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# Isolation by environment in the highly mobile olive ridley turtle (*Lepidochelys olivacea*) in the eastern Pacific

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Spatial and temporal scales at which processes modulate genetic diversity over the landscape are usually overlooked, impacting the design of conservation management practices for widely distributed species. We examine processes shaping population divergence in highly mobile species by re-assessing the case of panmixia in the iconic olive ridley turtle from the eastern Pacific. We implemented a biophysical model of connectivity and a seascape genetic analysis based on nuclear DNA variation of 634 samples collected from 27 nesting areas. Two genetically distinct populations largely isolated during reproductive migrations and mating were detected, each composed of multiple nesting sites linked by high connectivity. This pattern was strongly associated with a steep environmental gradient and also influenced by ocean currents. These findings relate to meso-scale features of a dynamic oceanographic interface in the eastern tropical Pacific (ETP) region, a scenario that possibly provides different cost–benefit solutions and selective pressures for sea turtles during both the mating and migration periods. We reject panmixia and propose a new paradigm for olive ridley turtles where reproductive isolation due to assortative mating is linked to its environment. Our study demonstrates the relevance of integrative approaches for assessing the role of environmental gradients and oceanographic currents as drivers of genetic differentiation in widely distributed marine species. This is relevant for the conservation management of species of highly mobile behaviour, and assists the planning and development of large-scale conservation strategies for the threatened olive ridley turtles in the ETP.

## 1. Introduction

Panmixia (i.e. random mating within a breeding population) is an unusual pattern in widely distributed marine species that challenges expectations of population structure over large and environmentally heterogeneous regions [1]. Patterns of population-genetic structure emerge over time as a result of different dispersal schemes, life-history traits, and environmental and geographical features [1,2]. Population structure has been generally related to 'isolation-by-distance' (IBD), a model where genetic distance between populations is correlated to their geographical separation [3]. However, in the last decade, evidence has accumulated for correlations between environmental and genetic discontinuities [4–6]. In the model known as 'isolation-by-ecology' or 'isolation-by-environment' (IBE), differentiation among populations can arise as a result of non-random mating due to adaptation to different environments (i.e. mismatch on reproductive timing),

and non-random mating due to environmentally mediated phenotypic plasticity (i.e. selection of feeding environments based on learned experiences) [7]. While testing for IBD may be a simple task, analysing the influence of environmental factors driving genetic differentiation in the marine environment, which lacks obvious barriers, can be very challenging [8].

Recent statistical advances have promoted the combination of high-resolution population-genetic data with environmental information to account for the effects of landscape or seascape features on gene flow [9,10]. This multidisciplinary approach, known in marine systems as seascape genetics, has been successfully applied to address a range of ecological questions [11–13]. Most studies have focused on species with larval stages where the influence of specific oceanographic variables is expected, allowing a more straightforward quantification of biological parameters across heterogeneous environments [12,14,15]. This is not the case for marine top predators, where the application of models that adequately depict both relatively static and dynamic seascape features is seen as a major challenge [10] (but see [11,16]). Advances in oceanographic modelling and the application of biophysical models, as tools by which dispersal probabilities can be estimated, promise to offer an exciting alternative to overcome this challenge. These models integrate data from the time-varying ocean circulation variability and biological parameters of the species and allow direct comparisons with information about the distribution of observed genetic variability (i.e. [15,17]).

Sea turtles are among the most ancient reptiles on earth and represent a group of high conservation concern, making them target organisms for many evolutionary and population-genetic studies that can inform conservation and management [18–21]. Yet, to date, no studies have tested for IBE in sea turtles, hampering our ability to understand the relative influences of spatial scales and environmental heterogeneity in population connectivity of this group of marine top predators. Like other highly mobile marine species, sea turtles perform long-distance migrations using a variety of habitats (varying among neritic and oceanic habitats depending on the species) during their lifetime [22]. Population structure in sea turtles is fundamentally promoted by females' natal homing behaviour or philopatry (return of adults to their natal beaches) and site fidelity (precision with which they return to the same beach in subsequent years) to nesting beaches (but see [23] on fidelity of breeding males to courtship areas). These processes reduce gene flow among groups of individuals that breed in geographically distant locations, resulting either in marked population-genetic structure when high philopatry and site fidelity are present, or the opposite when they are lower or take place at broader scales (reviewed by [24]). High philopatry and site fidelity are also common in several other aquatic and terrestrial species [25], but these traits do not apply universally to all sea turtles. This is the case of the olive ridley turtle, *Lepidochelys olivacea*, recognized as a panmictic species at regional levels (i.e. the eastern Pacific [24,26]; but see [27,28]). In olive ridley turtles, the absence of population structure has been associated with low site fidelity and high nomadic behaviour, the latter potentially linked to their use of highly productive pelagic and oceanic areas in the eastern Pacific [29,30]. In this region, fidelity to nesting areas has been documented primarily at synchronous *arribada*-nesting females, while solitary nesting females are known to exhibit low levels of fidelity, spreading their reproductive efforts among multiple beaches separated by hundreds of kilometres [31].

In the eastern Pacific, olive ridley turtles are found from Mexico to Ecuador, a region that represents the main area of reproduction of the species worldwide [32]. This region is considered of great oceanographic variability, with circulation influenced by wind forces and permanent meso-scale features (i.e. spatial scales of less than 500 km and time scales of less than 100 days) known for affecting the distribution of marine vertebrates [33]. Additional significant impacts on oceanographic and biological processes relate to the interdecadal variability by El Niño–Southern Oscillation (ENSO), and its warm (El Niño) and cold (La Niña) phases [34]. Ocean currents and oceanographic cues are recognized as having an important influence on dispersal and habitat preference of sea turtles [35]. Nonetheless, the complex interplay between biological and environmental features, and in particular the relationship between oceanographic and genetic discontinuities, remains an understudied topic in sea turtle ecology. Exploring this frontier may answer key ecological questions related to natal homing and ecological processes influencing individual dispersal and population distribution in sea turtles.

Here we carried out a seascape genetic analysis to (i) test for panmixia in olive ridley turtles over a region with marked oceanographic discontinuities and (ii) assess the influence of environmentally dynamic seascapes on population divergence of a marine top predator. We analysed nuclear genetic variation of 634 individuals sampled across a vast geographical area in the ETP and implemented a biophysical model based on a hydrodynamic numerical ocean model in combination with a Lagrangian trajectory toolset. The re-assessment of panmixia in this species is relevant given the vulnerable status of populations worldwide [32] and the endangered status of local populations (i.e. in Mexico, US Endangered Species Act, ESA). Our study clarifies management units (MUs) for conservation in this charismatic species and exemplifies an integrative framework for studying population movements and addressing large-scale threats in marine vertebrates distributed across oceanographically heterogeneous regions.

## 2. Methods

### (a) Study area: the eastern tropical Pacific

The eastern tropical Pacific (ETP) includes the eastern and equatorial branches of the north and south Pacific subtropical gyres, the south and north equatorial currents, and two coastal counter-currents (California current and Peru current) [36]. The oceanographic dynamics are influenced by wind forcing that generates coastal eddies, impacting sea surface temperature (SST) as well as circulation. The main meso-scale features are the cyclonic and anticyclonic eddies of the Costa Rica Dome and Tehuantepec Bowl that originate off the coast of Costa Rica and southern Mexico, respectively (figure 1*a*; electronic supplementary material, figure S1). These features result from highly seasonal trans-isthmic wind jets, fertilizing marine zones that extend up to 1000 km offshore [36]. These main features are considered to influence the distribution of cetaceans and seabirds [33]. In addition, coastal and equatorial upwellings are biological hotspots offering a wide range of foraging habitat to sea turtles [37].

### (b) Sample collection and microsatellite genotyping

We collected samples of 634 olive ridley turtles across the ETP during the 2006 and 2010 nesting seasons (figure 1*a*). Skin biopsies were collected from nesting females; when this was difficult, one dead hatchling per nest was sampled. Analyses are based on

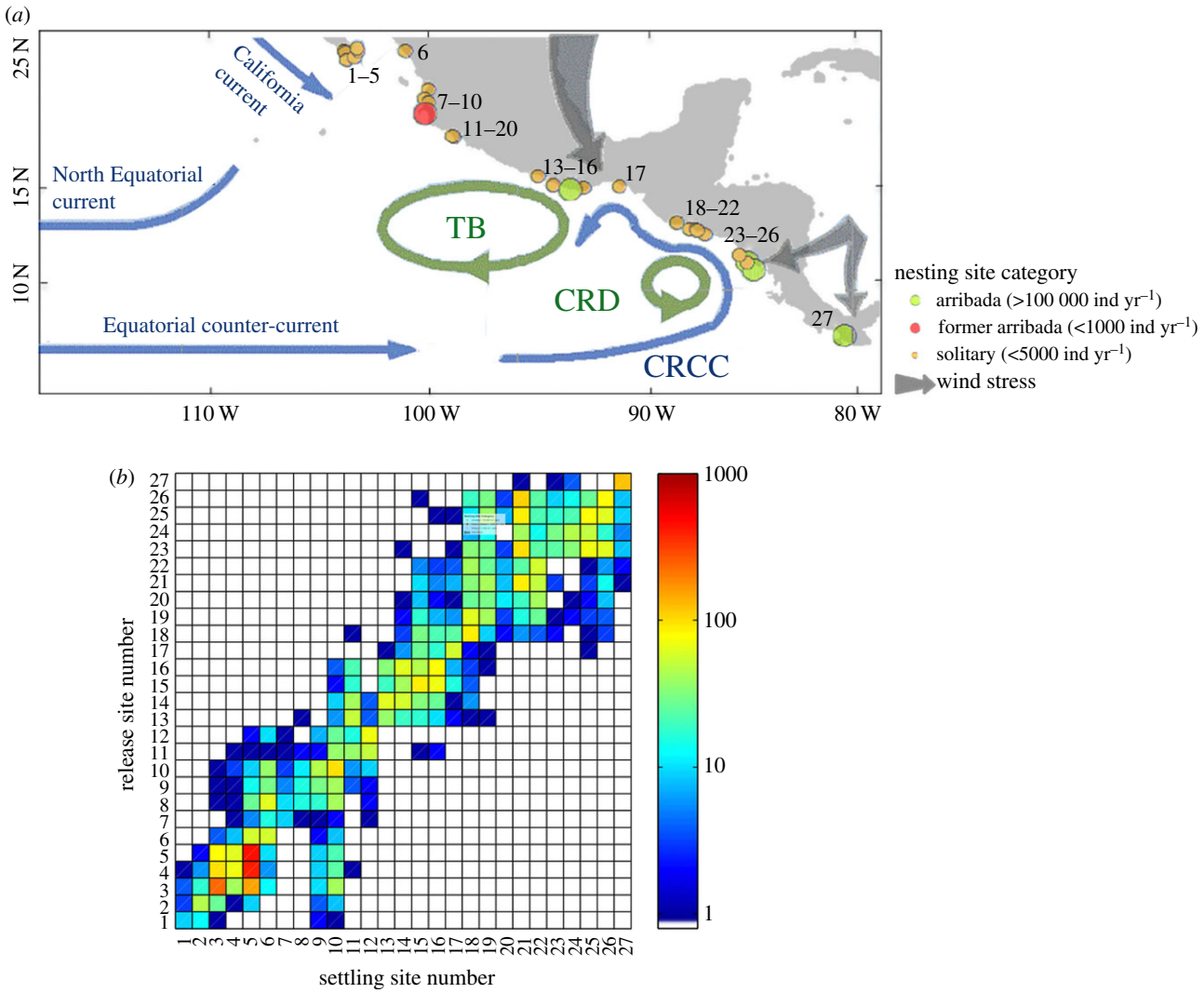


**Figure 1.** (*a*) Schematic of relevant meso-scale oceanographic features in the ETP and distribution of sampling sites of olive ridley turtles included for Lagrangian particle simulations. Oceanographic features: Tehuantepec Bowl (TB), Costa Rica Dome (CRD), Costa Rica Coastal Current (CRCC). (*b*) Connectivity matrix based on Lagrangian particle simulations. The matrix quantifies the degree of inter-site connectivity by tracking particles released on 27 nesting sites during the mating season and tracked back in time 150 days. The scale indicates number of particles settled per site up to 1000 particles (1–1000) with white colour indicating zero particles.

a maximum of 27 nesting areas; sites with fewer than 15 samples were assigned to major nesting areas ($n = 22$) using the criterion of the geographically closest neighbour. DNA extractions and collection of data from 10 olive ridley turtle microsatellite loci (electronic supplementary material, tables S1 and S2) followed [38]. Null alleles and large allele dropout were assessed for each microsatellite locus in Micro-Checker [39].

## (c) Genetic diversity and spatial population structure

Departures from Hardy–Weinberg expectations (HWE) and linkage disequilibrium (LD) among loci were tested in GenePop 4.0 [40]. Genetic diversity was estimated as expected (He) and observed (Ho) heterozygosity, allelic richness (AR) and FIS using FSTAT 2.9.3 [41]. Molecular variance (AMOVA) based on two genetic distance estimators ($F_{ST}$ and Jost's $D_{EST}$) was estimated in Arlequin 3.11 [42] and Genalex 6.5 [43], respectively.

We further tested for population differentiation across the ETP using a Bayesian clustering analysis in Structure 2.1 [44], using the standard and LocPrior admixture models. The identification of populations (K-clusters) followed [45], with 20 independent runs for each of $K = 1–22$ using $10^5$ iterations after a burn-in of $10^4$. To assess the spatial scale of genetic exchange we calculated autocorrelation coefficients of multilocus genotypes ($r$) among individuals sampled in the same locality (distance class 0) and among individuals separated by 100 km up to 3000 km using Genalex. We also used IBDWS 3.16 [46] to test for IBD patterns using $F_{ST}$ and $D_{EST}$ genetic distance.

## (d) Environmental predictors of genetic structure

We used four key oceanographic variables to assess whether genetic connectivity could be influenced by environmental heterogeneity in the ETP: night-time SST, chlorophyll *a* concentration (Chl_a, mg $m^{-3}$), sea surface height (SSH, cm) relative to a 450 m reference level and thermocline depth (obtained from remote sensing and float data; electronic supplementary material, appendix S1). In particular, SST and chlorophyll fronts influence spatio-temporal distribution of prey, and consequently migration patterns and habitat utilization of predators [47]. Environmental information was gathered for marine areas up to 1000 km offshore from each nesting area, corresponding to the scale of high habitat use by eastern Pacific olive ridley turtles (50 km up to 1000 km [30,48]), and our aim of depicting the influence of environmental heterogeneity on turtles' dispersal from foraging to coastal breeding grounds. Climatology maps for five seasonal periods were then reconstructed, and each pixel in the maps corresponded to the 10-year (2001–2011) average value for a 37 km grid (electronic supplementary material, figure S2a–Sd). The seasonal periods demarcate behavioural patterns for olive ridley turtles in the ETP:

**Table 1.** Hierarchical analysis of molecular variance (AMOVA) for olive ridley turtle populations in the ETP.

| source of variation | percentage of variation | *F*-statistics | *p*-value |
|---|---|---|---|
| among groups (putative populations) | 2.79 | $F_{CT} = 0.0279$ | 0.0000 |
| among nesting colonies within groups | 0.003 | $F_{SC} = 0.0008$ | 0.2849 |
| within nesting colonies | 97.12 | $F_{st} = 0.0288$ | 0.0000 |

MIG, migration to breeding areas (April); MATE, mating season (May–June); NES1, beginning of nesting season (July–September); NES2, ending of nesting season (October–December); FEED, migration and residence on feeding areas (January–March). Habitat utilization in sea turtle hatchlings has been linked to currents, eddies and convergent zones of high productivity [35]; therefore, maps were also coupled with data of geostrophic currents (gathered from AVISO). Data were processed using ArcGIS software v. 10.1 (http://www.esri.com).

We used a variety of analytical tools to assess the relative importance of environmental variables on the genetic structure of olive ridley turtles. By using the hierarchical Bayesian analysis in GESTE [49], we assessed the relative importance of SST, Chla, SSH and Therm on the genetic structure. As GESTE uses population-specific $F_{ST}$ as genetic data, the four environmental variables were transformed to make them population-specific, and coded as the mean absolute difference of a variable between a sampling locality and each of the other sampling localities [6]. To consider the effect of geographical distance, the mean distance between each locality and all other localities was calculated using pairwise geographical distances. A test for the effect of advection connectivity was incorporated using results from the Lagrangian particle simulation (see below). For the latter, we calculated a population-specific advection connectivity index as the proportion of immigrants in regard to the total number of particles reaching a specific locality. Overall, the influence of six factors (i.e. four environmental variables, geographical distance and advection connectivity) was tested for each seasonal period (MATE, MIG, NES1, NES2 and FEED). Using these five seasonal analyses, we identified the factors that best explained the observed genetic structure by calculating the posterior probability of all the models that include any given factor [6]. We then identified the best model using the estimated posterior model probabilities resulting from a final GESTE analysis that included only the previously selected five factors (i.e. with posterior probability $> 0.1$). Additionally, two separate complementary analyses (a BIOENV procedure and a partial redundancy analysis, pRDA) were implemented as described in the electronic supplementary material.

Mantel and partial Mantel tests were also used among nesting colonies (subpopulation level), and between putative populations to test for correlations between pairwise genetic ($F_{ST}$ and $D_{EST}$) and environmental distances, while controlling for the effect of geographical distance. Finally, we also implemented a stepwise multiple regression analysis of standardized distance matrices [50]. The stepwise procedure adds one variable at a time with each step resulting in a model modified in every successive step. Each model is then tested for statistical significance. Tests were performed using the package vegan in R v. 3.0 [51].

### (e) Seascape genetics

A hydrodynamical model was implemented to investigate potential effects of ocean currents on dispersal and population connectivity of olive ridley turtles. This model simulates movement of individuals by incorporating ocean dynamics from a hydrodynamic numerical ocean model in combination with a Lagrangian trajectory toolset. Three-dimensional velocity data were used to generate a connectivity distance matrix between nesting sites based on the maximum of sampled sites possible with available genetic information (27 sites). A more simplified connectivity matrix based on 22 sites, was also generated to test for the sensitivity of pooling sites. We used the Ocean Model for Earth Simulator (OFES) [52] at a global resolution of 0.1° (approx. 10 km in the region). While models with finer resolution exist, none of them spans the large area of the tropical Pacific over which olive ridleys move around, meaning that this resolution was optimal between resolving fine enough coastal details while capturing the flow in the entire Pacific. The Connectivity Modeling System v.1.1 [53] was used to integrate virtual Lagrangian particles within the velocity fields saved every 3 days for the period January 1980 to December 2010. For each site, one particle was released every day (with a total of 1891 particles per site) at 10 m of depth; and two-dimensional locations of the particles were saved every day. Particles were released in May and June (mating season) and their trajectories were tracked back 150 days. The results were combined into single matrices describing the proportion of particles (individuals) from a given source-nesting colony (rows) reaching a specific destination (columns) at a given time. The ocean circulation effect on sea turtle dispersal was assessed with a Mantel test by comparing connectivity distance matrices against $D_{EST}$ genetic distances. To test the hypothesis that ocean circulation influences population structure independent of distance and genetic clustering, a partial Mantel test was also performed.

## 3. Results

### (a) Regional genetic diversity and population structure

No deviations from HWE or evidence of LD were detected, and all microsatellite loci were variable (average of 10.9 alleles per locus, mean Ho = 0.72 and AR = 5.85; electronic supplementary material, table S1). Null alleles were identified for one locus (OR2) at only four out of 22 nesting areas; results remained unchanged with its removal so this locus was kept for analyses.

The hypothesis of random mating across the ETP was rejected ($F_{ST} = 0.015$, $p < 0.001$). Nesting colonies pairwise comparisons based on both $F_{ST}$ and $D_{EST}$ were significant in a pattern where Mexican nesting colonies were differentiated from those in Central America, but not different within each of the two inferred groups (electronic supplementary material, table S3). The same pattern was confirmed by hierarchical AMOVA ($F_{ST} = 0.027$, $p < 0.001$; table 1).

The Bayesian analysis of structure corroborated previous results by detecting two spatial clusters ($K = 2$), referred herein as the northern (all Mexican nesting colonies) and southern (all Central American nesting colonies) populations. Populations were well defined regardless of admixture model used (figure 2). These findings were consistent with results from other analyses (electronic supplementary material, figure S2, tables S3 and S4).

Results of spatial autocorrelation and partial Mantel tests indicated positive correlations of genetic variation with geographical distance at the regional level ($F_{ST}$: $r = 0.439$,

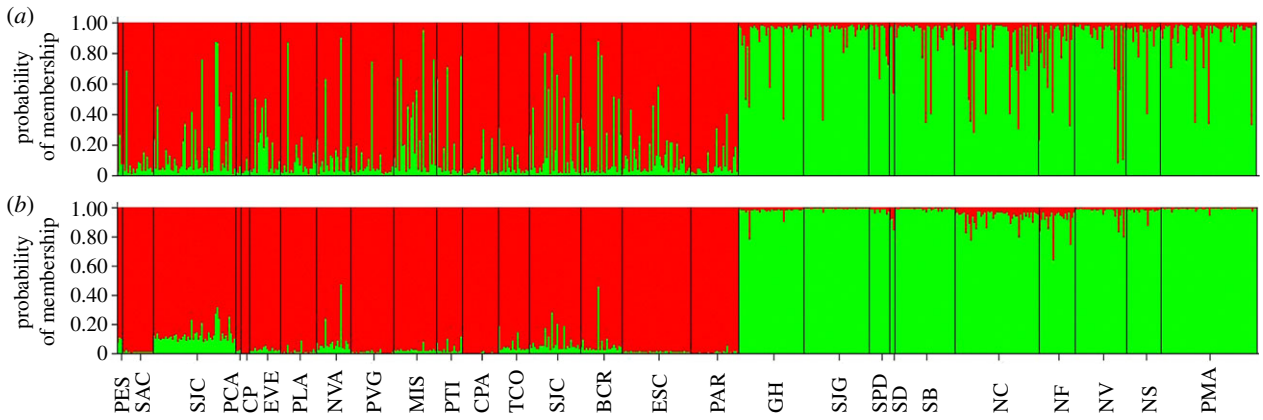


**Figure 2.** Estimated probabilities of membership coefficients for each individual turtle in the inferred clusters estimated by STRUCTURE based on two admixture models: (*a*) standard and (*b*) LocPrior. Each bar represents an individual from a total of 27 sampling sites with the proportion of colour representing assignment to cluster 1 or 2.

**Table 2.** Posterior probabilities of the most probable models for the final GESTE analysis including the five factors with highest posterior probability in each seasonal analysis. Also shown is the sum of posterior probability of models that included a particular factor. Chl_a, chlorophyll concentration; Therm, thermocline depth; MIG, migration to breeding areas; MATE, mating period; NES1, beginning of nesting season July to August; NES2, ending of nesting season.

| GESTE—final analysis | | | | |
|---|---|---|---|---|
| model | factors included | probability | sum posterior probability | |
| 2 | MIG_Therm | 0.27 | MIG_Therm | 0.37 |
| 3 | MATE_Therm | 0.25 | MATE_Therm | 0.34 |
| 1 | Null | 0.22 | NES1_Therm | 0.04 |
| 17 | NES2_Chl_a | 0.05 | NES2_Therm | 0.09 |
| 4 | MIG_Therm and MATE_Therm | 0.03 | NES2_Chla | 0.13 |

$p < 0.0001$; $D_{EST}$: $r = 0.361$ $p < 0.0003$), but not at the subpopulation level (northern population: $F_{ST}$: $r = 0.027$ $p = 0.351$; $D_{EST}$: $r = 0.025$ $p = 0.4003$; southern population: $F_{ST}$: $r = 0.0078$ $p = 0.446$; $D_{EST}$: $r = -0.0615$ $p = 0.558$; electronic supplementary material, figure S4 and table S5, respectively). Spatial autocorrelation of genotypically similar individuals across the region was observed for up to 400 km ($r = 0.008$, $p = 0.001$; electronic supplementary material, figure S4).

## (b) Influences of environmental heterogeneity on genetic structure

All analyses indicate that environmental heterogeneity influenced population divergence. They also pinpointed biologically relevant periods where this influence takes place and highlighted the relative contribution of ocean currents in genetic structure. GESTE provided evidence for an important role for Therm during two critical seasons (MATE and MIG), as well as contribution of Chl_a (table 2; electronic supplementary material, table S6). This was consistent with results from BIOENV (electronic supplementary material, table S6) and particularly with pRDA (electronic supplementary material, figure S8). The final RDA results included two environmental variables (MIG_Chl_a and MIG_Therm), plus the advection connectivity and geographical distance. This model was globally significant ($p = 0.002$) with environmental variation and advection connectivity explaining 49.4% of the total genetic variation even after controlling for IBD (the latter explained only 11% of total genetic variation).

In addition, Mantel tests indicated significant correlations with Chl_a and Therm, for the same MATE and MIG seasons, respectively. These are depicted in a pattern predicted by the presence of a spatially steep environmental gradient (e.g. [54]), as indicated by Mantel correlograms (electronic supplementary material, figure S6). The results remained significant after controlling for the effects of geographic distance and genetic clustering in the two groups (electronic supplementary material, table S7). Stepwise multiple regression analysis supported Mantel test results (electronic supplementary material, table S8). The variability of the main environmental predictors for the MIG and MATE seasons in the ETP is shown in electronic supplementary material, figure S1.

## (c) Biophysical model confirms the effect of an environmental gradient on dispersal

The connectivity matrices showed zones of moderate to high retention of particles, suggesting restricted connectivity among nesting sites during the turtle migration period. These findings were obtained for particles sampled back 150 days based on simulations including all 27 or 22 nesting areas (figure 1*b*; electronic supplementary material, figure S6). The pattern of restricted connectivity remained significant when

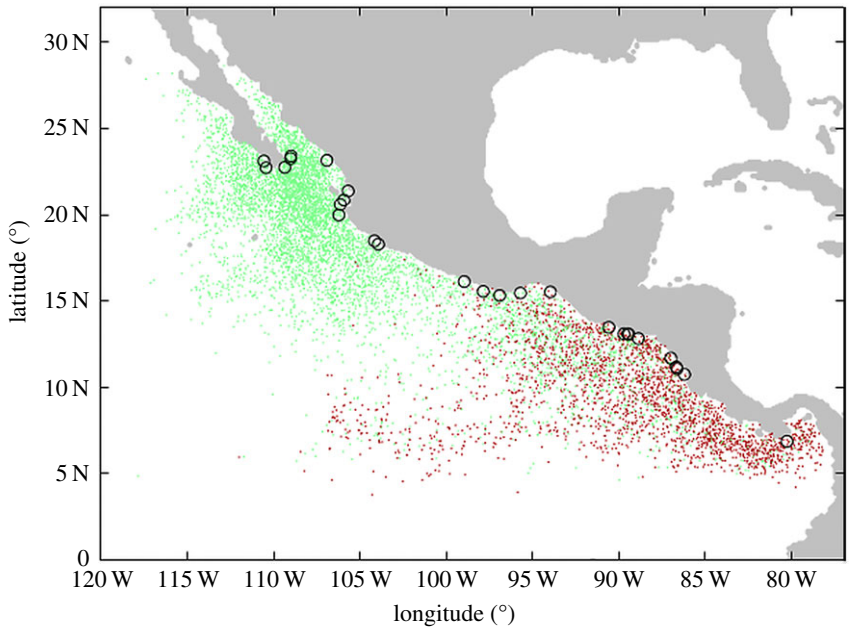


**Figure 3.** Lagrangian particle distribution for olive ridley turtles in the ETP released on 27 nesting sites during the mating season and tracked back in time 150 days. Distribution of particles shows two spatially distinct groups in the ETP (northern population: green particles; southern population: red particles).

connectivity matrices and genetic distances were compared and correlations controlled for geographical distance and genetic clustering ($r = 0.1972$, $p = 0.0482$, and $r = 0.2697$, $p = 0.0241$, respectively). The plots of particle distribution support the existence of two oceanographically dynamic but largely disconnected regions in the ETP, with a mixing zone located in southern Mexico (figure 3; electronic supplementary material, figure S7).

We also explored the possibility that connectivity during the nesting period influences the distribution of genetic variation in olive ridleys by sampling particles back to 185 days (July). Connectivity increased (electronic supplementary material, figure S7b,c) and was not correlated with genetic information when controlling for geographical distance and genetic clustering ($r = 0.005$, $p = 0.4559$, and $r = 0.1668$, $p = 0.0768$, respectively). This indicates that environmental heterogeneity during this period does not restrict dispersal of turtles. However, plots of particle distribution for this period still supported two spatially distinct groups in the ETP (electronic supplementary material, figure S7).

## 4. Discussion

This study challenges the paradigm of regional panmixia proposed for the highly migratory and nomadic olive ridley turtle in the ETP [24,26]. We report on population divergence across a steep environmental gradient linked to a dynamic oceanographic interface in the ETP. The gradient, and to a lesser extent the ocean currents, appear to influence dispersal of olive ridleys during both the mating and migration periods. These results held after accounting for the effects of geographical distance and represent, to the best of our knowledge, the first evidence for IBE [7,55] in a sea turtle. We propose a new paradigm for olive ridley turtles where reproductive isolation due to assortative mating is linked to its environment, which provides different cost–benefit solutions and selective pressures for sea turtles.

### (a) Meso-scale oceanography, environmental heterogeneity and population divergence

Oceanographic features and currents play an important role by reducing the associated costs of dispersal of many marine organisms including sea turtles [22,56], something particularly advantageous for females during the breeding season. In addition, habitat preference determined by particular cues [35,50] influences the dispersal of individuals and horizontal and vertical migration. The biophysical model implemented here showcased the role of ocean currents in influencing connectivity at a range of spatial scales (figures 1 and 3). Additionally, GEST and complementary analyses indicated that thermocline variation and primary productivity, which vary across the oceanographic interface, are proxies for the genetic structure of the species in the ETP. These results provide an environmental context to interpret the complex interplay between biological factors, oceanographic variation and habitat heterogeneity (i.e. [15]).

The biophysical model proved to be valuable in describing impeded connectivity at a regional scale by disclosing two main oceanographic zones of moderate to high retention of particles, particularly during the migration and mating period. The distribution of simulated particles reflected the spatial segregation of a northern and a southern population in the ETP (figure 2). These appear as largely isolated during the migration and mating season, but each is composed of multiple demes linked by high connectivity (figure 3; electronic supplementary material, figure S7). The latter is consistent with high gene flow among 13 nesting colonies of olive ridleys surveyed along the Mexican coast [38].

The low levels of genetic differentiation reported may have been the result of the region's recent colonization by olive ridley turtles followed by environmentally driven divergence. Distinguishing between ongoing ecological divergence in parapatry versus secondary contact of populations that initially diverged in allopatry is difficult (i.e. [52,54]). Nonetheless, strong support for the former comes from biogeographic studies of the species [26–28].

The Indo-West Pacific is thought to be the centre of radiation of olive ridleys, which first colonized the Atlantic and more recently (approx. 0.3 Ma), the eastern Pacific Ocean [26,28]. Phylogeographic analyses also suggested a constraint of species range to tropical waters during glacial periods with subsequent expansions from southern to northern areas in the ETP [27].

The genetic break identified here is located between the boundaries of the Costa Rica Dome and the Tehuantepec Bowl meso-scale features (figure 1*a*), suggesting that the seasonal dynamics of these systems generate an environmental gradient impacting on gene flow. This gradient may also be strengthened by vertical variation in thermocline depth, as shallow thermoclines, such as the one in the Costa Rica Dome, are known to aggregate marine life preventing prey from dispersing and providing abundant feeding opportunities for marine predators [57]. In Atlantic leatherback turtles, temporary residency areas have been found associated with meso-scale surface oceanographic features as depicted in altimetry features and chlorophyll *a* concentration [50].

The two meso-scale systems of high productivity develop during boreal winter and become particularly active during spring [58] (the time where olive ridley turtles start their migration to breeding areas). They exhibit strong current speeds around their edges of about 20–50 cm $s^{-1}$, weaker during summer [58], and comprise features of comparable primary productivity [36] that are relatively permanent and predictable [58]. Thus, dispersal during this key season (spring) and associated variation in thermocline depth might have influenced dispersal trajectories in sea turtles due to differential cost–benefit solutions and selective pressures. We envisage several benefits for turtles that remain associated with each of the two oceanographic systems of high productivity while migrating towards coastal areas for reproduction. These include: (i) reduction of feeding costs by decreasing diving time and energy spent when searching for prey, as the latter concentrates in upper layers of the water column due to variation in thermocline depth; (ii) increasing energy storage by females for mating and reproductive output (approx. one to three clutches per season); and (iii) reduction of migration cost, particularly for females, which are known to return to the same natal areas for reproduction.

Investigating the role of environmental heterogeneity in population-genetic divergence along the evolutionary continuum is becoming a popular topic in biology [7,52,55]. Critically, the relatively simple seascape genetic approaches applied here emphasize the synergistic interaction that natal homing behaviour, dispersal cost/benefit and environmental barriers might have on population structure of sea turtles. This lead us to propose a model where olive ridley turtles return to natal regions at broad spatial scales to nest. Hatchlings are then drifted by predominant currents to areas within the boundaries of both populations, where high productivity is likely to enhance hatchlings' survival. As adults, they will then return to natal beaches with low levels of philopatry, but dispersal beyond the boundaries of each population will be limited by the combined action of predominant currents and environmental discontinuities associated with meso-scale features.

Our findings highlight the need for additional regional-scale studies in marine top predators that assess gene flow across heterogeneous environments while controlling for spatial genetic autocorrelation. Such surveys would also benefit from *a priori* spatial delineation of ecologically relevant phenotypes (i.e. adaptive phenotypes) and from scenarios where environmentally driven population divergence can be disentangled from vicariant biogeographic history (*sensu* [52]). Lastly, it is expected that novel seascape computational methods become increasingly available to overcome well-known limitations in the use of $F_{ST}$ as a preferred measure of genetic distance for species with high levels of genetic diversity [59].

## (b) Conservation implications

The perspectives about connectivity and population divergence provided here contribute to the re-definition of MUs at regional scales and highlight the role of solitary nesting sites in maintaining regional connectivity within putative populations (figure 1*b*) that could in some cases benefit recovery trends. However, recent evidence indicates that despite high levels of metapopulation connectivity in Mexico, the recovery of genetically eroded nesting colonies may be compromised [38]. Olive ridley turtles are still listed as endangered by the US Endangered Species Act (ESA) due to increasing mortality associated with bycatch [60,61]. Thus, our results can add to ongoing efforts to quantify and address widely distributed US threat effects on sea turtle populations [60].

Finally, our understanding about population divergence in sea turtles would benefit from next-generation sequencing (NGS) approaches to identify gene regions targeted by natural selection and to link them to underlying landscape or seascape features [62]. An even greater contribution would probably be made by combining landscape genomics, transcriptomics and candidate gene approaches to identify genomic signatures associated with putatively adaptive traits in sea turtles. Such studies would be in a stronger position to clarify aspects of the biology of highly mobile marine species and to build a framework for conservation management that takes into account the functional role that heterogeneous seascapes might have in maintaining biodiversity structure and dynamics.

Ethics. Permissions for collecting samples were obtained separately in countries where it was required (MARN-AIMA 89-2010, El Salvador; CONAP 043/2010, Guatemala; SGPA-DGVS-04687-06, Mexico; 014-112010/DGPN, Nicaragua and SE/A-118-10/ANAM, Panama). CITES permits used to export/import samples were 2011-AU-624683, 07761, 509/2010, MX50499, 09025, SEX/A-18-11.

Data accessibility. Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.nj344m5 [63].

Authors' contributions. L.B.B. and C.J.R.-Z. developed the conceptual framework and devised analytical approach. C.J.R.-Z. and J.S.-C. performed most analyses. E.v.S. performed biophysical model simulations, C.J.R.-Z. and R.G.K. processed environmental data. L.B.B. and C.J.R.-Z. wrote the manuscript. A.R.-O. and J.U. contributed with fieldwork/samples.

Competing interests. We declare we have no competing interest.

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