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Hypoxia from depth shocks shallow tropical reef animals

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ABSTRACT

Coastal deoxygenation is poorly documented in the tropics. When the Isthmus of Panama separated the Caribbean from the Pacific, sister lineages diverged and adapted to changing oxy-thermal conditions along both coasts. This provides unique insight into the ecological consequences of ocean warming and deoxygenation. We find deoxygenated, or hypoxic, waters shoal to the shallow depths of 10 m on both sides of the Isthmus, with Caribbean waters generally warmer than those in the Pacific. We tested the performance of two Caribbean *Echinometra* sea urchin species and their Pacific sister species under different warming and oxygen scenarios. Performance, measured as righting ability, was reduced by 50–100% under hypoxia compared to normoxia in one species from each coast. Only one Caribbean species performed well under hypoxia and did so at ambient temperatures (≤ 29 °C) but not under warming. This tolerant species, *E. viridis,* appears to be specialized for living on protected Caribbean reefs, unlike its two sister species that occur on well-oxygenated reefs. Our results emphasize the danger of shoaling hypoxia compressing well-oxygenated habitat from beneath and the importance of evolved hypoxia tolerance. This highlights the underappreciated risk deoxygenation poses for shallow tropical ecosystems.

1. Introduction

When the Isthmus of Panama formed three million years ago (Mya), two distinct marine environments emerged as the Caribbean Sea was separated from the Tropical Eastern Pacific (TEP) [1]. The TEP remained nutrient rich but as waters began upwelling, it became more variable in time and space with respect to nutrients, temperature and salinity [2, 3].

In the Caribbean (CAR), waters became nutrient limited, more saline, warmer and relatively stable. Marine animals that were not driven to extinction either adapted to the novel warm, well-oxygenated, low nutrient conditions in the CAR [4], or the increased variability in temperature and nutrients associated with strong seasonal upwelling in the TEP [2, 5]. This history could impact how Neotropical reef animals respond to the novel stresses presented by rapid global change, especially by the threat of ocean deoxygenation (i.e., hypoxia), defined here as dissolved oxygen (DO) concentrations < 2 mg/L.

In the Pacific, upwelling of cold deoxygenated water is intensifying due to climate change [6], and the amount of oxygen in these upwelled waters is also decreasing [7], leading to devastating results in some locations [8, 9]. The Pacific oxygen minimum zone (OMZ) has expanded during the last 50 years, especially in the tropics where oxygen has declined faster than anywhere else in the world, accounting for over a fifth of total global ocean oxygen loss [7, 10]. Despite knowledge of these open-ocean oxygen conditions and the gravity of potential ecological impacts [8, 9], there is little documentation of how this cold, oxygen-poor, upwelled water affects coastal ecosystems in the TEP. In contrast, coastal hypoxia in the Caribbean is primarily driven by warming, stratification, and anthropogenic nutrient loading [11]. A number of dead zones and mass mortalities have resulted from hypoxic water shoaling in shallow eutrophic coastal areas [12-15]. These events have been most severe in protected locations during warm periods.

It is necessary to determine and document baseline conditions in these systems to contextualize extreme events and future changes [16] as temperatures are rapidly increasing [17] and hypoxia becomes more prevalent [18, 19]. Both coasts experience hypoxia on seasonal timescales, either associated with the cold, upwelling season in the TEP or the warm season in the Caribbean [20, 21], but virtually no information is available on how coastal Neotropical marine invertebrates respond to these stressors. Studies from other regions show that regardless of the source of deoxygenated waters, the impacts of low oxygen on benthic marine organisms are often detrimental [22]. Examples from sea urchins show that this is true on timescales as short as two hours [23]. For example, short-term hypoxia can limit the ability of some sea urchins to graze for food [24] or to right themselves, a common proxy for overall health and performance [23]. The addition of short-term temperature stress to hypoxic stress is likely to result in further synergistic, negative effects on growth, performance and survival [25, 26].

When the Isthmus of Panama formed, species were geographically divided, resulting in sister lineages on either side of the Isthmus that have been on independent evolutionary trajectories [27]. One such case

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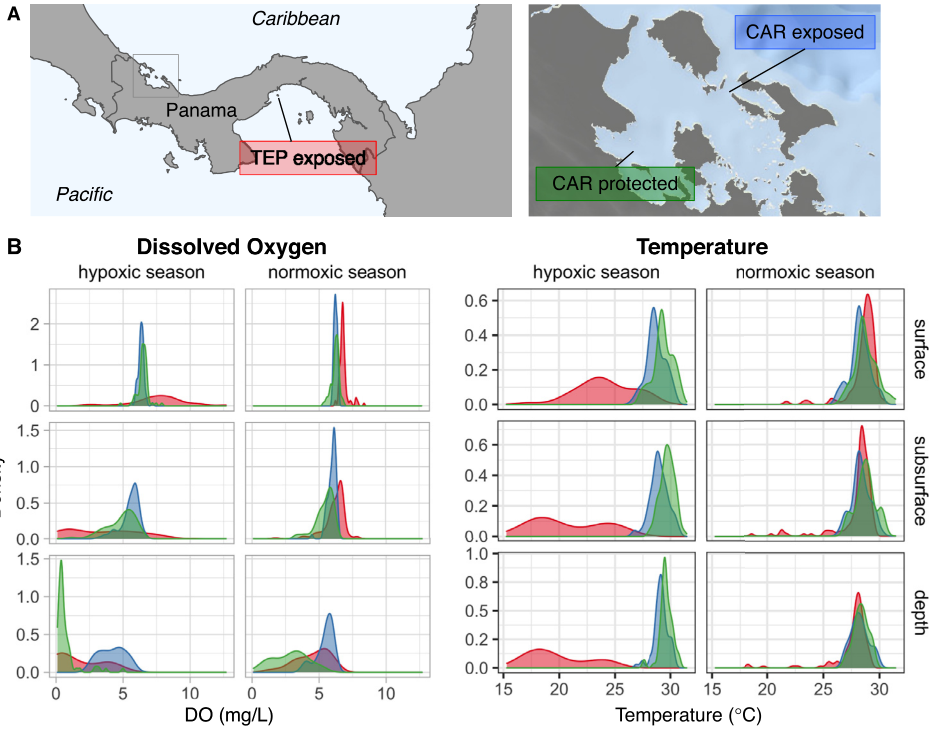

Fig. 1. Location of monitoring sites (A), and density plots of DO and temperature (B), measured weekly over 3 years at each site, during both the hypoxic and normoxic season at the surface (~1 m), subsurface (~10 m), and seafloor (~20 m).

occurs in *Echinometra,* a genus of tropical herbivorous sea urchins, in which a common ancestor diverged into three species: *Echinometra vanbrunti* in the TEP, and *Echinometra lucunter* and *Echinomentra viridis* both in the Caribbean (Fig. 1a) [27, 28]. The three species are significant herbivores on shallow Neotropical reefs between the surface and 45 m [29, 30], and their excavation of hard substrates makes them important ecosystem-engineers [31–33]. We document the environmental conditions experienced by these three *Echinometra* species and determine their tolerances to warming and deoxygenation under current and future conditions. We expect the Pacific species, *E. vanbrunti,* to be more susceptible to warming when combined with hypoxia because hypoxia occurs at the coolest temperatures in the TEP. We also expect both Caribbean species to be more tolerant to hot, hypoxic conditions that they may naturally experience in their habitats.

2. Materials & methods

2.1. Environmental conditions

Weekly depth profiles of temperature and dissolved oxygen (DO mg/L) were measured from July 2017 to March 2020 at three sites: one in the TEP near an exposed reef that experiences seasonal upwelling (TEP-exposed, Taboguilla Island), one near an exposed Caribbean reef (CAR-exposed; Hospital Point), and the last in a large, semi-enclosed bay (CAR-protected; Almirante Reef; STRI Physical Monitoring Program, Fig. 1). To determine the conditions at the surface, subsurface, and near the seafloor, measurements were taken with an YSI multiparameter sonde (EXO2 & EXO optical DO, accuracy ± 0.1 mg/L; pH Smart Sensors, accuracy 0.02 units; and Temperature Sensors, accuracy ± 0.01 C, Yellow Springs, USA) at 1, 10 and 20 ± 5 m respectively. These sensors were calibrated monthly following the manufacturer's instructions.

2.2. Experimental trials

Sea urchins were collected from the exposed CAR and TEP sites to test their righting performance and survival under different oxygen and temperature treatments. *E. viridis* (n = 131) and *E. lucunter* (n = 121) were collected from 0 to 3 m on March-April 2019 prior to the onset of the hypoxic season, and *E. vanbrunti* (n = 149) was collected from 0 to 10 m in November 2019 prior to the onset of upwelling so that all were field-acclimated to similar temperatures (~29 °C) and all incurred minimal hypoxia stress prior to the experiment. Experiments were run outside of all three species' spawning periods to minimize any reproductive effects [34]. All animals recovered from potential collection stress in 400 L flow-through holding tanks at 29 °C in the laboratory while awaiting trials. Animals were kept in three holding tanks for an average of three days (± 1.9 SD), and never more than seven days. Experiments on the CAR species took place at the Bocas del Toro Research Station on the Caribbean coast, while those on the TEP species took place at the Naos Marine Laboratory on the Pacific coast of Panama.

For each experimental trial, three individuals were taken from the holding tank and placed in a 4 L trial tank inside a heat bath and brought from the normoxic ambient temperatures in their holding tank to one of the fully factorial combinations of the following temperatures and oxygen concentrations over 15 min: 26, 29, 32, or 35 ± 0.1 °C with either normoxia (6.0 ± 0.12 mg/L bubbled with air) or hypoxia (1.4 ± 0.05 mg/L bubbled with nitrogen). Animals were kept in these treatments for two hours and water conditions were monitored every 15 min in each tank (Thermo Scientific Orion Star A320 optical DO probe; accuracy ± 0.1 mg/L, Omega high precision thermocouple; ± 0.05% reading accuracy). Following the two hour exposure, animals were gently turned upside-down and their ability to right within a 10 min period was recorded [23, 35-37]. Righting response is commonly used to assess the impacts of temperature on echinoderm performance and reflects coordinated sensory and locomotory functions [38-40]. After the trial, animals were placed in fully oxygenated recovery aquaria at ambient temperature (29 °C) to assess survival 24 h post-trial [24]. Each trial included three or four animals in one tank (i.e. 'replicates'). Between five and eight trials were performed for each treatment – at different times (i.e., sequentially). Trials of different treatments were performed on the same day so that the treatments were evenly distributed throughout the course of the experiments, accounting for potential variation between date of collection and holding times the animals experienced. An average of 17 animals (range 12–22) were exposed to each

Table 1
Minimum, median and maximum measured temperatures and DO concentrations at each site, grouped by hypoxic season.

		Tropical Eastern Pacific			Caribbean (protected)			Caribbean (exposed)		
Temperature (°C)										
	Depth (m)	min	med	max	min	med	max	min	med	max
	1	17.3	24.0	28.4	27.3	29.2	30.9	26.6	28.6	30.3
Hypoxic season	10	15.4	19.9	26.4	28.1	29.7	31.2	26.7	28.9	30.7
	20	15.3	19.2	24.7	27.6	29.6	30.8	26.9	29.2	30.4
	1	21.7	28.9	30.5	26.7	28.6	31.4	26.2	28.2	30.2
Normoxic season	10	18.6	28.4	29.6	27.0	28.8	30.5	26.4	28.2	30.3
	20	18.3	28	29.2	26.8	28.3	29.6	26.8	28.2	29.8
DO (mg/L)										
		min	med	max	min	med	max	min	med	max
	1	2.4	7.7	12.7	4.8	6.5	7.9	5.6	6.4	7.2
Hypoxic season	10	0.1	3.6	8.1	1.1	5.1	6.3	3.2	5.7	6.7
	20	0.1	1.3	5.3	0.1	0.4	5.0	2.4	4.2	6.0
	1	6.2	6.8	8.3	5.3	6.3	6.8	6.0	6.2	6.5
Normoxic season	10	1.6	6.3	8.0	3.2	5.6	6.2	4.5	6.0	6.5
	20	1.0	4.8	6.6	0.2	3.0	5.2	3.6	5.6	6.4

treatment. Test diameter did not differ significantly across the treatments for any of the three species (3.0 cm ± 0.8, mean ± SD).

Data were analysed and visualized with R v.3.6.2 [41]. To determine how temperature and oxygen impacted righting performance and survival, and if the species differed in their responses, we used fully factorial combinations of species identity, temperature, and oxygen level, with binomial Generalized Linear Mixed Models (GLMM) and the R Package *lme4* [42]. Trials were included as random effects nested inside the experimental treatments. However, for the analysis of survival, we used a Generalized Linear Model (GLM) without this nesting after the more complex GLMM failed to converge [43]. We used backward stepwise selection of fixed effects to identify the best model to explain the data without over-parameterization (R package*: Statistical Models*).

3. Results & discussion

Hypoxia rising from depth poses a particularly insidious threat to reefs. During this study hypoxia did not reach the surface waters at any of the three sites but it did shoal to 10–20 m at all sites. At just 10 m, a depth usually characterized by rich coral reefs in tropical locations, minimum DO concentrations reached extreme lows of 0.1 mg/L in the TEP, while in the CAR-protected site they were 1.1 mg/L (Table 1). The CAR-exposed site was the most oxygenated site with no DO concentrations below 2 mg/L. However, declines to 2.4 mg/L did occur at 20 m. While this is slightly above the conventional definition of hypoxia (2 mg/L), it should be noted that a global synthesis found about half of the benthic organisms tested have sublethal and lethal DO thresholds above 2 mg/L [44]. In the TEP, hypoxic conditions generally occurred with seasonally cool temperatures during the upwelling season between February and April (max: 26.4 °C) [21]. In both CAR sites, seasonally warm conditions occurred between July and January (max: 31.2 °C) [20]. Hypoxia was always more severe at the CAR-protected site compared to the CAR-exposed site, and temperatures were also generally 0.5 °C higher at the CAR-protected site (Fig. 1; Table 1). The frequency of hypoxia increased with depth. At 1, 10, 20 m depths, hypoxia occurred on 0%, 2%, 70% of the sampled days in the CAR-protected site and on 0%, 11%, 19% of the sampled days in the TEP site.

Infrequent acute *in situ* hypoxic conditions are simulated in our experiments. We subjected the benthic, reef dwelling sea urchins to a one-time exposure for just two hours. Previous work has shown that the diel cycle in DO creates a 2–3-hour window of particularly low DO every night in tropical shallow waters which was modelled by our short exposures [23, 45]. Our monitoring data from daytime measurements overestimates the minimum DO concentrations. Despite these known overestimations, we used measured values to parameterize the temperatures and DO concentrations in the experiments. We found clear evidence that hypoxia exposure, even at cool temperatures, has important negative impacts on righting success, a proxy for organismal performance. Sea urchins were more likely to right under normoxia than hypoxia ($p < 0.001$; Fig. 2), and at cooler rather than warmer temperatures ($p < 0.001$; Fig. 2). Under hypoxia, both *E. lucunter* (CAR) and *E. vanbrunti* (TEP) failed to right more than 50% of the time at 29 °C, a temperature commonly experienced at our sampling sites (Fig. 2; Table 1). The Caribbean species, *E. viridis,* was most likely to successfully right compared to the other two species, which did not differ from each other ($p < 0.001$, Fig. 2). This righting response reflects the neuromuscular coordination necessary for animals to remain securely attached to the substrate, to right and reattach if dislodged, and to actively forage [38–40]. Therefore the reduction in righting performance of *E. lucunter* (CAR) and *E. vanbrunti* (TEP) is likely to have real life fitness impacts, curtailing foraging which frequently occurs at night [46] when DO is lowest and reducing the ability to withstand dislodgement by predators.

Contrary to our prediction that both Caribbean species would be tolerant to hotter, hypoxic conditions, results show significant differences between these two species. *Echinometra lucunter* performed poorly under hypoxia, while *E. viridis* maintained a 75–100% success rate at temperatures up to 32 °C. The better performance of *E. viridis* under hypoxia appears to allow this species to utilize warm lagoonal habitats, which are not occupied by the less tolerant *E. lucunter. Echinometra lucunter* is primarily found on well oxygenated windward reefs like the CAR-exposed site, while *E. viridis* is most abundant on calm leeward reefs and protected habitats similar to the CAR-protected site [33, 47, 48]. Hypoxia appears to be the most important physiological determinant of this niche differentiation between the two species, as they have similar warming tolerances under normoxia [37] and in a previous experiment we failed to find any negative impacts of reduced pH on *E. lucunter* [23].

Projected ocean warming and deoxygenation suggest that *E. lucunter* is at risk of extirpation from sites in the center of its range, as conditions may exceed the tolerance of this more sensitive CAR species. *Echinometra viridis*, on the other hand, appears to be in little danger of decline. Although healthy herbivore populations are vital for coral reef health, an overabundance of herbivores may damage corals, particularly those that are already stressed from warm, high nutrient waters, and thriving macro-algae [49–51]. *Echinometra viridis* has recently been recognized for having some of the highest densities of sea urchins on Caribbean reefs, particularly on disturbed reefs [33, 47, 48] and it may become the dominant invertebrate grazer on such reefs [48]. In support of this possibility, we found large sections of shallow degraded *Porites* reefs near the CAR-protected site covered by *E. viridis* barrens during the course of this study (Fig. 2c). As *Echinometra* species are also important bioeroders [31, 32], such high densities at hypoxic sites, which also generally have low pH [23, 52], may further promote loss of the reef matrix [53].

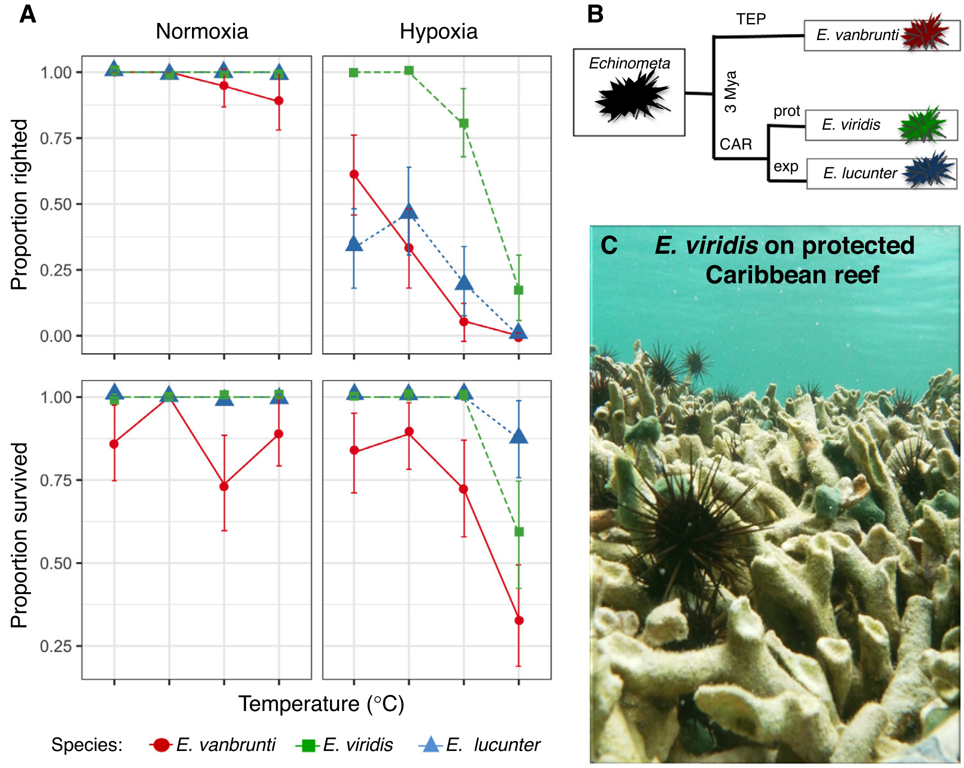

Fig. 2. Righting performance and survival (A) of each species after 2 hour experimental exposures combined with the phylogeny of Panamanian *Echinometra,* modified from [28], (B) suggest that hypoxia tolerance is a derived feature of *E. viridis*, which can result in the formation of *E. viridis* urchin barrens (C).

Although we did not correctly predict the physiological differences between the two Caribbean species, we did correctly predict that the Pacific *E. vanbrunti* was the most sensitive species in our study. Such sensitivity is highlighted by the post-trial survival results. Survival 24 h after the short two-hour exposure was significantly affected by species, DO, temperature and the interaction between DO and temperature (Fig. 2; Sup. Mat. Table 1A). All species experienced mortality when hypoxia was combined with the highest temperature tested (35 °C), but *E. vanbrunti* was least likely to survive compared to the other two species ($p < 0.001$, Fig. 2). It should be noted that temperatures of 35 °C are above those recorded at these study sites. The Pacific survey data did not record temperatures higher than 30.5 °C, and during the hypoxic upwelling season, temperatures were even cooler (max. 28.1 °C). The Caribbean was warmer with recorded temperatures reaching 31.4 °C. However, another study using permanently deployed loggers reported temperatures near the exposed Caribbean site as high as 33 °C during the same time period [23]. The fact that our weekly survey data did not capture the absolute highest temperatures across the sampled time period highlights how underestimated high temperature extremes and marine heat waves likely are [54]. The underestimation of high temperatures combined with our survival results suggest that previous hypoxia-related mortality events on reefs in the Caribbean, like that reported in Bocas del Toro in 2010 [15], may have been caused by a combination of thermal and hypoxic stress.

Hypoxia is associated with the cooler temperatures of upwelled water, suggesting marine life in the Pacific may escape the synergistic threat of heating and hypoxia in the Caribbean. However, environmental predictions indicate that conditions may nevertheless become more stressful in the TEP. The tropical Pacific Oxygen Minimum Zone (OMZ) is expanding [55], resulting in steeper temperature and oxygen gradients, increasing surface temperatures [7, 10, 56, 57], and shoaling hypoxia/anoxia that compresses oxygenated open-ocean habitat [58]. Considering the substantial reduction in *E. vanbrunti's* performance under hypoxia at all temperatures, this species is likely to experience negative effects as environmental changes impact coastal areas.

Echinometra viridis may become the most successful species in this *Echinometra* clade, with its opportunistic traits and apparent adaptations to survive hot, hypoxic waters. Yet, despite being particularly tolerant, *E. viridis* performance starts to decline at 32 °C under hypoxia, conditions which already occur in Bocas del Toro and at other hypoxic sites in the Caribbean [23]. From these results, it is clear that intensifying conditions in the near future will challenge these ecologically important herbivores. It also suggests that other hypoxia tolerant marine taxa may be at risk of extirpation due to the combination of warming and hypoxia [59–61].

The Caribbean and Pacific *Echinometra* species diverged from each other approximately three Mya, and *E. viridis* subsequently diverged from *E. lucunter* in the Caribbean [28] (Fig. 1). This relationship suggests that hypoxia tolerance is a derived trait of *E. viridis,* and that the common ancestor of the three species had a hypoxia sensitivity similar to that found in the other two more sensitive species. However, without knowing the physiological tolerances of the ancestor of the Panamanian *Echinometra* we cannot reconstruct the ancestral condition with certainty. Alternatively, our results could reflect plastic physiological responses to current environmental conditions, or local adaptation of each population. We consider local population-level adaptation unlikely as all three species have large population sizes, geographic ranges encompassing a wide range of environmental conditions and high gene flow between populations that minimize the potential for local adaptation [28, 62, 63]. We attempted to minimize plasticity effects by collecting all sea urchins during the time of the year when the conditions were most similar and animals were collected during the same season, from the same site on the CAR side. Explicit documentation of potential plastic responses to environmental conditions would be a highly relevant topic for future research [64–66].

Our results show hypoxic conditions that occur in both the Caribbean and Pacific have direct negative effects on organismal performance and survival. The shoaling hypoxia on both coasts may limit or eliminate deeper habitat, causing vertical habitat compression similar to that documented in the open ocean [58, 67]. Such hypoxia-driven habitat compression may limit deeper refuge from surface warming. However, under well oxygenated conditions we find sea urchins are able to withstand considerable short-term warming. This supports a counterintuitive conclusion that the best survival strategy may be to inhabit shallower, warmer habitats.

Author contributions

NML and RC designed the experiment; NML and EH collected the animals and conducted the experiments; NML and RC analyzed the data and prepared the manuscript.

Declaration of Competing interests

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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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100010.

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