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Field experimental evidence of sandy beach community changes in response to artificial light at night (ALAN)

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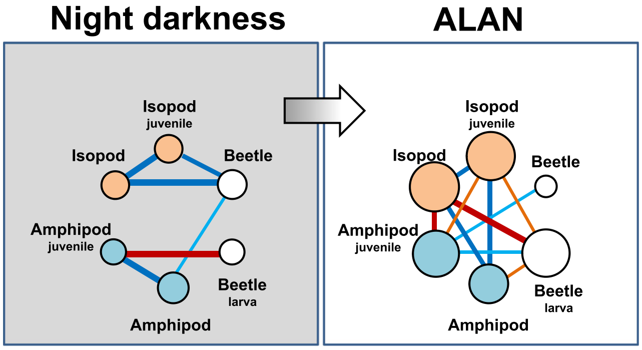
HIGHLIGHTS

- ALAN effects on life-stage and community structure were assessed.
- Abundance of adults and juveniles exhibited differential responses to ALAN.
- The zonation of adults and juveniles of all the species were modified by ALAN.
- ALAN effects had effects in community structure and likely beyond.

GRAPHICAL ABSTRACT



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ABSTRACT

Artificial light at night (ALAN) is a pervasive but still under-recognized driver of global change. In coastal settings, a large majority of the studies assessing ALAN impacts has focused on individual species, even though it is unclear whether results gathered from single species can be used to predict community-wide responses. Similarly, these studies often treat species as single life-stage entities, ignoring the variation associated with distinct life stages. This study addresses both limitations by focusing on the effects of ALAN on a sandy beach community consisting of species with distinct early- and late-life stages. Our hypothesis was that ALAN alters community structure and these changes are mediated by individual species and also by their ontogenetic stages. A field experiment was conducted in a sandy beach of north-central Chile using an artificial LED system. Samples were collected at different night hours (8-levels in total) across the intertidal (9-levels) over several days in November and January (austral spring and summer seasons). The abundance of adults of all species was significantly lower in ALAN treatments. Early stages of isopods showed the same pattern, but the opposite was observed for the early stages of the other two species. Clear differences

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were detected in the zonation of these species during natural darkness versus those exposed to ALAN, with some adult-juvenile differences in this response. These results support our hypothesis and document a series of changes affecting differentially both early and late life stages of these species, and ultimately, the structure of the entire community. Although the effects described correspond to short-term responses, more persistent effects are likely to occur if ALAN sources become established as permanent features in sandy beaches. The worldwide growth of ALAN suggests that the scope of its effect will continue to grow and represents a concern for sandy beach systems.

1. Introduction

Nighttime is fundamental for a wide range of organisms and is being increasingly threatened by human activities (Longcore and Rich, 2004; Gaston, 2018, 2019). Artificial Light at Night (hereafter ALAN) is a pervasive but still under-recognized driver of global change (Davies et al., 2014; Marangoni et al., 2022; Lynn and Quijón, 2022). A wide range of ecosystems are already exposed to some level of ALAN (Cinzano et al., 2001; Falchi et al., 2016), and exposure is expected to continue to increase (Hölker et al., 2010a; Bennie et al., 2015), particularly in Mediterranean and temperate ecosystems (Bennie et al., 2015). ALAN may alter natural light levels and the daily and seasonal light/dark cycles (Hölker et al., 2010b). These cycles represent a key ecosystem service (Abraham et al., 2019) that plays fundamental roles on physiological and behavioural traits of terrestrial and marine organisms (Davies et al., 2013a; Longcore and Rich, 2004). Therefore, it is reasonable to expect that ALAN may have effects at all levels of ecological organization from organisms to ecosystems (Davies et al., 2013b, 2014; Longcore and Rich, 2004; Duarte et al., 2019). Such organisms include a wide variety of plants (Bennie et al., 2016, 2018; Knop et al., 2017), invertebrates (Jelassi et al., 2014; Luarte et al., 2016; Ugolini et al., 2005), and vertebrates (McLaren et al., 2018; Raap et al., 2018).

Most of the studies assessing ALAN effects have focused on individual species (Bird et al., 2004; Dominoni et al., 2013; Moore et al., 2000; Pulgar et al., 2019). However, it remains unclear if the results gathered from single species can be used to predict community-level responses to this stressor (Sanders and Gaston, 2018). Studies assessing the response of communities remain scarce, particularly those associated to sensitive areas, such as biodiversity hotspots (Guetté et al., 2018). ALAN can modify community assembly through environmental filtering effects (physical factors) as well as by altering the strength of species interactions (Sanders and Gaston, 2018). For example, street lighting can change the composition of ground-dwelling invertebrate communities (Davies et al., 2012), and alter the detection of prey by visual predators, potentially modifying interactions and food web dynamics (Sanders et al., 2018), and indirectly top-down and bottom-up effects (Bennie et al., 2018).

One issue that has, so far, limited the studies assessing the influence of ALAN on communities is the common portray of species as single life-stage entities. Many species are polymorphic, changing with age in terms of size, morphology, and use of resources including time (Violle et al., 2012). In these cases, a careful examination of community responses to ALAN should consider both the different species within a community as well as different age classes (Polis, 1984). So far, the study of ALAN effects on different ontogenetic stages of a same species has been the subject of very few studies (e.g. Dananay and Benard, 2018; Farnworth et al., 2018), despite the fact that distinct stage responses may lead to whole community changes. An illustrative example is offered by the Chilean sand hopper *Orchestoidea tuberculata,* whose juveniles are active at dusk and dawn, whereas the adults are strictly nocturnal (Kennedy et al., 2000). Because the timing of their exposure to natural light differs, the known adult responses to ALAN (e.g. Luarte et al., 2016) may be very different from juvenile responses (see Duarte et al., 2019).

Sandy beach systems represent nearly 80 % of the ice-free world's coastline (Bascom, 1980) and are important socio-ecological systems (King and Symes, 2004; Pendleton et al., 2006; Schlacher et al., 2016), given the variety of economic, ecological, recreational and cultural uses of these coastal systems (Hyndes et al., 2022). Several species living in sandy beaches are nocturnal (Fallaci et al., 1999, 2002; Kennedy et al., 2000), displaying an activity that is controlled by natural day/night cycles (Ugolini, 2003; Jaramillo et al., 2003; Meschini et al., 2008). After feeding, these species require darkness to detect natural light signals and find their way back to their burrowing zone (Fallaci et al., 2002). ALAN may alter those natural processes (e.g Luarte et al., 2016; Duarte et al., 2019). Besides, only a few studies have documented the effects of ALAN on sandy beach organisms (Dimitriadis et al., 2018; Jelassi et al., 2014; Lorne and Salmon, 2007; Lynn et al., 2021; Quintanilla-Ahumada et al., 2021), but none, so far, has addressed community-level effects. Hence, we assessed ALAN effects on a sandy beach arthropod community in north-central Chile, which is composed of three semi-terrestrial burrowing species that emerges at night to feed on stranded macroalgae (Jaramillo et al., 2003). These species have shown to negatively interact with each other (competition), partitioning the use of space and activity time to avoid this interaction (Jaramillo et al., 2003). It follows that the potential effects of ALAN on the activity and distribution of these species could have unpredictable consequences on the balance of these interactions. Given that adults and juveniles of each species are well represented numerically, we also used them as models to put forward the following working hypothesis: ALAN changes community structure and this change is mediated by the differential response to ALAN of both species and ontogenetic stages.

2. Materials and methods

2.1. Study area and ALAN

The field experiments were conducted in "El Apolillado" sandy beach, north-central Chile (29°10′42"S, 71°19′17″, Fig. 1). The area supports large densities of the three species constituting the upper intertidal assemblage of sandy beaches in the region (29–34°S; Jaramillo et al., 2003): The oniscid isopod *Tylos spinulosus,* the talitrid amphipod *Orchestoidea tuberculata* and the tenebrionid beetle *Phalerisida maculata* (hereafter consistently referred to as isopods, amphipods and beetles, respectively). This sandy beach is also located far away from urban areas and large networks of coastal lighting, providing natural dark conditions at night (Duarte et al., 2019; and see Fig. 1).

2.2. Field experiments

Field experiments were conducted in November 17–19 2017 (Austral Spring) and January 15–17 2018 (Austral Summer) and involved two consecutive nights per period, starting at the beginning on the new moon of each month. To assess the influence of ALAN, two different experimental conditions were established: exposure to artificial light at night (ALAN) and exposure to natural daylight/dark conditions (control). ALAN conditions were created by installing three aluminum-pole structures equipped with light emitting diode (LED) lights at top (3 m high) and placed at the base of the dune (see below). These three structures were alternated with control conditions (no artificial light at night) in a systematic way (Hurlbert, 1984), and placed 100 m apart from each other (i.e., there was a 100 m distance between each ALAN and control area), that prevented the interference between conditions. As indicated below, this was confirmed with repeated light intensity measurements in control areas (Fig. 2). In each of these ALAN (3) and control (3) conditions, one transect was established from the upper to the low intertidal levels. Along each

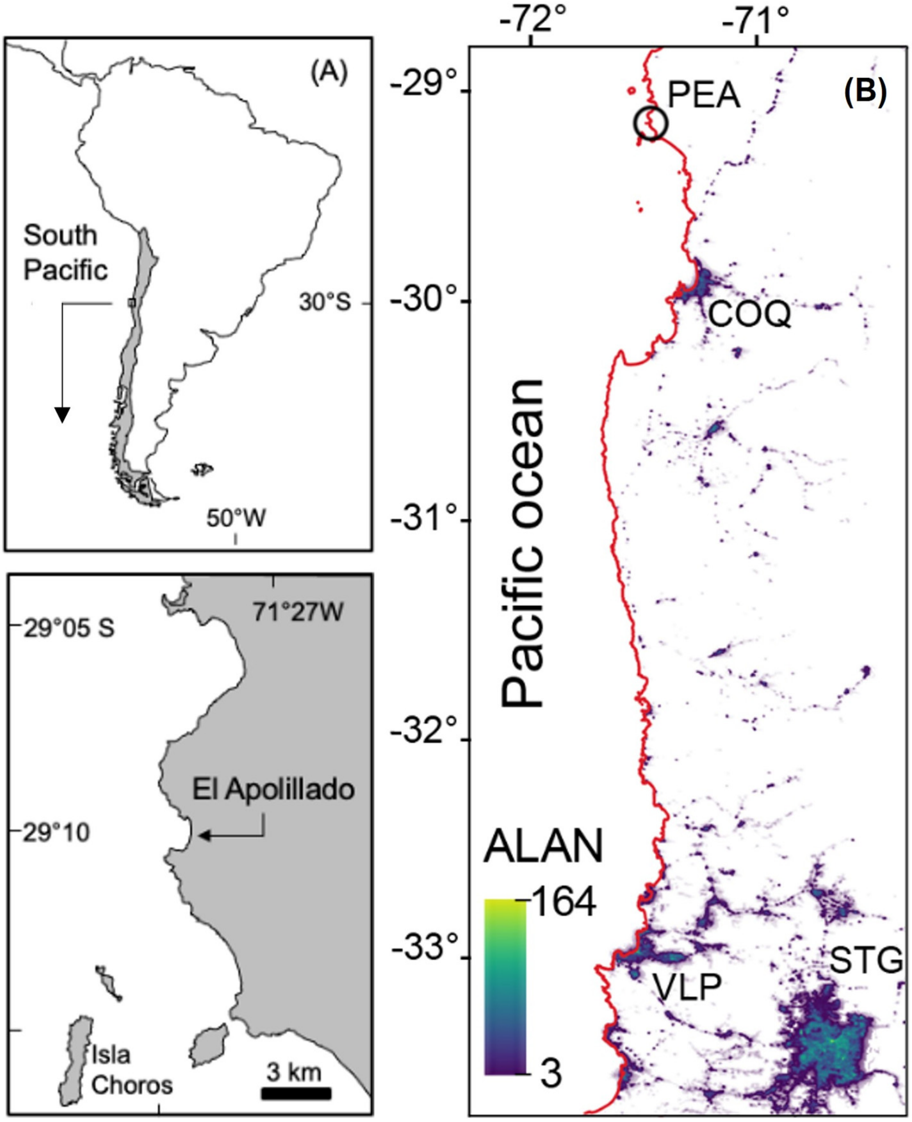

Fig. 1. (A) Map showing the approximate location of El Apolillado sandy beach in north-central Chile. (B) Map illustrating artificial light pollution at night (ALAN) along north-central Chile. Values plotted correspond to cloud-free mean nighttime radiances for 2016 using the Visible Infrared Imaging Radiometer Suite Day-Night Band (VIIRS-DNB) satellite (pixel of 0.55 km2; National Oceanic Atmospheric Administration, NOAA, 2018). Red contours depict the coastline, identifying also the location of the study site ("Playa El Apolillado", PEA) and for comparison, three more heavily polluted urban areas: Coquimbo (COQ), Valparaiso (VLP) and Santiago (STG). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transect, nine pitfall plastic traps (labelled 1–9; 5 cm diameter, 12 cm high) were buried into the sand with their rim flush to the beach surface at 3 m intervals (Fig. 2). Each trap was filled with a 5 % sea water-formalin solution to preserve organisms caught in the traps.

In the ALAN transects, the LED lights (SENTRY S 20 W driverless 5 K White-light; 220 V) mounted in the poles were connected to a distant (~100 m) power source (EP2500CX Honda generator; 2.2 KVA) placed behind the dunes. The poles were placed 2 m behind the first trap of the transect (Fig. 2) and provided an average ground-level light intensity of ~120 lx. Light intensity gradually decreased from there towards the low-tide, averaging 98 lx (level 2) 65 lx (level 3) 40 lx (level 4), 20 lx (level 5), 13 lx (level 6), 10 lx (level 7), 7 lx (level 8) and 4 lx (level 9). These measurements were repeatedly made using a PCE-L 100 light meter (sensitivity: 1 to 300.000 lx). As in previous studies (e.g. Pulgar et al., 2019; Duarte et al., 2019; Manríquez et al., 2021), the highest light intensity of the system recreated the one recorded under lighting networks of heavily polluted shorelines at night, where lights are located at the top of the shore, adjacent to beach boardwalks, roads and parking areas. Ground-level light intensities of <1 lx (the lightmeter sensitivity) were measured at all the control transects at night. Each field experiment was conducted along two consecutive nights: on November 17th we sampled at 2:00 and 3:00 AM and on the 18th at 1:30 and at 2:30 AM. On January 15th we sampled at 1:00, 3:00 and 5:00 AM, whereas on the 16th we sampled at 5:00 AM (8 h in total). In both experiments, traps were installed at midnight. During each sampling, the nine pitfall traps deployed along each transect were removed and quickly replaced (except on January 16th when only one sample was collected). The content of the pitfall traps was placed on labelled containers and transported to the laboratory where the species and ontogenetic stages (larvae/juveniles vs adults) were identified and counted. For beetles, larvae and adults were distinguished by their sharply different morphology. For amphipods and isopods, the cephalothoracic length was measured to distinguish between juveniles (≤7 mm) and adults (>7 mm) (Jaramillo et al., 2003; Duarte et al., 2010).

2.3. Community structure analysis

To assess how community structure-ontogenetic stage and species abundance and composition—change under ALAN, we fitted Joint Species

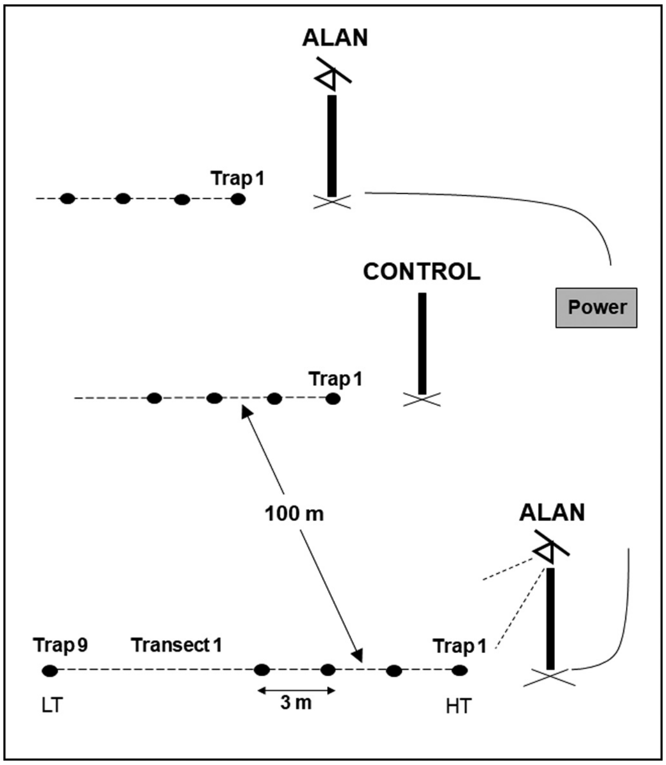

Fig. 2. An illustration of the field design with the relative position of traps, transects and ALAN and control conditions over the intertidal of the sandy beach. HT and LT stand for high and low tide levels, respectively.

Distribution Models (JSDM) in the package Boral in R (Hui, 2016; R Core Development Team, 2019). This package allows fitting joint models (using Bayesian Markov chain Monte Carlo estimation; MCMC) that are composed by separate generalized linear models fitted to each species and are able to incorporate latent variables to account for species correlations (Hui et al., 2015; Hui, 2016). Latent variables are variables that cannot be measured directly and therefore must be inferred from other empirical measurements (Hellgren and Sverke, 2003). These models have been applied in community ecology as a parsimonious approach to estimate unmeasured correlations across species, which could be caused by missing predictors or by species interactions, while studying their response to environmental variation (Ovaskainen et al., 2010, 2016, 2017; Pollock et al., 2014; Warton et al., 2015a).

The JSDM was fitted across the three species and their ontogenetic stages forming a 6 columns matrix, using a negative binomial distribution and a log link function (O'Hara and Kotze, 2010; Warton et al., 2012). The JSDM included the following: (1) predictors (dummy variables) including treatment (control vs ALAN), distance-to-light-source (vertical distribution including 9 traps or levels), the hour of the experiment (8 levels) and the interaction between these last two variables with the treatment; (2) two latent variables, which are usually sufficient to estimate correlations between species (Warton et al., 2015a); And (3) the micro-zone of the beach where a pair of transects (both control and ALAN) were located as a random effect (6 micro-zones, 3 in spring and 3 in summer) to account for confounding factors due to experimental design (i.e. micro habitat and seasonal differences, see Duarte et al., 2019). This was done using the row.eff argument in the boral function, which is analogous to a random intercept in mixed models (Hui, 2016). For model selection we used the Widely Applicable Information Criterion (WAIC, Watanabe, 2010), which is a natural extension of the Akaike's information criterion (i.e. smaller values suggest more parsimonious models) to the Bayesian and hierarchical modeling context (Gelman et al., 2013). The effect size of each component of the JSDM was assessed using the variance partition approach described by Ovaskainen et al. (2017). The explained variation was partitioned (0–100 %) into components attributable to predictive variables, latent variables and experimental design. This was done for each species using the calc.varpart function in the boral package. As an overall effect in community, for each term the average over species was considered (Ovaskainen et al., 2017).

To visualize compositional changes under ALAN, a pure latent variable (no-explanatory variables) model was fitted to perform model-based unconstrained ordination (Hui, 2016; Hui et al., 2015). Two latent variables and the micro-zones as random effect (see above) were included and the negative binomial distribution for the response matrix was used. The ordination resulting from this method can be interpreted in the same manner as distance-based ordination techniques such as nMDS, but has several advantages over those methods. For example, it accounts (using the negative binomial distribution) for a critical property of count-data such as the mean–variance relationship which usually is quadratic (Hui et al., 2015; Warton, 2005; Warton et al., 2012).

To assess how species co-variation changed between control and ALAN, JSDM was fitted to each condition separately. Models contained the vertical distribution (or the distance to light source in case of ALAN) and the hours of the experiment as predictors plus two latent variables and micro-zones as random effect. From these models, correlations between species abundances were extracted based on similarities or differences in their spatial and temporal distribution at control and ALAN conditions (with 95 % credible intervals excluding zero). This was done using the get.enviro.cor function in the boral package. These correlations are presented in networks and were performed using a circular layout in Gephi (Bastian et al., 2009). All JSDM were run using 400,000 iterations with the first 100,000 discarded as burn-in and with a thinning rate of 100. For checking overall goodness of fit and convergence, Dunn-Smyth residuals were used, as they are available in the boral package and trace plots of the MCMC chains through the coda package (Plummer et al., 2006) of R. A general overview of the statistical framework used here is provided by Warton et al. (2015a, 2015b) and Ovaskainen et al. (2017).

3. Results

The fittest JSDM (lowest WAIC) explaining sandy beach arthropod community included the interaction between the experimental conditions (control vs ALAN) with the distance to the light source and with the hour of the experiment (Table 1).

With regards to experimental conditions, the abundance of adults of the three species was significantly (i.e. 95 % HPD excluding zero, Table 2) lower in transects exposed to ALAN than in those exposed to natural conditions (controls). The same pattern was observed for the abundance of juvenile isopods, but the opposite was recorded for early stages of the other two species (amphipods and beetles), which showed higher abundances in ALAN transects compared to controls (95 % HPD including zero in the case of beetles, Table 2).

Table 1
Joint Species Distribution Model (JSDM) selection for the spatio-temporal variation of the sandy beach arthropod community in response to treatment (Control and ALAN), hour and distance to light source. JSDM are sorted by increasing WAIC values (from best to worst). Transect location was included as a random effect to account for the experimental design. Two latent variables (2LV) were also included to account for missing predictors. See Fig. 5 for variance partitioning of the best model (JSDM1) and Fig. 6 for the unconstrained ordination of the model JSDM6. × stands for interaction between predictor variables.

Model	Formula	WAIC	Δ WAIC
JSDM1	Treatment × Spatial + Treatment × Hour, 2LV, Transect location	14,415	–
JSDM2	Treatment × Hour + Spatial, 2LV, Transect location	14,447	32
JSDM3	Treatment × Spatial + Hour, 2LV, Transect location	14,526	111
JSDM4	Treatment + Hour + Spatial, 2LV, Transect location	14,563	148
JSDM5	Treatment + 2LV + Transect location	15,731	1316
JSDM6	2LV + Transect location	15,908	1493

Table 2
Arthropod community responses to ALAN effects. ALAN coefficients and their highest posterior density intervals (95 % HPD) are shown in comparison to control condition (intercepts), while accounting for experimental design and species correlations (JSDM5, Table 1). Values in bold identify 95 % HPD excluding zero.

Species	Stage	ALAN effect	95 % HPD lower	95 % HPD upper
Isopods (*T. spinulosus*)	Adults	**−2.84**	**−3.31**	**−2.43**
	Juveniles	**−1.79**	**−2.39**	**−1.31**
Amphipods (*O. tuberculata*)	Adults	**−0.55**	**−0.81**	**−0.31**
	Juveniles	**1.84**	**1.54**	**2.13**
Beetles (*P. maculata*)	Adults	**−1.85**	**−2.1**	**−1.63**
	Larvae	0.22	−0.3	0.84

With regards to zonation (Fig. 3), in natural (control) conditions, adult isopods showed their highest abundances at high- and mid-intertidal (levels 1–5), whereas adult amphipods and beetles showed highest abundances at mid- to low-intertidal (levels 7 and 5, respectively). In contrast, in transects exposed to ALAN adult amphipods and beetles showed a more uniform zonation patterns, whereas the highest abundance of the isopods shifted to lower tide levels (6 and 7) (Fig. 3). Regarding the early stages, in control conditions beetles and isopods were more abundant at high (1–2) tide levels, whereas amphipods were highest at the mid intertidal (levels 4–5). In transects exposed to ALAN, early stages of amphipods and *beetles* were highest at high tide (levels 1–2), whereas isopods increased towards low tide (levels 7–9) (Fig. 3).

With regards to temporal variation (Fig. 4), adults of the three species showed uniform abundances most of the night, with slightly more variation in those exposed to ALAN.

Meanwhile, beetle larvae showed little variation over time, whereas the other two species showed more changes across hours, particularly at 3:00 AM, when a rise and a sharp decline were detected in amphipods and isopods, respectively (Fig. 4).

Variance partitioning (JSDM; Table 1) identified a strong effect of ALAN accounting for 43 % (averaged over species) of spatio-temporal shifts in community structure (sum of mean effects of treatment and its interaction with the spatial and temporal components). Specifically, ALAN drove temporal (12 %) and spatial (distance to light source; 14 %) changes in the species distribution. In addition, 7 % of variation was associated to the experimental design (i.e., due to physical setting differences of transects location, for example, presence of stones, stranded seaweed or transect slope, among others) and 17 % of residual variation was accounted by the two latent variables (i.e. missing variables). Variance partitioning also showed that ALAN (treatment) modified in average a 14 % (range = 6–29 %) of the community (Fig. 5). In terms of species composition and their relative abundance, model-based unconstrained ordination (i.e. JSDM with no predictors and two latent variables) made evident a notorious community change in response to ALAN (Fig. 6). Compositional changes were related, in part, to the distance-to-light-source, with sharp control-ALAN community differences at levels 1–4 and with a gradual decrease of dissimilarity as the distance to the light source increased (levels 5–9; Fig. 6).

ALAN also drove intra-and interspecific shifts in species co-variations, particularly in relation to spatial distribution (Table 2; Fig. 7). In control conditions there was a strong intra-and interspecific segregation in space or time. For instance, isopods and amphipods showed strong intraspecific positive correlations with respect to their spatial distribution, but null or negative correlations in relation to time. Under ALAN conditions, a complex network of species correlations was found, with a loss or attenuation of intra-specific correlations (i.e. increases of spatial segregation) in some cases (e.g. adult and juvenile amphipods) or with an increases of inter-specific correlations (i.e. decreases spatial segregation) in other cases (e.g. adults of amphipods and isopods) (Fig. 7).

4. Discussion

Prior studies have shown the influence of Artificial Light at Night (ALAN) on various aspects of the ecology of sandy beach organisms, including abundance (Duarte et al., 2019), locomotor activity, feeding rates (Luarte et al., 2016; Lynn et al., 2021), growth rates (Luarte et al., 2016) and at least two physiology variables (Quintanilla-Ahumada et al., 2021: Lynn et al., 2022). However, to the best of our knowledge, this study is the first to provide field empirical evidence on the potential effects of this stressor on the spatial and temporal variation of the community structure

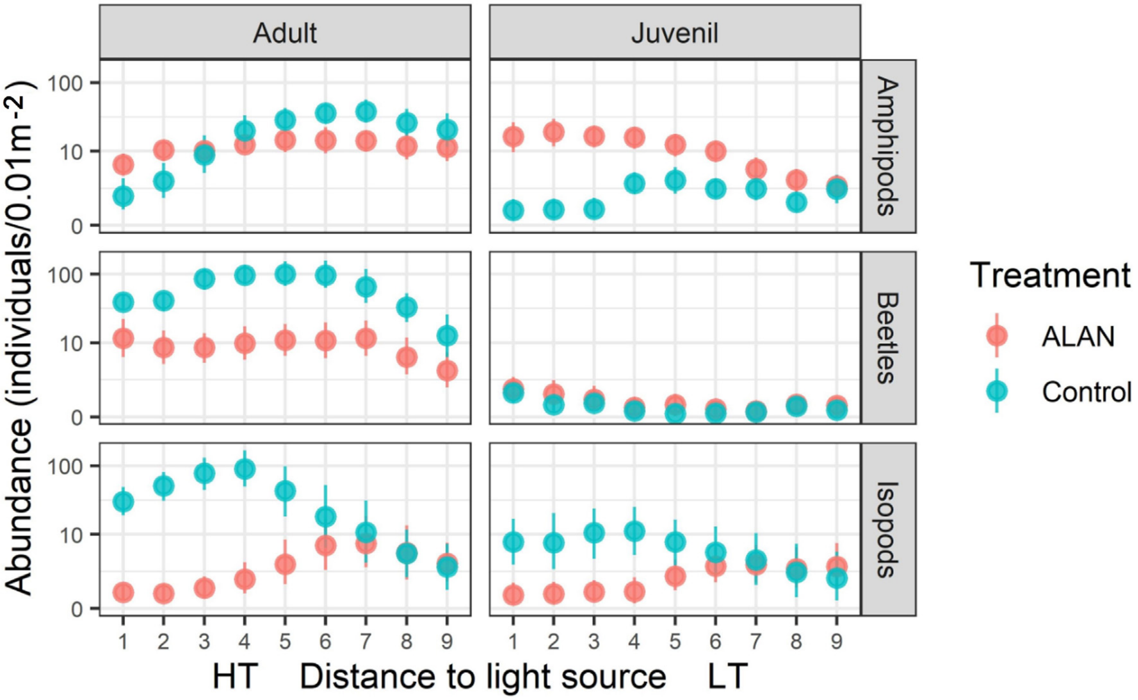

Fig. 3. Spatial variation of adult and juvenile abundances (mean ± bootstrapped 95 % confidence interval of individuals per pitfall trap) for different species in natural (control) and ALAN-exposed conditions (y-axis is on logarithmic scale). HT and LT stand for High and Low tide levels, respectively.

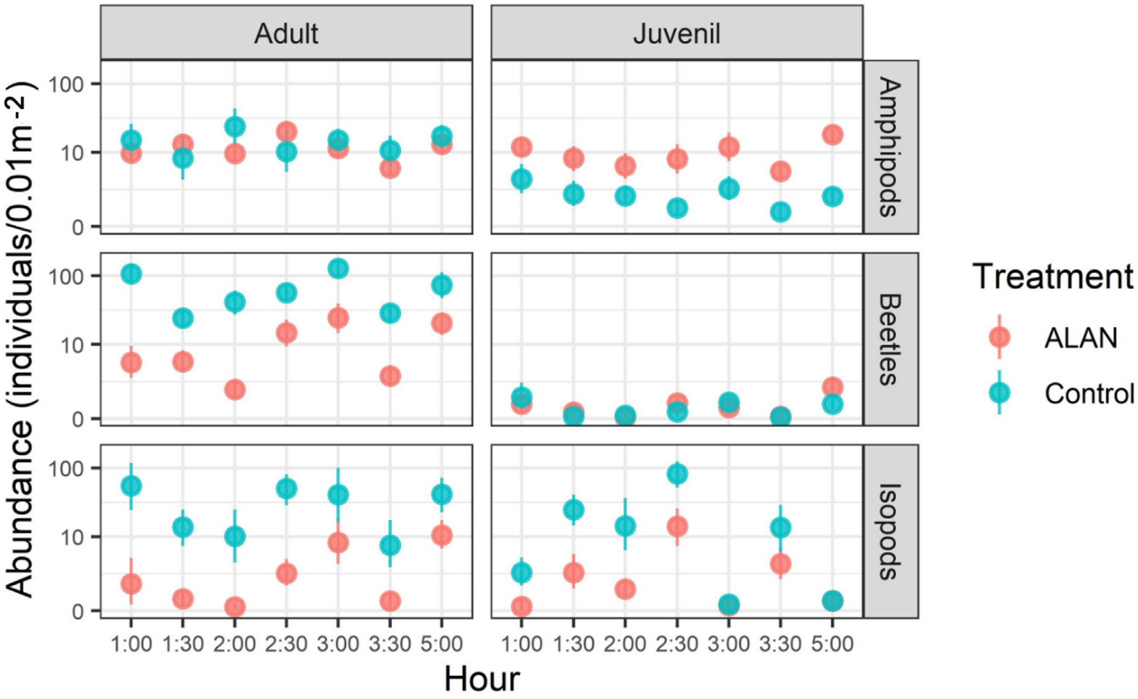

Fig. 4. Temporal variation of adult and juvenile abundances (mean ± bootstrapped 95 % confidence interval of individuals per pitfall trap) for different species in natural (control) and ALAN-exposed conditions (y-axis is on logarithmic scale). HT and LT stand for High and Low tide levels, respectively.

in these ecosystems. Our results support the hypothesis proposed by showing that ALAN has differential effects on early and late life stages of upper-shore arthropods and these effects contribute to substantial changes in community structure. Natural responses to stressors like ALAN may take many generations to become engrained in the behavioural repertoire of species and their life stages (Brown, 1996; Scapini, 2014). Based on the spatial and temporal scope of our experiments we are not attempting to infer such long-term effects: short-term exposure to ALAN does not necessarily have lasting effects on distribution, abundance or activity levels of species, life stages, and ultimately communities. However, we argue that the changes triggered by a rather brief period of light pollution exposure are meaningful and shed light onto the direction of the changes that these communities may endure as ALAN further spread and intensifies in near-shore habitats (Davies et al., 2014). If ALAN sources–such as light networks associated with sidewalks, parking lots, roads or buildings–become a permanent feature along or nearby upper shore sediments, the effects measured here may become a consistent factor contributing to the structure of these communities. Future studies addressing the influence of long-term exposure to ALAN would provide the evidence to know how species and communities cope with this stressor in the long-term.

As highlighted in two recent reviews (Marangoni et al., 2022; Lynn and Quijón, 2022), only a scarce number of studies has shown that ALAN can modify the community structure of vertebrate and invertebrate species from different ecosystems (e.g. Barker and Cowan, 2018; Davies et al.,

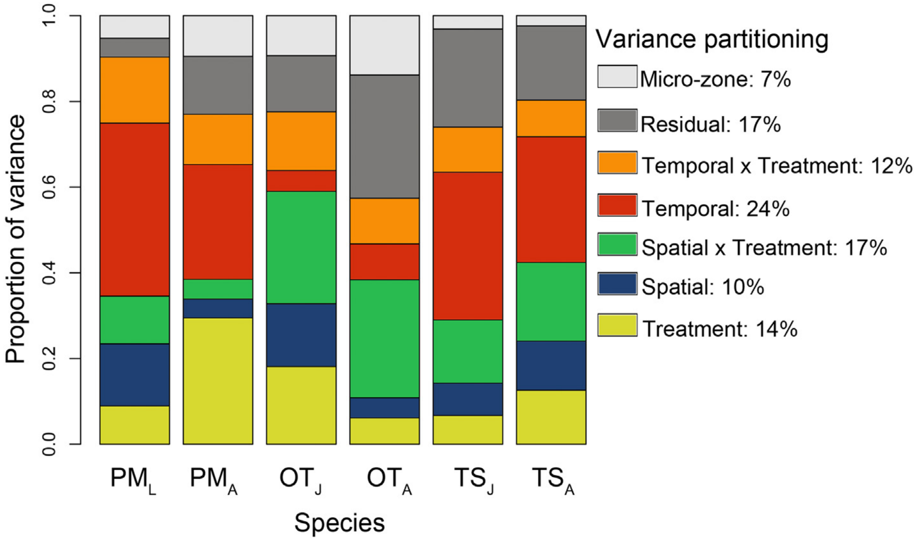

Fig. 5. Variance partitioning (from JSDM1, Table 1) for each arthropod species. Variation in species abundance were partitioned into responses to the treatment (control versus ALAN), the spatial component (vertical distribution at control condition and distance-to-light-source at ALAN), the temporal component (hours), the interaction between these last variables with the treatment, the latent variables (i.e. correlations between species due to missing predictors) and the experimental design (i.e. location of transects). Species codes are based on their initials and ontogenetic stage (e.g., TS_A = *T. spinulosos* adults).

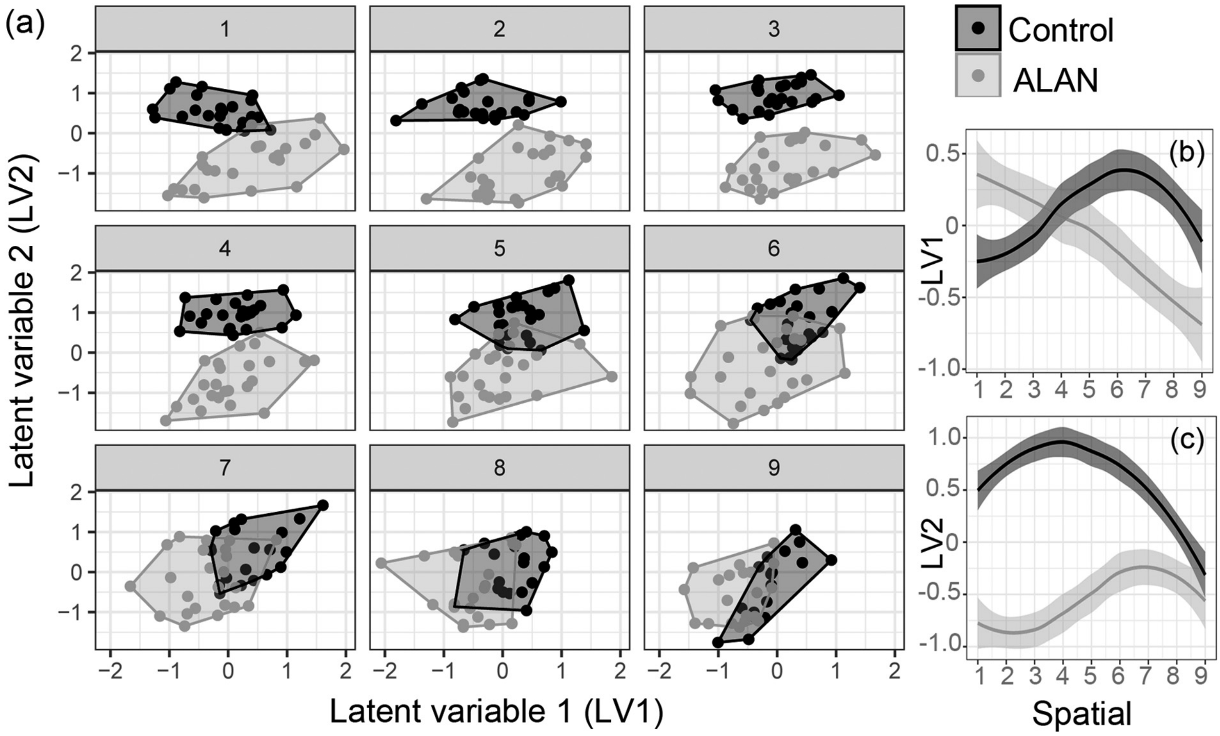

Fig. 6. Model-based unconstrained ordination showing arthropod community structure in natural (control) and ALAN-exposed conditions. The plot was constructed based on the posterior medians of a model with two latent variables and no covariate (JSDM6, Table 1). Once obtained, latent variables were shaded with the treatment conditions and faceted according to the distance to light source (a). Latent variable 1 (b) and 2 (c) in response to distance-to-light-source (mean ± standard error, using local polynomial). Values 1–9 stand for levels across the intertidal.

2012; Garratt et al., 2019). For example, Garratt et al. (2019) registered an increase in the species richness and total biomass with the illumination level in a sandy beach of the west coast in UK. Maggi et al. (2019) exposed a rocky shore epilithic microbial community to ALAN, showing an increment in the diversity of cyanobacterial families in presence of this stressor. The ALAN effects on the community structure can be direct or indirect through changes in biological interactions (see Bolton et al., 2017; Maggi et al., 2019). In this context, it is difficult to tease out the effects of biotic interactions and physical factors (i.e. environmental filtering; see Kraft et al., 2015) to explain the response of these species to ALAN. However, a combination of both types of factors seems likely (Maggi et al., 2019). Thus, the experimental manipulations can help to separate the effects of these concomitant factors as carried out in this study. On the one hand, prior studies have shown that in the absence of other species, the response (e.g. spatial distribution) of amphipods (Luarte et al., 2016) to ALAN is very similar to the one documented here. Such similarity suggests a prevailing role of physical factors over biotic interactions. On the other hand, one of the most striking responses to ALAN has been a reduction in the locomotor activity of these and other species (Luarte et al., 2016; Duarte et al., 2019; Lynn et al., 2021). In peracarid species, such activity is controlled by circadian rhythms (Jaramillo et al., 2003; Nourisson and Scapini, 2015; Rossano et al., 2018) which appear to be engrained in the behaviour of these species to minimize biotic interactions (Dhouha et al., 2017; Jelassi et al., 2014; Farnworth et al., 2018; Pulgar et al., 2019). As discussed below, the coexistence of these species and their life stages is facilitated by the timing of activity and their spatial distribution across the intertidal (Jaramillo et al., 2003; Rossano et al., 2018).

Under natural dark conditions at night (control), our results show clear zonation patterns and intra- and inter-specific variations in activity times. For instance, the isopods used primarily the upper intertidal whereas amphipods and beetles migrated down to mid- and low-tidal levels. Such patterns changed when exposed to ALAN, prompting isopods to move down and overlap with amphipods, potentially triggering negative interactions with the amphipods. The latter species are known to compete with isopods and beetles (Jaramillo et al., 2003), and prolonged exposure to ALAN would likely be most harmful for the isopods (Jaramillo et al., 2003). Similarly, although adult and juvenile isopods showed the same response to ALAN, the same cannot be said about early stages of amphipods and beetles, which in comparison to adults showed contrasting responses to ALAN: rather than migrating down with the adults, juveniles and larvae of these species increased in abundance at the upper intertidal, close to light sources. This novel example of phototaxis adds to the list of cases previously reported primarily in fish larvae and aerial terrestrial invertebrates (Rydell, 1992; Frank, 2006; van Langevelde et al., 2017). In addition, juvenile amphipods are also known for being active both during day and night hours (Kennedy et al., 2000), which may partially explain their high abundances under ALAN exposure. Furthermore, as expected in natural dark conditions, we report here strong negative spatial correlations between juvenile and adult amphipods, and a temporal segregation in the timing of their activity. Such segregation is critical to avoid cannibalism (Kennedy et al., 2000; Duarte et al., 2010), a behaviour that is deterred under ALAN exposure, and that would explain the change in zonation in juveniles as an alternative mechanism to avoid mortality.

The influence of ALAN has a strong spatial component, and this was made evident by the community-wide patterns depicted by the model-based unconstrained ordinations. The assembly of species and life stages was altered primarily at the upper levels of the intertidal, closer to the edge of dunes where ALAN sources such as boardwalk and lighting networks are normally placed (González et al., 2014; Manríquez et al., 2019). As expected, visual differences between control and ALAN-exposed communities were obvious between levels 1 and 4, but these effects gradually faded away further down the intertidal, as light intensities rapidly declined from 120 to 4 lx (see Luarte et al., 2016; Duarte et al., 2019). One hundred and twenty lux corresponds to the light intensity measured underneath light sources. However, ALAN effects in this and some of our prior studies (Luarte et al., 2016; Quintanilla-Ahumada et al., 2021, 2022) were detected at lower light intensities. Such spatial variation was also evident in the polygons representing communities (see Fig. 6), which

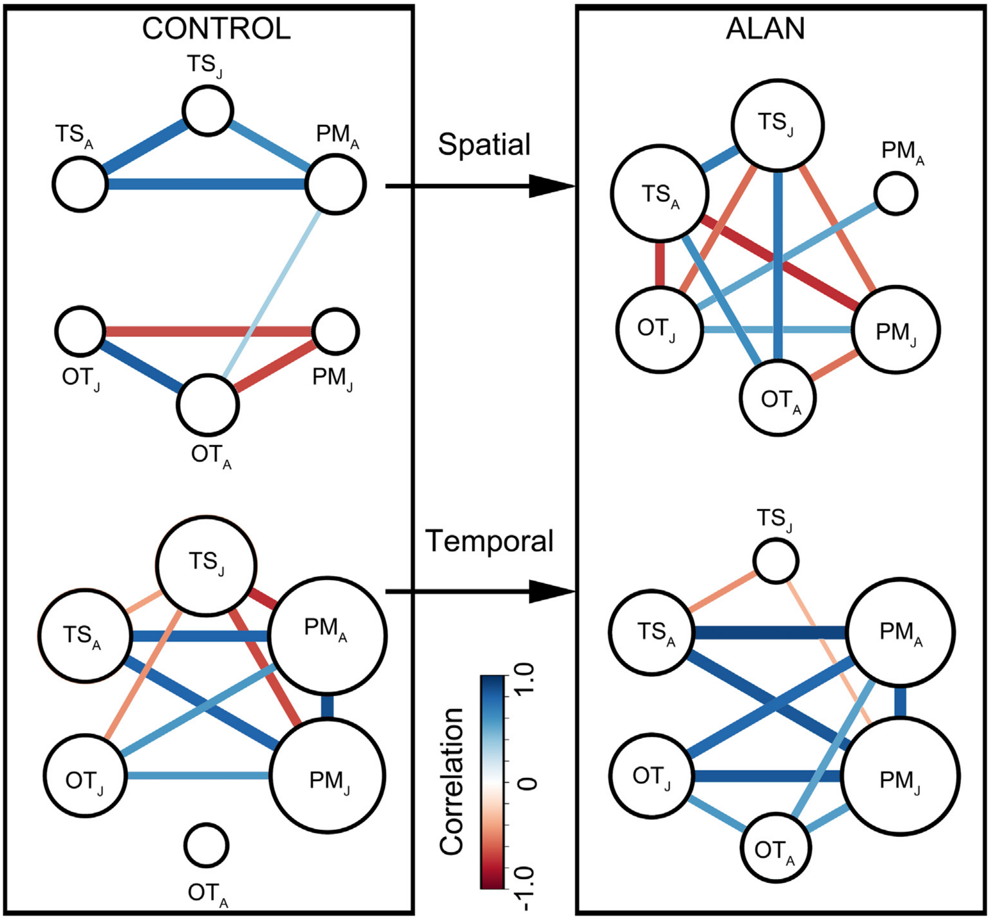

Fig. 7. Networks of correlations between species due similarities or differences in their spatial and temporal co-variations under control and ALAN conditions. Panels distinguished spatial (top) and temporal (bottom) correlations between species and stages under both conditions. Colour and thickness of lines linking species and stages are equivalent to species correlations (red and blue for negative and positive correlations respectively). Only significant correlations are shown (based on the 95 % credible intervals excluding zero). The size of the nodes or circles (i.e. species and stages) is proportional to the absolute sum of their correlations. Species codes are based on their initials and ontogenetic stage (e.g., TS_A = *T. spinulosos* adults). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

increasingly overlapped towards low tide levels. Our design reflected the position of ALAN sources in the field and in areas with heavy light pollution, and the dilution of effects detected, represents rather well what seems to happen as ALAN intensities fade with distance. The stronger influence of ALAN at the upper intertidal was also evident on the network plot of correlations between species and stages. The number of correlations between species abundances and stages was low in control transects, which suggests a lack of correlation between the distribution of isopods and amphipods and only a weak correlation between adults of beetles and amphipods. In contrast, correlations among species and stages were stronger and more numerous under ALAN conditions, probably because of spatial shifts among species. Although the focus of our study was not on the assessment of species interactions, those correlations likely reflect various changes on these interactions (or lack of in some cases) that should be studied further if ALAN exposure continues to grow in this and other sandy beaches of the region and elsewhere.

Beyond the interaction between species and between life stages, and how they regulate community structure at a particular intertidal level, the disruptive influence of ALAN should also be examined with regards to the ecosystem role of these organisms. The natural emergence and downshore migration of amphipods, isopods and beetles are directly related to feeding, specifically, grazing on seaweeds (Jelassi et al., 2014). Therefore, an ALAN-induced reduction in activity forces these organisms to remain buried in the sediment for extended periods of time (Rossano et al., 2018; Lynn et al., 2021), ultimately affecting the rates of feeding and processing of stranded seaweeds (Colombini et al., 2000; Cruz-Rivera and Hay, 2001; Rodil et al., 2015; Luarte et al., 2016). Such a role is critical for these consumers as well as for the seaweeds, which represent a main trophic subsidy for these ecosystems, and are relevant in the recycling of nutrients and the transport of carbon and nutrients between different ecosystems (Dugan et al., 2011; Krumhansl and Scheibling, 2012; MacMillan and Quijón, 2012; Rodil et al., 2015; Rodil et al., 2019). It follows that the fate of these communities and the primary producers forming wrack deposits may be altered by a growing influence of ALAN (Cinzano et al., 2001; Falchi et al., 2016). Further studies should therefore forecast the direction of the changes documented here in order to understand how light intensity or other features of ALAN sources (Davies et al., 2014) can further modify these and other species and life stages. Only the growth of that research would be able to properly inform management measures aiming to mitigate the future influence of ALAN in sandy beaches and other coastline habitats.

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Data availability

Data will be made available on request.

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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