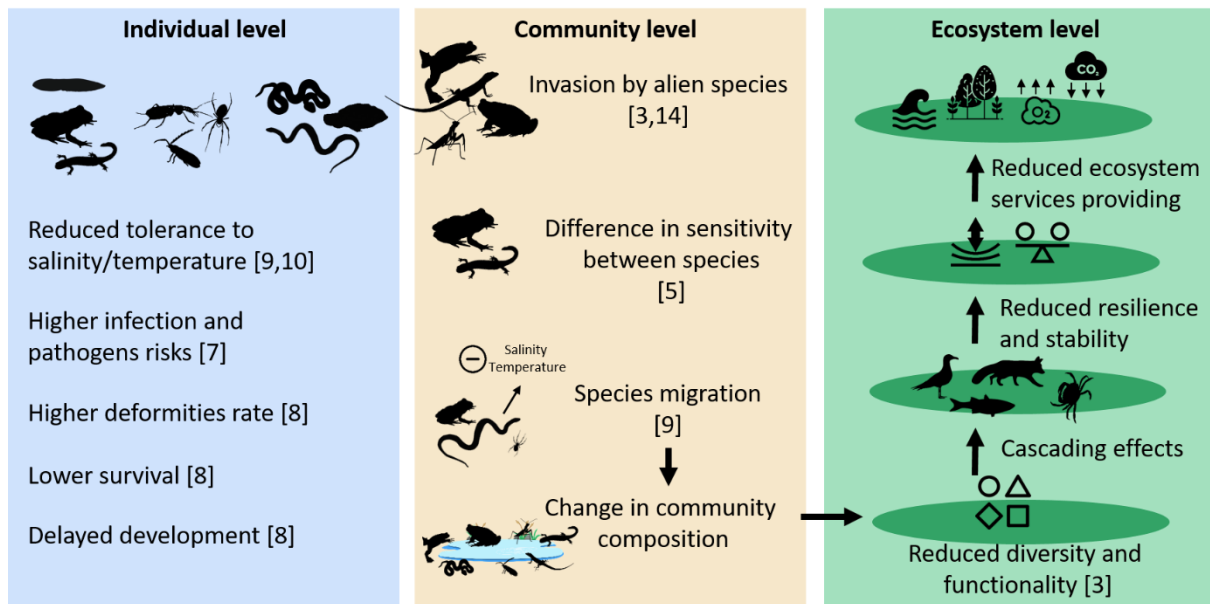


291

292 Figure I: Causes of salinization and increased temperature in coastal ecosystems (a
 293 continuum between intertidal sandy area, mudflats and seagrass beds; through salt
 294 and freshwater marshes or swamps), as well as expected responses of ectotherms
 295 (represented here by arthropods, reptiles and amphibians) to temperature (for
 296 thermal generalists or specialists) or salinity (for salt-tolerant or salt-sensitive
 297 species).

298

299 Figure 1 - Expected individual, community and ecosystem levels influences of
 300 salinization and global warming on coastal ectotherms.



301