Rita Castilho

Relatório Unidade Curricular

[Relatório Unidade Curricular apresentado nos termos da alínea c) ii) do n.º 3 do artigo 4.º do Regulamento de atribuição do título académico de agregado da Universidade do Algarve, publicado no Diário da República, 2.ª série, n.º 33, de 17 de fevereiro de 2020]

Marine Biogeography and Evolution

“RELATÓRIO DA UNIDADE CURRICULAR”

Framework, Contents and Methodologies

Rita Castilho

[Relatório da unidade curricular apresentado nos termos da alínea c) ii) do n.º 3 do artigo 4.º do Regulamento de atribuição do título académico de agregado da Universidade do Algarve, publicado no Diário da República, 2.ª série, n.º 33, de 17 de fevereiro de 2020]

Table of Contents

1. Preface

This document is part of the instruction process for Rita Castilho's candidacy to "Agregação", under the terms of Decree-Law nº 239/2007 of 19 June, of the Ministry of Science, Technology and Higher Education. It constitutes the pedagogical report of the curricular unit of Evolution and Marine Biogeography and is presented in English because the UC is part of the course plan of the (international) Master's Degree in Marine Biology at the University of Algarve, which is entirely taught in English. This document contains the contents of the program presented in detail and serves as a basis for the lessons of the curricular unit.

2. Course Basic Information

Module Title.
Marine Biogeography and Evolution

Discipline (field).
Marine Biology and Evolutionary Biology

Study level.
Graduate students.

Brief Description.
This unit has a total of 6 ECTS, corresponding to 156 total hours divided into 48 of contact (roughly a third of total hours) and 108 independent work. The course format will consist of lectures, discussions, and computer-based activities. The contact hours per week are divided into three hours of lectures and four hours of computer and tutorial classes per week, a total of 6 weeks. Computer-based exercises intend to reinforce and expand on key concepts introduced during the lectures providing opportunities to think critically, formulate questions and explanations, and communicate these effectively. This inherently multidisciplinary area integrates data and approaches stemming from many fields within the abiotic and biotic factors that govern the assembly of species diversity across space and through time. Understanding the biogeographic principles that drive the species distributions is central for studies of biodiversity, global change, and conservation in today's changing world.

Class functioning.
My goal is to facilitate the learning of Marine Biogeography and Evolution. To do so, I combine traditional expository lectures, computer-based activities, and discussions to illustrate diverse problems and techniques in this field. Because learning is not a passive process, students are expected to (1) attend all class sessions, (2) actively participate by asking questions in class, (3) come prepared - read assignments before class, and (4) communicate and work cooperatively with their peers.

Slides from class lectures are available on the dedicated website after class. Students are informed that slides have limited text, and I do not post lecture notes. I, therefore, suggest that students take notes during class and review notes and the lecture slides after class.

Class size.
The ideal class size is 30 students for the theoretical classes divided into groups for the computer labs. However, frequently we need to accommodate more students, and although not ideal, it is possible to still bring class discussions to fruition.

Objectives.

This course will examine the basic concepts of evolution and biogeography relating to the marine realm. It will focus on applying methods used to study evolution and biogeography. It will draw on a wide range of evidence from molecular data, distribution records, fossil records and life history traits to larval duration to explain biodiversity in the marine environment. It will review several case histories to demonstrate the role of historical events in determining distributions of marine taxa and contrast this with the role of ecological factors in maintaining marine populations.

Learning outcomes.

The main learning outcomes expected from this course are:

1. understand the evolutionary history, life history, distribution patterns, and speciation patterns of marine organisms;
2. understand the methods used to study the phylogeography of marine organisms;
3. understand the role of historical (geological) events in shaping the planet and influencing the volume and bathymetry of main water bodies.
4. synthesise current concepts of marine species and factors influencing speciation and distribution patterns;
5. knowledge of several marine organisms' evolutionary history, distribution patterns, and speciation patterns.
6. have demonstrable knowledge of the current literature relevant to marine evolution and biogeography.

Summary of contents.

1. Classe presentation (myself and students). Course outline (working schedule, topics, assessment, a dedicated webpage, moodle resources, preferred communication channels). Historical and Ecological biogeography. Main topics in biogeography. The phylogeography of sardines: a case study.

2. Early Biogeography. Pivotal biogeographers. Historical biogeography. The discovery of continental drift. The dispersal versus vicariance dilemma. Centres of origin, overlap and accumulation of species.

3. Ecological biogeography. Main contributing factors for limiting the distribution of marine organisms. Patterns of biodiversity. Measures of diversity. How many species are there? Overview of ocean biogeographic regions.

4. The evolution of Planet Earth's Oceans. Knowledge of the geological history of Earth's Oceans is essential for understanding contemporary diversity patterns. Continental drift. The formation and extinction of oceans and seas: formation and closure of Tethys, the opening of the Atlantic, formation of the Indian Ocean. The desiccation of the Mediterranean, the closure of the Isthmus of Panama, and the opening of the Bering Strait.

5. Biogeographic responses to glaciations. Milankovitch cycles. Measuring paleotemperatures. Isostatic and eustatic sea level. Lower sea levels in the past. Typical biogeographic responses to climate. Geographical barriers.

6. What is phylogeography? Most commonly used genetic markers. Molecular estimates of gene genealogies within species and between closely-related species. Statistical phylogeography. Avise's phylogeographic hypothesis.

7. The equilibrium theory of island biogeography. Species-area and species-distance relationships. Limitations of the equilibrium theory of island biogeography. Relevance of the concepts for marine conservation and the establishment of Marine Protected Areas.

8. Connectivity and genetic differentiation. Patterns of genetic differentiation in populations: definitions and examples of closed and open populations, cline populations, abrupt genetic changes due to geographical barriers, stepping stones and chaotic genetic patchiness type-populations.

9. The Atlantic-Mediterranean divide: a transitional zone. The geological history of the Mediterranean Sea. Hypotheses of biogeographic scenarios to explain genetic patterns between the Mediterranean and the Atlantic. Case studies: *Salaria pavo*; diverse genetic patterns in Sparidae from the Mediterranean and the Atlantic; responses to Pleistocene glaciations.

10. Marine Island evolution: what makes islands so interesting? The North Atlantic archipelagos. Evolution of marine organisms. Case studies: molluscs and fish, differences and similarities in colonisation and differentiation.

Adequacy and adjustment of content according to students' background.

Most of the MBM selected students are from Environmental Sciences, Life Sciences and Biology or Marine Biology. To these students, all the class content is intellectually accessible, and students are given enough supporting documentation to take up the individual study. Over the years, there was no specific need to make any specific adjustments to cater for eventual students' background mismatches. The adjustments this unit suffers are related to the need to update examples or approaches.

3. Justification

Marine biogeography is a research field that studies the patterns and processes governing the geographic distribution of marine taxa. It is a vibrant research field that aims to understand the role of historical factors in determining biodiversity and to advance predictive abilities for measuring how biodiversity will react to our unstable planet. Traditionally, biogeography was mostly a descriptive science. In the last decades, with the advent of technology, it has crossed the threshold of becoming a rigorous, measurable, hypothesis-driven science. The field compounds information from a wide range of other research areas, too many perhaps to list them all. The diversity of biogeography is vast, including basic sciences such as historical biogeography, ecology, evolutionary biology, oceanography, geology, and climatology, and social sciences such as linguistics, cultural biogeography, and more applied disciplines, such as invasion biogeography, disease ecology, environmental health. This course was developed to provide a historical background for the field of biogeography and the evolutionary foundations needed to understand the distribution and abundance of species and their changes over time. For instance, we aim to examine the relevance and contribution to global change biology, conservation, and invasion biology.

Historically, the development of marine biogeography has lagged behind its terrestrial counterpart for a few centuries, chiefly due to obvious logistical constraints in acquiring information in the ocean. The marine realm offers particular and often singular biophysical, environmental, and biotic features that shape unique environmental responses, such as (1) higher phyletic diversity than in the terrestrial realm (there are thirty-five marine phyla, compared to only eleven terrestrial phyla); (2) complex life cycles with unique challenges to understand biogeographic patterns and processes (possession or lack of a planktonic larval phase is one among many factors intervening at the scale of dispersal, gene flow, size of the geographic range, and duration in the fossil record); (3) air and seawater behave in quite different ways, shaping different adaptations by marine organisms and (4) the marine fossil record is comparatively much richer in preservation than that of terrestrial taxa, allowing phylogenetic dating of trees and testing evolutionary and historical factors shaping present-day biogeographic patterns.

What is marine biogeography, and why does it matter?

Marine biogeography aims at understanding the patterns and processes governing the distribution of marine taxa at different geographic and chronological scales. Marine biogeography has strong links and dependencies to numerous areas of knowledge, including broader disciplines such as marine biology, ecology, geography, geology, palaeontology, physical and biological oceanography, ecophysiology and genetics.

Regarding marine conservation, biogeography can play a fundamental role in systematic marine conservation planning by specifying (1) geographical distribution at different scales (ecosystems, species, populations, genes); (2) area cladograms which represent areas with ecological and or historical meaning and (3) information on several different processes that determine biological distributions and the spatial and temporal scales at which they operate. The role of marine biologists is to diffuse this possibility to promote the use of already existing data or of the need to produce new data to integrate conservationist decisions. Excellent examples can be found in Lourie et al. (2004) as the establishment of the Northern Gulf of Mexico Plans (TNC) (Beck et al. 2000; Beck & Odaya 2001); the National Representative System of Marine Protected Areas (Australia) created 11 “broad areas of interest” (CSIRO 1996; Environment Australia 1998) and the Extension of Florida Keys National Marine Sanctuary and creation of an ecological reserve and a no-take reserve in 2001 (National Oceanic and Atmospheric Administration 2000).

Curricular offers in Marine Biogeography and Evolution in Portuguese universities

There is only one Marine Biogeography course in Portugal, the “Biodiversity, Population Biology and Marine Biogeography”, taught at the Institute of Psychological, Social and Life Sciences (ISPA) in Lisbon. This is a 9-ECTS mandatory course for the Marine Biology and Conservation master's degree. The remaining courses are generally devoted to terrestrial biogeography (Table 1). The units offered are optional, except “Island Biogeography”, which is a 6 ECTS-undergraduate mandatory subject. There are many Biogeography courses at the international level, but only one devoted to the marine realm: Marine Biodiversity and Biogeography for undergraduates and Marine Biogeography for post-graduate students, both courses at the James Cook University, Australia. This is a prestigious course given by Profs. Bellwood and Bellwood are well known for their work on the ecology and evolution of coral reef fish (1). The syllabus for that course is not public; therefore, we cannot compare the contents of Marine Biogeography from James Cook University and Marine Biogeography and Evolution from the University of Algarve.

Table 1. Examples of Biogeography courses in Portuguese Universities.

Name	University	Study Cycle	Degree name	ECTS
Biogeografia	Clássica de Lisboa	Undergraduate	Meteorology, Oceanography and Geophysics	3 - optional
Ecologia e Biogeografia	Porto	Undergraduate	Biology	5 - optional
Biogeografia	Coimbra	Undergraduate	Tourism, Territory and Patrimony	6 - optional
Biogeografia	Porto	Undergraduate	Landscape Arquitecture	5 - optional
Biogeografia	Évora	Extra-curricular		6 - optional
Biogeografia Insular	Madeira	Undergraduate	Biology	6 - mandatory
Biogeografia	Porto	Master	Biodiversity, Genetics and Evolution	3 - optional
Biodiversity, Population Biology and Marine Biogeography	ISPA - Instituto Universitário	Master	Marine Biology and Conservation	9 - ECTS

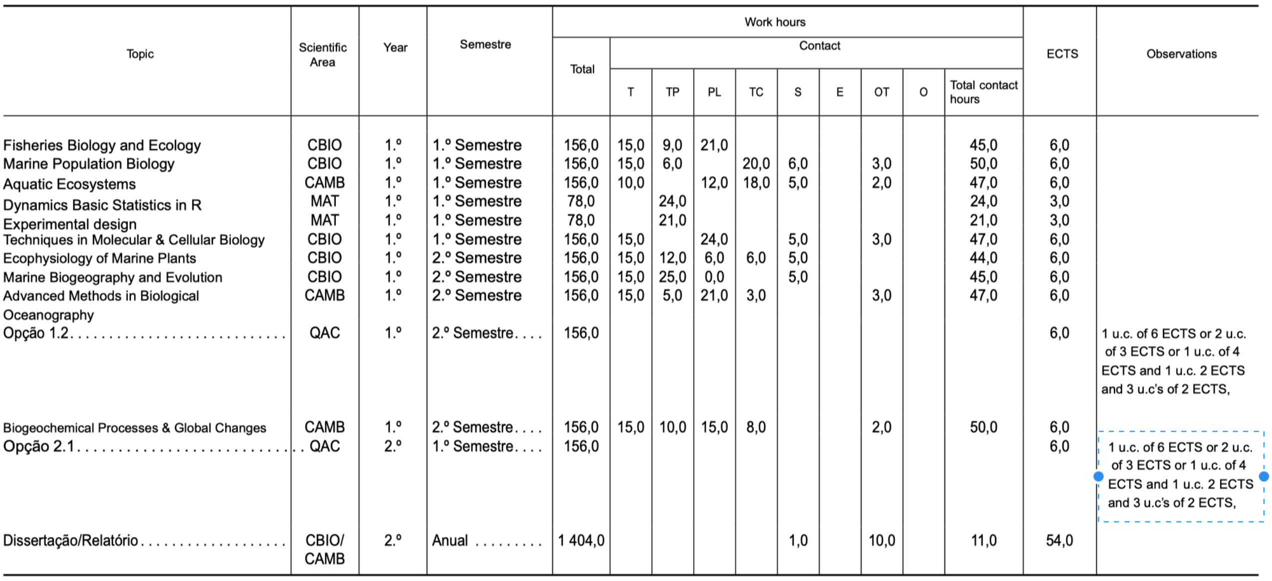
(1) Bellwood, D. R., & Wainwright, P. C. (2002). The history and biogeography of fishes on coral reefs. Coral reef fishes: dynamics and diversity in a complex ecosystem (pp. 5–32). Academic Press.

4. Integration in the course structure

Marine Biogeography and Evolution curricular unit is part of the international Masters in Marine Biology, a cycle of studies accredited by the Agency for Assessment and Accreditation of Higher Education (A3ES). I proposed this Curricular Unit when this program was created in 2015 and have coordinated it ever since.

Table 2. Study plan of the master's program.

Abbreviations: CBIO - Biological Sciences; CAMB - Environmental Sciences; CBIO/CAMB - Biological Sciences/Environmental Sciences; MAT - Mathematics; QAC - Any other area.



Topic	Scientific Area	Year	Semestre	Work hours										ECTS	Observations
				Total	Contact										
					T	TP	PL	TC	S	E	OT	O	Total contact hours		
Fisheries Biology and Ecology	CBIO	1.º	1.º Semestre	156,0	15,0	9,0	21,0						45,0	6,0	
Marine Population Biology	CBIO	1.º	1.º Semestre	156,0	15,0	6,0		20,0	6,0		3,0		50,0	6,0	
Aquatic Ecosystems	CAMB	1.º	1.º Semestre	156,0	10,0		12,0	18,0	5,0		2,0		47,0	6,0	
Dynamics Basic Statistics in R	MAT	1.º	1.º Semestre	78,0		24,0							24,0	3,0	
Experimental design	MAT	1.º	1.º Semestre	78,0		21,0							21,0	3,0	
Techniques in Molecular & Cellular Biology	CBIO	1.º	1.º Semestre	156,0	15,0		24,0		5,0		3,0		47,0	6,0	
Ecophysiology of Marine Plants	CBIO	1.º	2.º Semestre	156,0	15,0	12,0	6,0	6,0	5,0				44,0	6,0	
Marine Biogeography and Evolution	CBIO	1.º	2.º Semestre	156,0	15,0	25,0	0,0		5,0				45,0	6,0	
Advanced Methods in Biological Oceanography	CAMB	1.º	2.º Semestre	156,0	15,0	5,0	21,0	3,0			3,0		47,0	6,0	
Opção 1.2.	QAC	1.º	2.º Semestre. . . .	156,0										6,0	1 u.c. of 6 ECTS or 2 u.c. of 3 ECTS or 1 u.c. of 4 ECTS and 1 u.c. 2 ECTS and 3 u.c's of 2 ECTS,
Biogeochemical Processes & Global Changes	CAMB	1.º	2.º Semestre. . . .	156,0	15,0	10,0	15,0	8,0			2,0		50,0	6,0	
Opção 2.1.	QAC	2.º	1.º Semestre. . . .	156,0										6,0	1 u.c. of 6 ECTS or 2 u.c. of 3 ECTS or 1 u.c. of 4 ECTS and 1 u.c. 2 ECTS and 3 u.c's of 2 ECTS,
Dissertação/Relatório	CBIO/ CAMB	2.º	Anual	1 404,0					1,0		10,0		11,0	54,0	

5. Teaching Philosophy

My overall teaching goal is to allow students to develop the skills of imaginative and sceptical scientists, to be inquisitive about evolutionary processes and anchor them with well-founded knowledge of biological patterns and mechanisms. The information presented in classes provides background that is intended to allow students to discuss biogeography and macroevolution in a hypothesis-testing framework. Class slides are profusely illustrated with figures and graphs, and during class, students are called upon to interpret, extrapolate and contribute to the general understanding of the concepts and results at hand.

From its inception, the “Marine Biogeography and Evolution” designation and content were proposed and developed entirely by me. This is one of the few worldwide courses focusing specifically on marine biogeography. In the course, I apply diversified teaching-learning techniques, working with students on understanding the questions that can be addressed rather than focusing on the details of current methods. The class is a mixture of lectures, small group discussions, class discussions, and computational investigations. Lecture aids such as computer lab classes constitute a way for students to grasp the influence of evolutionary and ecological drivers through ready-made apps or simple introductory programming techniques. I emphasise how we learn about these things, how to perform experimental tests of these ideas and formulate hypotheses. I also try to incorporate current work on the topics so students see science as an ongoing discovery process rather than a static set of facts.

The two last classes will gravitate entirely around case studies. Students will have by then acquired knowledge on the main contemporary and historical factors to consider when engaging in the several case studies. I have found that case studies are powerful tools for learning and engaging students. In class, we explore the story behind scientific research to understand the phenomenon being studied, the question asked, the thinking used to investigate it, and the data collected to help students better understand the process and content of science. A strength of this approach is that it gives students a chance to consider how they would investigate a topic and the possibility of coming up with novel perspectives and unique approaches to the problems. Students can access the papers that are the focus of the class in advance to read and prepare for their participation - individual study - because students are specifically prompted to participate actively in the class. Rather than sitting in class watching yet another series of presentation slides flash by, students are encouraged to think and talk about science.

I implement several simple rules across classes to hopefully increase participation and interest. I have discouraged the use of laptops or other electronic devices for note-taking. The justification for this is based on Mueller & Oppenheimer (2014), which shows that hand-written notes are far better than laptop retention. I specifically mentioned the Cornell note-taking method and talked to students about time-planning and study techniques such as Pomodoro (Cirillo, 2018), chunking (Oakley et al. 2021), recall, and testing, which most students are not aware of. I employ real-time assessment of my teaching: I give students a link to an anonymous form they can use to give feedback on any part of the class at any time. This allows me to improve the class for the students in it rather than just waiting for the official university results.

Communication. E-mail is the primary means of communication between students and me, as it was shown to be the best way for students to contact me outside of class. Students are expected to check their e-mail regularly throughout the semester for updates and course information. More often than not, students came to see me with various vague questions denoting a lack of study or lack of preparation. I have instated a rule by which, before discussing with them, they must write down all their questions to make them realize exactly what the problem needs clarification. I also have direct contact with the students' representatives and regular two-way contact via WhatsApp.

References

Cirillo, F. (2018). The Pomodoro technique: the acclaimed time management system that has transformed how we work, First edition. New York, NY: Currency.

Mueller, P. A., & Oppenheimer, D. M. (2014). The pen is mightier than the keyboard: advantages of longhand over laptop note taking. Psychological Science, 25, 1159–1168.

Oakley, B. A., Rogowsky, B., & Sejnowski, T. J. (2021). Uncommon sense teaching: practical insights in brain science to help students learn. New York: TarcherPerigee, an imprint of Penguin Random House LLC.

6. Attendance and Assessment

Attendance policy. Class attendance is an important part of the academic process and should be considered both a privilege and a responsibility. The theoretical literature on student achievement emphasises that class attendance is associated with better performance (Nieuwoudt, 2020). I expect students to attend classes regularly and to arrive on time. If students must miss class for any reason, I encourage them to contact me, get notes from classmates and go through the recommended readings. Attendance, however, is not compulsory, and I do not keep attendance records. University students are adults and should be responsible for their own commitments.

Assessment. Students are queried through re-class reading quizzes questions made through, for instance, Polleverywhere. These live queries are a way for the students and myself to learn how learning is progressing without the pressure of studying for a grade. These quizzes match the pace of assigned readings, as students are expected to read them on time. This will ensure that students will be ready to cover the material during the lecture, and any topic less clear can be addressed in detail during class.

The assessment of this course is based on a three-pronged approach: an individual assignment (30%), an online or in-person exam (50%) and two short reports from the computer class work (2 x 10%).

The individual assignment topic can be chosen from a pre-existing list of topics or can be autonomously proposed by the students, which in this case, needs to be approved for suitability. The students should develop the topic by researching the literature and express ideas or concepts in their own words to demonstrate understanding; apply relevant concepts to a situation or phenomenon; analyse ideas and concepts and consider relationships among them; evaluate a decision, perspective or particular way of doing something and/or create new ideas or perspectives.

Each year students are given a choice of three preferred modalities for the individual assignment:

(1) Written paper

> The objective of the written assignment is to allow the student to choose a topic of their liking and research
>
> The written assignment is to be handed in at the end of classes at a pre-announced date but will be accepted later at a deduction of 20% per day. The assignment must have the content and structure of a review article seeking to understand gaps and future research needs. The total length is between 2500 to 4000 words, roughly 5-8 A4 pages, excluding references. Using figures adapted, redrawn, or originals and tables are highly recommended. Evaluation criteria are communicated beforehand (Annexe 1).

(2) Poster

A scientific poster is an illustrated summary of research to present scientific topics to larger audiences.

Students will make a 3-minute poster presentation in front of the class, a digital poster which will be projected, not printed. The poster will have an A0 size formatted horizontally to better fit the data show specifications for in-class presentation. The evaluation criteria for the posters are visual presentation, vocal delivery, clarity, vocabulary and content quality, with equal weights. Annexe 2.

(3) Flash oral presentation

A flash talk is a very short presentation lasting three minutes in which students will present a scientific concept or idea in a manner understandable to fellow colleagues. In the allocated time, students can present 4 slides. Students are encouraged to follow the suggestions in Annexe 3. The evaluation criteria for the posters are visual presentation, vocal delivery, clarity, vocabulary and content quality, with equal weights.

In practice, there is not much difference between the oral presentation of the poster and the flash talk, and it is only the visual presentation means that is different. The poster is equivalent to one slide with all the information, while in the flash presentation, students may present up to four slides.

The objective of the online or in-person exam is to assess the extent to which the student has achieved the academic objectives stipulated for the subjects/subject elements of the programme in the curriculum of the Marine Biogeography course. The exam contains a mix of essay-based topics or questions to develop into longer answers (see below) and multiple-choice questions.

The reports resulting from the computer lab classes are just one A4 page (500 words, excluding references) describing briefly the two tasks' objectives, methods, results and conclusions. Evaluation criteria are presentation, clarity of exposition, vocabulary and content quality, and weighting equally.

Examples of essay topics and questions.

An overview of corals adaptations to climate change in Pacific Ocean
Tsunami-driven rafting: Transoceanicspecies dispersal and implications formarinebiogeography
Humpback whale song (r)evolution: how, where, and why?
Drivers of zoogeographic composition and endemism of the ichthyofauna of Cabo Verde
Origins of marine Mediterranean biodiversity

Dispersal on Oceanic Islands
The role of the Panama Isthmus on octopod species diversification
Climate change impacts on the biogeography and biodiversity in the Mediterranean fish
iogeographic diversification of killer whale ecotypes
Biogeography of polar bacteria
Climate Change driven Tropicalization processes under-studied in Macaronesia
Biogeography and genetics of the invasive lionfish in the Western Atlantic and Caribbean
Colonization routes of the Loggerhead Sea Turtle across the Atlantic Ocean and Mediterranean Sea
Hippocampus sp. dispersal and population connectivity in the Atlantic Ocean along the Gulf Stream
Climate change affecting migratory patterns of cetaceans
The potential influences of anthropogenic noise pollution on the biogeography of marine organisms
Galápagos Islands: Paleogeography and Biogeographic patterns
Identifying the main factors responsible for an increased marine biodiversity in the coral triangle (Indo-Pacific)
Biogeography and Evolution of Pygmy Blue Whale in Assessing Safe Areas in the Indian Ocean
Biogeographic Diversification of Smoothhound shark (Genus Mustelus)
Opening of the Suez Canal and consequent Lessepsian migration
Oceanic Volcanic Islands impact on Coral reef distribution and diversity
Biogeographic “barriers” related to Pleistocene glacial cycles in Australian waters: recent shark radiation
Ecological Speciation by Thermal Selection
Biological invasions: the new face of the Mediterranean Sea
Biogeographical marine barriers affect seahorse diversification in the Atlantic Ocean
An overview on the evolutionary diversification of cetaceans
An approach of the hybridisation and its role in the coral’s evolution
Ice loss effects on the biogeography and biodiversity of Arctic species
How are corals adapting to global change?
Evolution, Biogeography & Species richness of coleoid cephalopods
Evolutionary History and Phylogeography of Sea Turtles with a Focus on Chelonia mydas
Historical biogeography of smoothhound sharks (genus Mustelus) and climate change
Biogeography and ecology of deep sea Chemosynthec ecosystems
The Biogeography of Macaronesian Marine Molluscs: An Overview of Dispersion and Range Expansion Processes
Functional morphology of diatom frustules: Evolution and Diversification
Island biogeography: a comparison of the Caribbean and Indonesian archipelagos
Dispersion of Sargassum fluitans and natans in the North Atlantic Ocean

Influence of large paleo-biogeographical events on the radiation of Elasmobranchii
In general, speciation on islands takes place at a faster rate than on mainlands. Discuss.
What kind of evidence supports the conclusion that a geographical distribution is the result of vicariance or dispersal?
Center of origin concept: how is this idea still around today?
What does the theory of Island Biogeography have to teach us? What does it assume?
What effects did the formation of the land bridge between North and South America have on marine species?
Which species do you think are more common: the ones with endemic distribution or the ones with cosmopolitan distributions?
What are the two factors that MacArthur and Wilson suggest are key to spatial patterns of species richness on islands? Explain the general trends proposed by the model of the equilibrium theory of island biogeography. Additionally refer to (1) general applicability of the ETIB; (2) limitations of the model.

References

Nieuwoudt, J. E. (2020). Investigating synchronous and asynchronous class attendance as predictors of academic success in online education. Australasian Journal of Educational Technology, 15–25.

7. Class roadmap

Note

At the end of each class, there is a list of references, in some cases quite extensive. These are references mentioned in slides and to which the students should have access to. Those lists are merely for reference, as the mandatory readings are clearly marked and are not more than two, the exception being the two last classes, which are case-study classes, and students have a longer list of readings to enable high-level participation.

Class 01

Summary: Classe presentation (myself and students). Course outline (working schedule, topics, assessment, a dedicated webpage, moodle resources, preferred communication channels). Historical and Ecological biogeography. Main topics in biogeography. The phylogeography of sardines: a case study.

This first class is an ice-breaker event. By the time we start this course, students are in the second semester, so they already know each other. So in this class, I present my background and research work, and I ask students to individually identify their background and expectations for this course. The course presentation will be based on the dedicated webpage and will mention all the topics covered, the schedule, computer classes and assessment.

The most fundamental split in biogeography is between the historical and ecological aspects of the subject. Historical biogeography deals with evolutionary time-scale questions, often including global geographic distribution areas and both intra and interspecific questions on extinct and extant taxa. In contrast, ecological biogeography approaches more contemporary aspects of intra-specific geographic distributions and the influence of both environmental abiotic and biotic variables.

We will mention the four main persistent transversal themes in biogeography that can be traced back to 18th- and 19th-century naturalists or geologists: (1) the delineation and classification of terrestrial and marine biogeographic regions; (2) the reconstruction of the history of diversification, distribution, and extinction of lineages and biotas, often in the context of events in Earth history; (3) explanation of differences in the numbers and types of species between geographic areas, and biotic turnover along gradients of area, isolation, latitude, elevation, and depth; (4) examination of geographic variation in characteristics of individuals and populations within and among closely related species, including trends in morphology, physiology, behaviour, genetics, and demography (Riddle, 2017).

The class will then be based on the phylogeography of sardines (Grant and Bowen, 1998) which presents an ideal setting for a study case introductory overview to the course. Although the students are not yet familiarised with the terminology and concepts of this discipline, I have found it useful to show them the end product of a phylogeographic study. Most intraspecific studies on marine fish using mitochondrial DNA (mtDNA) show low sequence divergence between haplotypes compared to the observed between sister taxa. Whether this pattern is due to sweepstakes, historic population size bottlenecks, founder events, or natural selection is unclear. All of these can delay the accumulation of deep mtDNA lineages. Paleoclimate research has prompted a reexamination of oceanographic processes as a fundamental factor affecting the distribution pattern of genetic diversity. Evidence from ice cores and anaerobic marines document a strong regime shift in the world's oceans consistent with periodic climate change. These changes in sea surface temperature, current path, upwelling intensity, and eddy currents can be a precursor to large population fluctuations or regional extinctions. Sardinas (genera Sardinops and Sardina) are found in temperate boundary currents around the world, and populations in these areas are known to vary widely in size. Biogeographic and genetic data show that the Sardinops have existed for at least 20 million years. Still, the mtDNA genealogy of this clade has converged in less than 500,000 years at the edge of the Indo-Pacific. The closure of the Tethys seaway probably triggered the differentiation between the two genera. Results indicate that the populations of the sardines follow a boom and bust cycle with regular crashes and regrowth. Such climate-related dynamics may explain the mtDNA genealogy's low nucleotide diversity and shallow coalescence. These findings may generally apply to marine fish management strategies need and the need to consider the idea that even very abundant populations can be relatively vulnerable on ecological and evolutionary timescales.

This paper allows the general introduction of the ideas such as geological events (the closure of the Tethys seaway); paleoclimate and paleocurrents; haplotypes; nucleotide and haplotypic diversities; haplotype networks; historical demography. It is not intended for the students to take immediately everything on board, and these concepts will be revisited throughout the course. Still, a window is open, and the general view is lay-out hopefully, the student's interest in this field of work will be sparked, and they will feel motivated to attend classes and participate.

Because there is no Marine Biogeography textbook, basic or advanced, I recommend Lomolino, Riddle and Whittaker (2017) and Cox et al. (2016) as a general approach. For this first class, the first section on “The Science of Biogeography”, which focus on “What Is Biogeography?” gives an overview of the “Integrative nature of the field” and its “Relationships to other sciences” and the second section on “The History and Reticulating Phylogeny of Biogeography” are highly appropriate.

At the end of the class, I retrieve the initial class objectives and give a take-home message summarising the main class contents.

References

[* students mandatory readings]

[references for building up the lecture]

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Class 02

Summary: Early Biogeography. Pivotal biogeographers. Historical biogeography. The discovery of continental drift. The dispersal versus vicariance dilemma. Centres of origin, overlap and accumulation of species.

Early Biogeography. Observations on the diversity of life and the geographic distribution around the world have been common since the days of ancient Greek philosophers and perhaps even earlier. However, the high point of scientific exploration in the 18th century greatly expanded our knowledge of biodiversity and led to a corresponding increase in attempts to explain the patterns observed in that diversity. We will briefly mention the first known biogeography maps (Ebach & Goujet, 2006). Terrestrial biogeography was initially, and until quite recently, much more explored than marine biogeography due to obvious limitations and constraints in studying the marine realm.

Pivotal biogeographers. There are five main founders of biogeography: Georges-Louis Leclerc, conde de Buffon (1707 — 1788), Alexander von Humboldt (1769 — 1859), Alfred Russel Wallace (1823 — 1913), Robert MacArthur (1930 — 1972) and E.O. Wilson (1929 — 2021). Buffon's observations led him to posit that geographically distinct areas with similar environments have different assemblages of species, which became the first principle of biogeography known as Buffon’s Law (Lomolino et al., 2017), which became the first law of biogeography. The explorer and naturalist Alexander von Humboldt's contributions to the topics of ecology, global change and earth science have fundamentally changed our view of nature and our position within it. His comparisons between Latin American fauna and flora and the comparisons to European specimens and their distributions to local environmental conditions would eventually give birth to the field of biogeography. Biogeography research became popular with Alfred Russel Wallace's work in the late 19th century. Originally from England, Wallace was a naturalist, explorer, geographer, anthropologist, and biologist who studied extensively, first in the Amazon and then in the Malay Archipelago (the islands between mainland Southeast Asia and Australia). While in the Malay Archipelago, Wallace studied flora and fauna and developed the “Wallace line” concept. The “Wallace line” divided the distribution of Indonesian land animals into two different regions, depending on the climate and conditions of those regions and the proximity of their inhabitants. Instead of focusing on the differences between species assemblages, as Buffon, Wallace took a key step in developing his theory of evolution by recognising that “species found close together are likely to share their common ancestor more recently than species found farther apart”. For wildlife in Asia and Australia, organisms are more related to Asian fauna, and the ones closer to Australia are more related to Australian fauna. Due to his extensive early work, Wallace is often referred to as the "father of biogeography." Wallace was followed by many other biogeographers who studied species distribution, most of whom turned to history for explanation and made it a descriptive field. In 1967, Robert MacArthur and E.O. Wilson published the theory of island biogeography (MacArthur & Wilson, 2001). This publication made it important for biogeographers to change the way they see species and to study the environmental characteristics of the time to understand their spatial patterns. As a result, island biogeography and island-induced habitat fragmentation have become popular research areas because it was easier to explain the patterns of plants and animals in the microcosm that developed on isolated islands. Since then, the study of habitat fragmentation in biogeography has led to the development of conservation biology and landscape ecology.

Historical biogeography. Biogeography can be divided into three major areas of research: historical biogeography, ecological biogeography, and conservation biogeography. Historical biogeography, called paleobiogeography, studies the past distribution of species. It examines their evolutionary history and such things as past climate change to determine why a particular species may have evolved in a particular region. For example, the historical approach posits that there are more species in the tropics than in high latitudes because the tropics do not experience less severe climate change during the ice age, are less extinct, and have long-term population stability. [although there may be other contemporary reasons as well].

The discovery of continental drift. Many have noticed how well Brazil fits under Africa's belly, at least since the introduction of the first world map. Alfred Wegener (1880 – 1930) sought other connections. He found studies on the same fossil on the coasts of Africa and South America. Therefore, geologists were convinced of the immutability of the world map and provided a more incredible explanation. An overpass that disappeared after animals and plants were allowed to move from one continent. Separately. In January 1912, a German meteorologist and explorer, Alfred Wegener, unveiled an amazing new vision of the Earth's past. According to Wegener, the world we see today is the result of a huge land split into individual continents that have been moving since then. It moves as a whole, not just the highest part of the continent. This new theory, plate tectonics, also explains that when two plates rub against each other, an earthquake and a tsunami occur, and when they collide head-on, a large mountain range is formed.

The dispersal versus vicariance dilemma. Biogeography was, in the past, dominated by two schools of thought, the one that defended vicariance, that is, distribution patterns chiefly determined by geological, tectonic-isolating events, and another defending that current distribution patterns are largely the result of recent dispersal events. These two processes are at the core of virtually all species' geographic distribution. The integration of different sources of evidence, such as estimates of the divergence time between lineages (usually based on DNA sequences), and external sources, such as information on past climate and geography, the organism's fossil record, or its ecological tolerance, allowed biogeography to “escape the dispersal versus vicariance dilemma” (Sanmartín, 2012). However, vicariance and dispersal concepts remain critical to biogeography and distinguishing their contribution (Ludt & Myers, 2021). We will illustrate these two concepts using a selected group of case studies (Cowman & Bellwood, 2013, Boo et al., 2022, Portnoy & Gold, 2012).

Centres of origin, overlap and accumulation. In the Indo-Malay-Philippine region, the taxonomic diversity decreases both latitude and length with distance from the region known as the Coral Triangle (Veron et al., 2009). This pattern was identified in corals by Stehli & Wells (1971) and recognised in various other taxa such as molluscs (Paulay, 1990) and fish (Briggs, 1999). Due to the generality of this pattern, many researchers conclude that a common mechanism may be responsible for the high biodiversity of the region. Several hypotheses have been proposed to explain the species richness of IMP hotspots, which can be divided into four main categories: (1) centre of origin (Ekman, 1953) [the high number of species in the Indo-Malay-Philippine hotspot is a product of an unusually high rate of speciation in the region, with new species radiating from this centre of origin], (2) centre of accumulation (Ladd, 1960) [speciation in peripheral locations with subsequent dispersal of novel taxa into the IMP hotspot] and (3) centre overlap (Woodland, 1983) [the high species diversity in the IMP hotspot is due in part to the overlap of distinct faunas from the Pacific and Indian Oceans]. A good discussion of these different hypotheses can be found in (Gaither & Rocha, 2013).

At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 03

Summary: Ecological biogeography. Main contributing factors for limiting the distribution of marine organisms. Patterns of biodiversity. Measures of diversity. How many species are there? Overview of ocean biogeographic regions.

Ecological biogeography. One generally accepted definition for ecological biogeography is “the study of aspects of biogeographical phenomena that focuses on the interactions between organisms and their environments.” (Cox et al., 2016). The study of the environmental factors shaping the distribution of individual organisms at a local spatial scale and short temporal scales. These factors are mainly abiotic environmental factors such as temperature, salinity, currents, substrate, light, nutrients, and biotic factors, the living components of the ecosystems, and their interactions. In the field of ecological biogeography, we first study the dispersal of organisms (usually individuals or populations) and the mechanisms that influence that dispersal and then use this information to explain the spatial distribution patterns of these organisms. increase. Therefore, ecological biogeography is typically associated with short-term time periods and often intraspecific questions, such as what constraints the present range of a species, what is the role of specific environmental variables, and what may explain the higher number of species in the tropics than temperate or cooler environments? What seems to govern the diversity of organisms in a particular area?

Main contributing factors for limiting the distribution of organisms. Not all species are cosmopolitan, that is, species that may inhabit both icy and warmer water and deep and shallow seas. Indeed, most species experience some sort of intrinsic and extrinsic limitations to their geographic distribution. There is no single, general all-encompassing explanation for geographic distribution limits (Willi & Van Buskirk, 2019). Some evolutionary models predict that populations at the edge of the range are not well adapted to the local environment. In contrast, others posit that populations near the edge of the range can adapt independently to the marginal environment (Bontrager et al., 2020). Many studies have highlighted these ideas, such as reviews of adaptation to marginal conditions (Geburzi et al., 2021) and meta-analyses of the abundant-centre hypothesis (Eckert et al., 2008; Pironon et al., 2017; Sagarin & Gaines, 2002). In this third class, we will mention two main physical properties of seawater determinants of the geographical distribution of organisms: temperature and salinity. While other characteristics are also important, we challenge the students to investigate those in the individual study. Temperature affects species distribution through physiological and ecological processes and is one of the most important modern factors in global biodiversity patterns (Chaudhary et al., 2021). Understanding how and where temperature limits species distribution can highlight important evolutionary and biogeographical processes and predict future biodiversity responses to global warming. However, it was partly difficult to determine if there was a generalisable relationship between species between geographic areas and the thermal niche. This is because the effects of temperature are usually confused by many other interacting factors that promote species distribution (Stuart-Smith et al., 2017). The thermocline is defined as the layer within the water column where the vertical temperature gradient is maximal. Below the thermocline, the temperature slowly decreases with depth, with an average temperature of about 3.5°C. As a result, the deep sea is permanently cold. These cold waters are formed by the cooling of water masses by the polar atmosphere. Cold, dense water sinks to the bottom of the ocean, fills deep-sea basins, gradually rises to the surface, and replaces the submerged water formed in the polar regions, forming global circulating cells. This thermally driven abyss circulation is called thermohaline circulation (Huang, 2015).

Changes in salinity are a significant factor in marine and estuary species distribution. Therefore, salinity is fundamental in changing the structure and function of aquatic ecosystems. The impact of salinity changes on the ecosystems of different habitats is ultimately determined by the underlying physiology and tolerance of the organism and its ability to cope with salt changes on both long and short time scales. Many marine species are stenohaline and are limited by their narrow physiological tolerance. Salinities at the limits or outside the tolerance range of certain species will restrict their occurrence, modify their behaviour, or constrain reproduction and germination, reducing their fitness for survival in that environment (Smyth & Elliott, 2016).

Patterns of biodiversity. Biodiversity is distributed heterogeneous all over the world. Some areas are biodiversity hotspots (e.g. Coral triangle), while others are almost lifeless (e.g. polar regions or abyssal plains). Between these two extremes lay most of the areas of the planet. Why there is such an array of variation in the number of species among regions of the world is a core objective of biogeographers. In this class, we will present several global patterns of spatial variation in biodiversity, including patterns in hotspots and coldspots (highs and lows) of diversity; variation with spatial scale (for example, species-area relationships and relationships between local and regional richness); variation along gradients across space or environmental conditions (for example, latitude, longitude, altitude, depth, peninsulas, bays, isolation, productivity/energy) (Gaston, 2000).

Measures of diversity. It is well well-known that species diversity is unequally distributed across space, following a latitudinal gradient, with increasing diversity from the poles toward the tropical regions (MacArthur, 1965). These differences in spatial diversity patterns have led to the formulation of three levels of species diversity: alpha, beta, and gamma diversity (Whittaker, 1960). Alpha diversity represents the species diversity measured at a given site on a local scale. It describes the species diversity (richness) within a functional community. Alpha diversity, for instance, describes the observed species diversity within a defined plot or within a designated ecological unit, such as a sand beach or a coral patch. The scale of such ecological units is quite variable, depending on the group of species of interest. Some species have more restricted geographic distribution, such as some sessile invertebrates, while others have vast distribution ranges, e.g. sharks. The second diversity measure, beta diversity, defines the degree of differentiation between species communities. Unlike other levels of species diversity, the accurate interpretation and quantification of beta diversity vary significantly between studies. Presently, a commonly used measure of beta diversity is the Sørensen dissimilarity index which captures spatial turnover and differences in diversity between sites (Koleff et al., 2003). Gamma diversity describes the overall species diversity across communities within a larger geographic area. It can be summoned from within cells of a spatial grid of fixed cell size or summarised across biogeographic units, such as ecoregions or countries. Gamma diversity more broadly and loosely describes the diversity of species that can be found in the whole area (Andermann et al., 2022).

How many species are there? It is estimated that over 90% of marine species are still unknown (Mora et al., 2011), while according to NOAA, more than 80% of the ocean is unmapped. These staggering statistics were meant to be addressed in part by the Project "Census of Marine Life, a decade-long international project that took place during the first decade of the new millennium to chart the diversity, distribution and abundance of marine life (Snelgrove, 2016). The Census of Marine Life identified three world regions as having the highest number of species: Australia and Japan, each reporting over 32,000 species, and China, which had over 22,000 species with three taxa—Crustacea, Mollusca, and Pisces— contributing to almost half of all species richness, while Protozoa and algae contributed 10% each (Costello et al., 2010).

Overview of ocean eco-regions, provinces and realms. Biogeographic classifications are critical for developing ecologically representative systems of protected areas and supporting identifying patterns in marine biodiversity while understanding processes and shaping marine resource management and conservation efforts. The first marine biogeographical regions were proposed by Ekman (1953) based on zoogeographical characteristics, environmental barriers, and levels of endemism. But it was only more recently that two main biogeographic classifications of the world's coasts and shelves made a considerable contribution. First, in 2007 was published a wide-ranging marine classification system with defined boundaries and definitions of ecoregions nested within the broader biogeographic tiers of realms and provinces (Spalding et al., 2007). These authors propose a nested system consisting of 12 realms, 62 provinces, and 232 eco-regions covering all coastal and shelf waters of the world. In this class, we will focus on the North Atlantic Temperate realm, which includes the Lusitanian province, consisting of the South European Atlantic Shelf, the Saharan Upwelling and the Azores, Canaries and Madeira eco-regions (Spalding et al., 2007). The later publication aims to delineate biogeographical entities for reef fishes on a global scale (Kulbicki et al., 2013). The Eastern Atlantic region reveals the presence of 403 reef species, of which 241 are endemic, which is modest compared to all other regions. However, a significant gap exists as none of the publications has considered the pelagic or deep benthic environment so far.

At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 04

Summary: The evolution of Planet Earth’s Oceans. Knowledge of the geological history of Earth’s Oceans is essential for understanding contemporary diversity patterns. Continental drift. The formation and extinction of oceans and seas: formation and closure of Tethys, the opening of the Atlantic, formation of the Indian Ocean. The desiccation of the Mediterranean, the closure of the Isthmus of Panama, and the opening of the Bering Strait.

Continental drift. The Earth's conformation is shaped by plate tectonics. The theory of plate tectonics is a modern update of continental drift, an idea first proposed by Alfred Wegener, in which the Earth's continents moved across the planet over time. Plate tectonics determines the shape and placement of continents and defines the shape of ocean basins. The Earth's outer crust is divided into large slabs of solid rock called "plates" that slide across the Earth's mantle, causing breakups and collisions that cause the tallest mountains on Earth (e.g., the Atlantic Ocean. With the breakup of Pangea) The result was a long-duration (>10 million years) continental rift that eventually resulted in the emergence of new ridges extending across the ocean floor.

The formation and extinction of oceans and seas.

The opening of the Atlantic. After the Early Jurassic (200-174 million years ago - Mya), the Central Atlantic Ocean began to open between West Gondwana and Laurussia. However, the spreading between Europe and North America started only during the Cretaceous 145 to 66 Mya. The oldest seafloor in the mid-Atlantic is estimated to be around 175 Mya (Klitgord & Schouten, 1986). Existing data suggest that the rift began well before 175 Mya, but the extent of the rift spread between the two continents is poorly understood (Voo, 1993). The widening of the Atlantic Ocean during the Cretaceous is responsible for the initial isolation between the West and East Atlantic. Presently the Atlantic continues to expand on average, about 1 cm/year in the south and about 4 cm/year in the north.

The formation and closure of Tethys. The Tethys Sea existed between Gondwana and Laurasia from the Triassic (252 - 201 Mya). The transformation of Thetis began with the splitting of the supercontinent Pangea into Laurasia and Gondwana in the Triassic. The gradual separation of North America from Laurasia in the Middle Cretaceous and the breakup of Gondwana about 110 to 84 million years ago opened the Atlantic Ocean, a deep-sea basin between Europe and America. In the early Eocene (about 50 Mya), India moved north and collided with Asia. Then, in the late Eocene, another intracontinental convergence closed Tethys. At the Eocene-Oligocene boundary (34 Mya), the Southern Mediterranean was formed at the western extremity of He Tethys and the intercontinental

Paratethys north of the tectonic belt. During the early Miocene (24–20 Mya), counterclockwise rotation of the Afro-Arabian block drove the opening of the Red Sea, and collisions between the Arabian Plate and Eurasia formed a long chain of islands. In the Middle Miocene (18–12 Mya), the Apocalyptic Tethys Event gradually closed the Tethys Sea between the Mediterranean and Indian Oceans, resulting in the emergence of a land bridge between Eurasia and Africa. The closure of the Tethys Sea region in the Middle Miocene seems to have cut off the global equatorial currents and isolated the Atlantic/Mediterranean, Indo-West Pacific, East-Atlantic, Mediterranean and Indo-West Pacific. This closure disrupted trade between the Atlantic and Indian Oceans and forever changed the Atlantic community.

[main reference: Hou & Li, 2018]

The formation of the Indian Ocean. The origin and development of the Indian Ocean are the most complex of the three major oceans. Its formation resulted from the collapse of the southern supercontinent Gondwana (or Gondwanaland), beginning around 180 Mya. The northeastward migration of the Indian subcontinent (beginning about 125 Mya) began colliding with Eurasia about 50 Mya. And with the westward migration of Africa and the separation of Australia from Antarctica by about 53 Mya. 36 Mya, the Indian Ocean took on its present shape. Although it first opened about 140 Mya, most of the Indian Ocean basin is less than 80 Mya.

[main reference: Morgan et al., 2021]

The desiccation of the Mediterranean. About 6 Mya, the Mediterranean Basin was the site of one of the most extraordinary events in the Earth's recent geological history, the Messinian Salinity Crisis (Duggen et al., 2003; Hsü et al., 1977, 1973). The Mediterranean Sea was isolated from the Atlantic Ocean. The collision of African and Eurasian tectonic plates raised the Rif and Betic mountains (northern Morocco and southern Spain, respectively), closing at least two significant straits or channels that connected the oceans at the time. Restriction to seawater exchange between the Atlantic and Mediterranean oceans has led to excessive evaporation, the deposition of a 1.5 km-thick layer of salt on the bottom of deep Mediterranean basins, and a sharp increase in the salinity of residual waters in the Mediterranean Sea. When the Strait of Gibraltar reopened 5.33 Mya, the dry Mediterranean era may have ended quickly, with massive floods replenishing empty waters in just two years. Reflection seismic imaging, a technique that uses sound waves to map what lies beneath the surface of the Earth, has revealed that vast erosion channel stretching across the straits beneath kilometres of Quaternary sediments. This channel has hundreds of meters deep and 390 kilometres long, stretching from the Bay of Cadiz (Atlantic Ocean) to the Algerian Basin (Mediterranean Sea). Researchers believe the channel may have been carved during high tide when waters from the Atlantic rushed in to replenish the Mediterranean Sea (Duggen et al., 2003; Hsü et al., 1977, 1973). The Zanclean flood hypothesis has its critics. Many researchers studying MSC are unsure if the Mediterranean was much drier than it is today. One of the main problems with the drying theory is the enormous amount of salts and gypsum believed to have been deposited in the MSC. If that water evaporated quickly, the present-day Mediterranean Sea would be left with a salt layer less than 30 meters thick. In contrast, the salt layers associated with MSCs are up to 1 kilometre thick in some places. To accumulate so much salt, critics of the Zanclean hypothesis argued that water should flow from the open ocean into the sea. It may precipitate. The alternative implies a deep-sea non-dry scenario in which large bodies of water persist in the Mediterranean through the Messinian salt crisis. Still, the Atlantic connectivity is significantly reduced (Garcia-Castellanos et al., 2020).

[main reference: Roveri et al., 2016]

The closure of the Isthmus of Panama. The establishment of the Isthmus of Panama caused significant changes in the prevailing environmental and oceanographic conditions (Haug & Tiedemann, 1998; Bartoli et al., 2005; Schneider & Schmittner, 2006) and affected the dispersal and speciation processes of marine biota (Leigh, O'Dea & Vermeij, 2013). The closure of the Atlantic-Pacific link is considered the most important secondary event of the Cenozoic (O'Dea et al., 2016). It provides a unique system for studying evolutionary processes in the natural environment. Offers. The age of the Isthmus of Panama's eventual closure, and its role in fundamental evolutionary processes, remains controversial (Stone, 2014), with two main hypotheses proposed to explain this event: the "late Pliocene model" and the "Middle Miocene model". Using three independent data types: geological, fossil, and molecular, several authors suggest that the final closure of the isthmus occurred in the late Pliocene, about 2.5 to 3.5 million years ago (Ma) (Coates et al., 1992; O'Dea et al., 2016). However, recent studies based on terrestrial propagating waves and geochronological information suggest that the closure of this seaway occurred in the Miocene (15 Ma) (Bacon et al., 2015; Hoorn & Flantua Montes et al., 2015). According to the late Pliocene hypothesis, this lengthy process began with the collision of Central and South America around 15–24 Ma and the formation of volcanic arcs around the early Miocene (Coates & Stallard, 2013). During the middle Miocene (~10 Ma), successive collisions caused widespread ocean flattening and major changes in oceanic conditions, disrupting the exchange of deep and intermediate waters between the Atlantic and Pacific oceans. (Coates et al., 2004; Keigwin, 1982). Approximately 6–4 Ma ago, ocean conditions such as water temperature, salinity, sediment carbon content, and habitat availability changed significantly on both sides of the isthmus (Haug & Tiedemann, 1998; Leigh, O. `Dea & Vermeij, 2013). By 3 Mya, the Isthmus of Panama uplift completely separated the tropical western Atlantic and tropical eastern Pacific waters (Coates & Stallard, 2013; O'Dea et al., 2016). Uranium-lead geochronology-based studies in Andean detrital zircons, Panamanian river sediments, and inferences about terrestrial and underwater distributions provide another insight into the early closure of the Isthmus of Panama. An alternative hypothesis, the "Middle Miocene hypothesis" (Montes et al., 2012; Bacon et al., 2013; Bacon et al., 2015; Montes et al., 2,015), posits the isthmus formation about 38–28 Ma ago and the southern tip of Central America and South America collision occurring in the late Oligocene (28.1–23.0 Ma). The water link between the eastern Pacific and western Atlantic was completely closed about 14–15 Ma ago (Montes et al., 2015). There are recent examples how these changes have influenced speciation processes e.g. Lima et al., 2020; Quintão et al., 2022.

The opening of the Bering Strait. The Bering Strait is a passage that has divided the previous supercontinent that joined Eurasia and North America. Before its opening the Bering Strait prevented the marine connection between the North Pacific and the North Atlantic-Arctic oceans. Therefore, the first opening of the Bering Strait was an important palaeogeographical and biogeographical event for marine and terrestrial biotas in Asia and North America, and an oceanographic event of global importance. The opening event, however, has never been precisely dated, so it has not been accurately incorporated into global biogeography and oceanography models. The dates vary between 3.1 - 4.1 Mya (Barron & Gladenkov, 1995), 4.8 - 5.5 Mya (Barron & Gladenkov, 1995), and 4.8 and 7.3 - 7.4 Mya (Marincovich & Gladenkov, 1999). Examples of the biogeographic impact of the opening of this strait are abundant in the literature (e.g. Laakkonen et al., 2021).

Climate change throughout geological time. The Earth's climate has changed dramatically over and over since the formation of the planet 4.5 billion years ago (Zachos et al., 2001). These changes were caused by changes in continental and oceanic composition, changes in the intensity of the Sun, changes in Earth's orbit, and volcanic eruptions. Natural changes in atmospheric greenhouse gas concentrations, the evolution of life, and the effects of meteorites have also caused climate change. For example, millions of years ago, the Earth's average temperature was several degrees higher than today's, and warm tropical waters reached far from the equator, resulting in a very different ocean and atmospheric circulation patterns. Was there. Over the past million years, the Earth's average surface temperature has risen and fallen by about 5 ° C in glacier cycles about every 100,000 years (Annan & Hargreaves, 2013). During the coldest part of the Last Glacial Period, between 18 and 20,000 years ago, sea levels dropped to at least 120 meters than today due to more water trapped in polar ice sheets (Lambeck et al., 2012). The past 8000 years, which make up most of the recorded human history, are relatively stable at the warmer ends of this temperature range. This stability has enabled agriculture, settlement and population growth. Most of the past changes in global temperature have occurred slowly over tens of thousands to millions of years. But there is also evidence that some sudden changes have occurred, at least at the regional level. During the last ice age, temperatures in the North Atlantic region plunged by more than 5°C in just a few decades (Capron et al., 2010) due to the sudden collapse of the Northern Hemisphere ice sheets or changes in ocean currents (Barker et al., 2010. (Böning et al., 2008). Some ocean currents have changed in response to changes in surface winds, ocean temperature and ocean saltiness, e.g. southward shift of the Antarctic Circumpolar Current (Böning et al., 2008).

At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 05

Summary: Biogeographic responses to glaciations. Milankovitch cycles. Measuring paleotemperatures. Isostatic and eustatic sea level. Lower sea levels in the past. Typical biogeographic responses to climate. Geographical barriers.

The alternation between inter-glacial and glacial cycles has immensely defined the distribution of organisms. In this class, we will look into the triggers of those cycles, methods of measuring temperatures of the distant past, and the environmental and biogeographic consequences of those cycles.

Milankovitch cycles. The pattern of solar radiation (insolation) falling on a planet at a particular location and time is vital in understanding the directional trends and variability observed in many palaeoclimatic records, especially for the Quaternary Ice Ages (Laskar et al., 2004). Changes in solar irradiance are caused by the Earth's natural orbital oscillations known as Milankovitch cycles. The three components of the Milankovitch cycle are eccentricity, obliquity, and precession. Eccentricity (shape of Earth's orbit) describes the degree to which the Earth's orbit around the Sun varies from circular to elliptical. Eccentricity has two main periods: cycles of 100,000 years on average and longer cycles of 413,000 years. Obliquity describes the tilt (angle of axis) of the Earth's axis related to the orbital plane and ranges from 22.1 to 24.5 degrees with a period of approximately 41,000 years. Precession (the direction of the Earth's axis) describes the movement of the Earth's axis of rotation and does not point to a fixed, cardinal direction over time. Instead, the axis of rotation represents a clockwise circle in space with a period of 19,000 to 23,000 years, like the spinning of a rod. These Milankovitch cycles affect the insolation, or sunlight exposure, of different regions and, thus, the behaviour of ice formation. How is this relevant for glaciations? There is a good correlation between the Milankovitch cycles and Earth's regular inter-glacier and glacial periods. The average length of ice ages varies over time, from about 40,000-year cycles more closely coinciding with changes in the tilt of the Earth's axis (obliquity) to about 100,000-year cycles coinciding with changes in the orbit (eccentricity). The transition between the 40,000- and 100,000-year cycles occurred in the mid-Pleistocene. But scientists are having trouble pinpointing exactly how ice ages begin, why they coincide with these cycles, and why the lengths and gaps between ice ages change over time (Lee et al., 2017).

Measuring paleotemperatures. Oxygen is an essential key to deciphering the past's climate. Oxygen has heavy and light varieties or isotopes that are useful for paleoclimate studies. Every oxygen atom has 8 protons, but the nucleus can contain between 8 and 10 neutrons. The oxygen molecule with 8 neutrons is the most abundant in nature and is called "light" oxygen-16, with 8 protons and 8 neutrons, is the most abundant isotope in nature. In comparison, the much less "heavy" oxygen-18 (^{18}O) has 8 protons and 10 neutrons. The ratio between these two types of oxygen in water changes depending on the climate. Water molecules containing light oxygen are slightly easier to vaporize than water molecules containing heavy oxygen atoms. At the same time, water vapour molecules containing heavy oxygen condense more easily. Water vapour gradually loses ^{18}O on its way from the equator to both poles. Water molecules containing heavy ^{18}O isotopes condense more quickly than normal water molecules, so the air gets less ^{18}O and dries colder as it moves to higher latitudes. Conversely, the snow that makes up most of the glacier ice is also exhausted at ^{18}O. As the glacier ice melts, ^{16}O-rich freshwater returns to the sea. Oxygen isotopes preserved in marine sediments provide clues to the past ice age and salinity records. Therefore, less heavy oxygen in frozen water means cooler temperatures in polar ice cores.

Isostatic and eustatic sea level. Sea level changes significantly over time. Every day, the sea level changes due to the tide, but the sea level also changes on larger time scales. These sea level changes are usually caused by ice ages or other major global events. Sea level change can be due to eustatic and isostatic changes, depending on whether they affect sea level globally or locally (Rovere et al., 2016). Eustatic change occurs when the sea level changes due to changes in the amount of water in the ocean or changes in the shape of the ocean basin and, thus, the amount of water the sea can hold. Eustatic changes are always global effects and occur during and after the ice ages. When the Ice Age began, temperatures dropped, and water froze and was stored in inland glaciers, disrupting the water cycle. This pulls water out of the ocean but not back, resulting in a general drop in sea level. Conversely, temperatures rise at the end of the ice age, and water stored in glaciers reenters the hydrological cycle, replenishing the oceans and causing sea levels to rise. Changes in isostatic sea level result from increases and decreases in land elevation. During ice ages, isostatic changes are caused by ice accumulation on land. When water is stored in glaciers on land, the weight of the land increases, the land subsides slightly, and the sea level rises slightly. When the ice melts at the end of the Ice Age, the land begins to rise again, and sea levels fall. These two cycles are called compression and decompression or hydrostatic rebound. Isostatic rebounds occur incredibly slowly and have occurred since the last ice age to this day. Isostatic sea level changes can also be caused by tectonic uplift or subsidence. This type of isostatic change only occurs in some parts of the world, as it only occurs along plate boundaries. The effects of the glaciation cycles led to a concentration of ice in the polar caps, and a consequent accentuated global sea level drop, which in the last glacial maximum (LGM — 19[1] - 30ky) (Yokoyama, 2011) corresponded to a sea-level fall to about 120 to 135 m (Haq & Schutter, 2008; Lambeck et al., 2002; Milne et al., 2002;

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[1] ky represents thousands of years.

Peltier, 2002).

General principles of species distribution. Every species has its particular geographic distribution range. Some species occupy large spaces and are ubiquitous in different environments - generalists. Others live only in small areas limited by specific geographical, environmental, or ecological factors - endemics. The factors that define species occurrence can be broadly categorised as (i) environmental conditions, including climate. (ii) the resources necessary for the survival of the species; (iii) negative (competitive, predatory, parasitic) and positive (mutualistic and symbiotic) biological interactions; (iv) the ability to move or disperse in space to determine the environment the species has access to (Soberón, 2007). These factors result in highly dynamic species distributions in space and time. Interestingly, the locations where species are found (realised niche) are often not the same as those potentially suitable for the species (fundamental niche).

Typical biogeographic responses to climate. The geographic distribution of species is generally shaped by climate. In the northern hemisphere, species distribution was shaped by alternating series of glacial and interglacial periods during the Quaternary period that began 2.58 Mya and is ongoing. Since the middle Quaternary, the glacial-interglacial cycle has been about 100,000 years long (Abe-Ouchi et al., 2013). During and between these ice ages, abrupt changes in climate and sea levels occurred, changing the world's environment. These changes have resulted in rapid alterations in the distribution of both flora and fauna life forms. There is evidence that the relatively extreme climatic conditions of the Pleistocene glacials drove continental European temperate species to southern regions. Terrestrial organisms have found refuge in the three peninsulas in south Europe, the Iberian Peninsula, the Apennines and the Balkans (Hewitt, 2004). After deglaciation, the species dispersed northwards, recolonising open habitats. These movements of species were genetically traced and resulted in southern populations becoming generally more diverse than northern populations (the "southern richness, northern purity" paradigm) (Hewitt, 2000; Vitales et al., 2016). These large and rapid latitudinal shifts, particularly in the Pleistocene climate change, are well documented in pollen and fossil data, particularly following the end of the LGM and gave rise to the expansion-contraction model. In the marine environment, there is no equivalent of peninsulas to limit the southwards advancement of individuals. Therefore, the main consequence of the organisms' distribution is displacement until they reach their physiological optimum. Because most marine organisms are ectotherms, they depend on environmental temperature to regulate body heat and maintain a proper internal environment for physiological functions. Hence, an accentuated temperature drop allied to the global sea level fall drastically affected the species' geographic distribution.

Geographical barriers. Geographical barriers are essential determinants of the evolution and distributions of species. In marine ecosystems, range distributions can be defined by different types of barriers: biotic and biological barriers, "soft" and "hard" barriers. The hard barriers are obvious physical obstacles such as landmasses (e.g., the Isthmus of Panama separating the Pacific and the Atlantic Ocean). In contrast, the "soft" barriers (Luiz et al., 2012) are permeable filters that constrain the distribution of some species but not others. Large stretches of deep oceanic water, such as the Mid-Atlantic region; near-shore gradients in physical and chemical properties of seawater, such as the freshwater discharge forming the Amazon-Orinoco Plume; or the relatively cool Benguela/Agulhas Current that separates southern Africa into two provinces, are a few of the most striking examples of soft barriers (Briggs & Bowen, 2013).

We will focus in this class on chosen case studies by Marko et al. (2010), Jenkins et al. (2018), Kettle et al. (2011), Maggs et al. (2008) and Silva et al. (2014) that illustrate the effects of the LGM on the distribution of organisms as inferred by hindcast of species distribution modelling and population genetics. At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 06

Summary: What is phylogeography? Most commonly used genetic markers. Molecular estimates of gene genealogies within species and between closely-related species. Statistical phylogeography. Avise's phylogeographic hypothesis.

What is phylogeography? The term was coined by John Avise (1987) and designated the field of study that seeks to reveal relationships between individual genotypes within species or groups of very closely related species and to correlate these relationships with their spatial distribution. Derived genealogical relationships can be used to trace the biogeographic history of subspecies populations and answer evolutionary questions such as gene flow, fragmentation, range expansion and colonization. It is an integrative discipline where biogeographical, phylogenetic, population genetics, life history, ecological, and paleontological information is combined to draw a past history of species.

Most commonly used genetic markers. Although the most commonly used molecular marker in first-generation phylogeographic studies was animal mitochondrial DNA (mtDNA), other markers have also been used, particularly plant chloroplast DNA. Several features of animal mtDNA are particularly suitable for studying the geographical distribution of evolutionary lineages. First, animal mtDNA genomes are usually inherited in a single parent (maternal line), so the effective population size is one-fourth that of the nuclear genome (Avise et al., 1987). Second, the molecular evolution rate of the mtDNA genome is relatively fast (Brown et al., 1982). These features of the mtDNA genome result in (1) non-reticular (branching) gene trees and (2) rapid geographic sorting and genetic divergence of populations in the absence of gene flow. As a result, phylogeographic studies using mtDNA typically provide better resolution of intraspecific patterns of geographic variation than non-molecular methods (Avise, 2000).

Molecular estimates of gene genealogies within species and between closely-related species. Individuals are usually obtained from the entire geographic range of the species, and a gene fragment of the mtDNA genome is sequenced for each individual. The most commonly used genes are the control region, also called the displacement loop, the cytochrome c oxidase I (COI or COX1 – the "barcode gene") (Hebert et al., 2004), or D-loop, and cytochrome b. The resulting haplotypes are used to construct a network of haplotypes that reflects the evolutionary relationships of the individuals and locations of origin. The combination of genetic and geographic information can elucidate the haplotypes shared among sampling locations, the geographic distribution of the major gene lineages (if they exist) and the genetic structure of the species.

Statistical phylogeography. Theoretical developments allowed the application of a variety of probability-based approaches (reviewed in (Excoffier & Heckel, 2006; Kuhner, 2009) and coalescence (model of how alleles sampled from a population may have originated from a common ancestor) methods (e.g. Beerli & Palczewski, 2010; Kuhner et al., 1995), integrating climatology and geology to molecular and evolutionary genomics (e.g. Morim et al., 2019, Provan & Maggs, 2012, Fisher et al., 2022, Fonseca et al., 2022). These methods, although computationally intensive, provide detailed historical estimates of population size, growth, subdivision, admixture, gene flow patterns, divergence timing, etc. Alternatively, instead of considering the total probability of the data, a method based on summary statistics can be used (reviewed by Hickerson et al., 2005; Knowles, 2004), providing a framework for comparing competing scenarios and estimating parameters and computations while combining processes (e.g., population divergence, admixture, size change, and migration). Because phylogeography is hypothesis-driven, it can test the role of historical processes (such as vicariance events and environmental changes) in the evolution of species. This has improved our ability to infer many taxa's most likely evolutionary history (Avise, 2000). Phylogeographic approaches are commonly used to study intraspecific genetic phylogeny (Avise, 2009), and increasingly comparative approaches (e.g. comparing co-distributed species affected by common climate change) are employed to explore the links between microevolutionary and macroevolutionary processes in communities (Dawson, 2014; Pascual et al., 2017; Robalo et al., 2020).

Avise's phylogeographic hypothesis. In the inception of phylogeography, three main hypotheses were put forward to explain the observed patterns observed (Avise et al., 1987): (1) Most species consist of geographic populations whose members occupy recognizable phylogenetic branches of intraspecific lineages; (2) Species with "shallow" phylogeographic population structures have life histories conducive to dispersal and have occupied areas free of longstanding barriers to gene flow and (3) Intraspecific monophyletic groups characterized by large genealogical gaps usually arise from long-term extrinsic (biogeographic) barriers to gene flow. These broad hypotheses cover the possibilities of outcome and constitute a basis for any phylogeography study.

At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 07

Summary: The equilibrium theory of island biogeography. Species-area and species-distance relationships. Limitations of the equilibrium theory of island biogeography. Relevance of the concepts for marine conservation and the establishment of Marine Protected Areas.

The equilibrium theory of island biogeography. The equilibrium theory of island biogeography (ETIB) was first proposed by MacArthur and Wilson in 1963 as "An Equilibrium Theory of Insular Zoogeography," and expanded in 1967 into a book (MacArthur & Wilson, 1967). The theory addresses the common observation that the number of species on an island generally increases with increasing area. The fundamental tenet of the ETIB is that species distributions in island ecosystems are highly dynamic, governed by simple birth and death process. Species richness on islands results from an equilibrium between colonization and extinction. Colonization is considered as frequent, measured in decades or centuries, or at most in millennia, and extinction is roughly equally frequent as colonization, leading to several species on an island reaching a dynamic equilibrium (Heaney et al., 2013). However, the composition of species changes frequently due to ongoing turnover. MacArthur and Wilson's theory allows general predictions about future island biodiversity patterns. Although ETIB has been essentially overthrown by the emergence of field data and more realistic concepts, there are key aspects of the ETIB paradigm that continue to influence basic biogeographical thinking and its application in conservation science today. Moreover, ETIB changed the prevailing view that island ecosystems remain relatively static over geological time (Dexter, 1978) by understanding that island community display a dynamic equilibrium between species colonization and extinction (species turnover). Although the theory was initially developed for the Indo-Australian archipelago's terrestrial ecosystems (and extended to many other regions in the world), its inception did not specifically contemplate the marine habitats.

Species-area and species-distance relationships. ETIB proposes two main parameters affecting the number of species on an island: the distance of the island from source areas and the island area. The interplay between these two events determines the colonization and the extinction rate. The colonization rate decreases with the increasing distance of the island from source areas, as it is more difficult for organisms to reach more distant locations. In contrast, the extinction rate decreases with increasing island size. Therefore, the interaction between colonization and extinction results in a constantly changing species composition (species turnover) on the island. Small and distant islands will have high extinction and low colonization rates; large and remote islands, low extinction and low colonization rates; small and near islands, high extinction and high colonization rates and small and distant islands, high extinction and low colonization rates, comparatively.

Limitations of the equilibrium theory of island biogeography. A model is a deliberately oversimplified representation of reality and of how a system should behave if only a few significant factors are considered. Basically, we assume all other things are equal, we should obtain a specific outcome. Often more insight into a system is gained with a model, which results deviate from the expected (e.g. the fundamental principle of Hardy-Weinberg). In the ETIB case, its predictions are intended to ask relevant questions about why the system is not in equilibrium, thereby focusing on the process rather than solely on a pattern (Whittaker, 2000). The main limitations of the ETIB are manifold. The first main limitation is that faunas and floras of many islands and small archipelagos are not well known, imposing a bias due to uneven sampling efforts between islands and endemic species inventories are still largely incomplete (Gray & Cavers, 2014). There are a few other practical limitations, such as the ability to distinguish true colonizers from in-situ evolved species and the difficulty in estimating colonisation and extinction rates on our temporal scale. Other limitations include disregarding large-scale environmental alterations causing changes in species composition between sampling intervals, considering that all habitats are biodiverse equivalents and considering that all species are alike, e.g., affected by competition and predation in the same way. The model is neutral at the species level and at the habitat-type level. These limitations have prompted the conceptualization of other models, such as the neutral spatially implicit model (NSIM), which considers individuals and not species and hence introduces the possibility of predicting patterns of species abundances rather than just presence and absence (Rosindell & Harmon, 2013).

Relevance of the concepts for marine conservation and the establishment of Marine Protected Areas. The island biogeographic theory used to explain species richness on oceanic islands can be adapted to isolated patches that do not conform to the usual island definition but that ecologically are also islands. The ETIB is probably the most iconic connection between metacommunity ecology and conservation biology. Ideas emerging from the ETIB and related theories have been instrumental—albeit not without controversy—in examining the role of habitat loss and fragmentation for patterns of biodiversity, as well as reserve design (Fahrig, 2017; Haddad et al., 2015; Harrison & Bruna, 1999; Simberloff & Abele, 1982). Biogeography sensu lato is pivotal for conservation and hence for a sound establishment of protected areas, marine or terrestrial (for a review, see Fredston-Hermann et al., 2018). Research on MPA design has incorporated highly sophisticated models of physical oceanography dynamics such as advection-diffusion of currents, temperature, and pH. Other more traditional models of ecological dynamics (e.g., species interactions, within-range species distributions, migrations and range shifts) have not been included at the same level (Brown et al., 2016; Levy & Ban, 2013; Makino et al., 2015; Mumby et al., 2011).

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Class 08

Summary: Connectivity and genetic differentiation. Patterns of genetic differentiation in populations: definitions and examples of closed and open populations, cline populations, abrupt genetic changes due to geographical barriers, stepping-stone and chaotic genetic patchiness type-populations.

“Defining the scale of connectivity, or exchange, among marine populations and determining the factors driving this exchange are pivotal to our understanding of the population dynamics, genetic structure, and biogeography of many coastal species” (Cowen et al., 2006). Across species and within species, contemporary patterns of genetic diversity are modelled by the interplay of various ecological and evolutionary processes such as gene drift, gene flow, natural selection, survival and reproduction (Hellberg, 2009). These processes are strongly influenced by populations' spatial distribution and size, which fluctuate over time according to historical and contemporary biotic and abiotic factors. Negative gradients of neutral genetic diversity from core to marginal populations have been reported in various species (Eckert et al., 2008; Hampe & Petit, 2005; Pironon et al., 2017). However, the underlying processes are still controversial (Guo, 2012; Hardie & Hutchings, 2010). Two non-mutually exclusive hypotheses can usually explain these negative gradients, including contemporary and historical processes. According to the "central-peripheral hypothesis" (Sagarin & Gaines, 2002), genetic diversity is closely related to peripheral habitats (e.g., Johannesson & Andre, 2006). The alternative "postglacial range expansion hypothesis" posits a series of recolonization founder events (see Austerlitz et al., 1997; Slatkin & Excoffier, 2012) that shaped negative genetic gradients from the source to the edge of the distribution range. This pattern is primarily caused by increased genetic drift along the expansion routes due to contrasting demographic histories when comparing marginal and central populations. Elucidating the relative impact of these processes on current diversity patterns is complex and relies primarily on assessments of historical impacts (Eckert et al., 2008; Guo, 2012). However, this is an important conceptual and practical step in developing a good conservation plan (Frankham, 2010; Hampe & Petit, 2005).

The spatial genetic structure of observed marine species rarely fits models developed for terrestrial populations, such as island and stepping stone models (Hellberg et al., 2002; Neigel, 1997). In the ocean, dispersal usually occurs during the pelagic larval stage, which lasts for days to weeks in offshore waters (Levin, 2006). Surface currents and winds contribute to pelagic larvae dispersing, ultimately affecting most populations' connectivity. At fine geographic scales, surface flow is highly turbulent and nonlinear (Gaines et al., 2003), so linear distance can be a poor predictor of gene flow (White et al., 2010). Early estimates of gene flow in marine species relied solely on simplified models based on unidirectional ocean currents acting on passive particles (Cowen et al., 2006). Recently developed multi-biophysical models provide better estimates of gene flow, including the possible influence of biological factors such as larval mortality and larval active vertical placement behaviour on dispersal pathways.

We will look closely at types of populations along the axis of no differentiation - total differentiation that exists in nature as a gradient of possibilities. Here, we will use the six categories of Hellberg et al. (2002) as the anchor for this class. These are mainly based on the relationship between gene flow and effective population size. Although there may be many models of population structure or population differentiation, we will focus on only a few as part of a continuum from open populations to closed populations: cline, stepping stone and chaotic patchiness populations. Obviously, these are models, which by definition, greatly simplify reality. They are, however, important to grasp the main characteristics at play.

Open populations. These populations have broad geographic scale homogeneity. Numerous closely related mtDNA haplotypes are shared between distant populations, suggesting gene flow. The high global variability observed also indicates that genetic connectivity is not solely due to one single recent founder event. Examples of species with such populations are the blister worm *Polydora websteri* (Rice et al., 2018) or the Pacific thread herring (*Opisthonema libertate*) (Pérez-Quiñonez et al., 2019).

Closed populations. These populations are consistently genetically different from other conspecific populations. This may happen because a substantial fraction of the offspring produced in an area persists, is retained or returns to the same area. The populations may be more or less different, and the extent of this differentiation depends on the combined effects of mutation, drift, migration and selection and their interaction with time and population size. In the absence of gene flow between two populations, the effects of drift and selection will most heavily influence the differentiation. Over time, mutations lead to the emergence of "private" alleles - genetic variants inherent to a specific population – and these will reach high frequencies (by drift or selection) in some populations and do not appear in others. Another interesting aspect is the phylogenetic relationships between haplotypes because new alleles arise from those already present in the population, creating a pattern in which the most similar haplotypes are distributed within (rather than between) populations. With time and sustained self-recruitment, a reciprocal monophyletic pattern emerges in which all alleles in each population are more closely related to each other than alleles in the foreign population (Cunningham & Collins, 1998). Closed populations are expected to occur more often in species with limited dispersal capability, such as gastropods with direct development (Kyle & Boulding, 2000), or in species with strong natal philopatry, such as the bonnethead sharks (Sphyrna tiburo) (Portnoy et al., 2015). Nonetheless, closed populations have also been described in species with pelagic larval stages, such as the burrowing crustacean *Challichirus islagrande* (Bilodeau et al., 2005), and the tidepool copepod *Tigriopus californicus* (Burton, 1998).

Cline populations. Although gene flow exists among populations, allele frequencies vary geographically in a continuum. This is often due to the direction and strength of natural selection correlated with environmental gradients. The textbook example is the change in the Lactate Dehydrogenase allele frequencies of the Mummichog *Fundulus heteroclitus*, which are an adaptation to cold and warm temperatures (Powers & Place, 1978). Another relevant example is the change in allele frequencies across latitudes in the temperature-adapted Atlantic cod *Gadus morhua* (Bradbury et al., 2010). Geographic clines can also arise from secondary contact (populations that have diverged by genetic drift or selection during a period of isolation before contact) between genetically divergent populations, such as in rainbow smelt, *Osmerus mordax*, which had undergone a geographical separation, or vicariance, during the Pleistocene, but currently has no barriers to gene flow (Bradbury et al., 2011).

Abrupt genetic changes due to geographical barriers. Gene flow between populations on either side of the barrier is restricted for a period sufficient for genetic differentiation to occur. These barriers separate different genetic lineages and are called phylogeographic breaks when their locations coincide with past or present barriers. Phylogeographic discontinuities such as the Indo-Australian Archipelago (Barber et al., 2002), Point Conception (California) (Pelc et al., 2009), and the Alboran Sea (Mediterranean-Atlantic divide) (Patarnello et al., 2007) have been observed, with some species exhibiting genetic discontinuities in these regions. The Alboran Sea, in particular, is crossed by a complex ocean circulation system that may act as a gene flow barrier for some organisms and not for others (Bargelloni et al., 2003).

Stepping stone gene flow. This is also known as isolation by distance, meaning that gene flow decreases with increasing geographic distance among populations. There are many examples of marine fish and invertebrate species showing this isolation by distance patterns, such as nosestripe klipfish (*Muraenoclinus dorsalis*), super klipfish (*Clinus superciliosus*) and bluntnose klipfish (*Clinus cottoides*) (Wright et al., 2015).

Chaotic genetic patchiness. The populations exhibiting this pattern have exchange genes at high rates, but the effective population size, a number that corresponds to the number of breeding individuals in the population, is small so that the results in genetically similar adult populations coexisting with genetically different juvenile populations (cohorts of recruits). This pattern is observed in several species with pelagic larvae and might be due to several factors, such as switching population sources, selection (mainly on early life stages), sweepstakes reproductive success, collective dispersal, or temporal shifts in local population dynamics leading to asynchronous spawning (Eldon et al., 2016). In the Atlantic stalked barnacle (*Pollicipes pollicipes*), the isolation by distance pattern is congruent with Iberian Peninsula hydrodynamics, which can produce chaotic genetic patchiness at small temporal scales due to sweepstake reproductive success, collective dispersal and/or self-recruitment (Parrondo et al., 2022).

Broad scale homogeneity. This pattern in practice corresponds to a situation of panmixia, i.e., gene flow is constant and effective population sizes are large, resulting in genetic homogeneity over broad geographic scales. Because of the particular characteristics of the physical environment, it is not trivial to find species that will exhibit broad-scale genetic homogeneity. Examples of such a pattern are the jellyfish *Pelagia noctiluca* in the North Atlantic Sea (Glynn et al., 2016) and the bluespine unicornfish (*Naso unicornis*) (Horne et al., 2008).

At the end of the class, I will retrieve the initial class objectives and give a take-home message summarising the main class contents.

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Class 09

Summary: The Atlantic-Mediterranean divide: a transitional zone. The geological history of the Mediterranean Sea. Hypotheses of biogeographic scenarios to explain genetic patterns between the Mediterranean and the Atlantic. Case studies: Salaria pavo; diverse genetic patterns in Sparidae from the Mediterranean and the Atlantic; responses to Pleistocene glaciations.

Transitional zones are of great evolutionary interest because unique patterns of spatial change are often preserved. The Atlantic-Mediterranean divide or transition has been associated with the existence of a genetic break represented by the Almería-Oran front (AOF), a common feature observed in many species (Pascual et al., 2017, Patarnello et al., 2007), but is by no means universal (Bargelloni et al., 2003). The AOF is situated east of the Strait of Gibraltar by the convergent Atlantic and Mediterranean water masses, stretching from Almeria on the Spanish coast to Oran on the Algerian coast, and its characteristic oceanography may promote differentiation between populations on either side of the break.

The geological history of the Mediterranean Sea. The geological features of today's Mediterranean Basin essentially arise from two main processes: (1) crustal deformation caused by the subduction of the African plate under the Eurasian plate and (2) gradual closure of the Mediterranean sea involving a series of submarine-insular sills (sea floor barrier of relatively shallow depth that restricts water movement). The development of the Mediterranean Basin begins with the breakup of the Mesozoic supercontinent Pangea. During this period, the Triassic seafloor's expansion triggered the Atlantic Ocean's development, separating the African and Eurasian plates from the North American plate. The seafloor spread at different geographic locations triggered the development of the Tethys Ocean, separating the African plate from the Eurasian plate. This ancient sea remnant is now known as the Mediterranean Sea. The Mediterranean Sea is a completely enclosed sea, except for a 12.9 km wide, 286 m deep connection with the Atlantic Ocean between Cape Trafalgar and Cape Spartel (Strait of Gibraltar). The depth of the Mediterranean Sea is about 3400 m in the West Basin and 4200 m in the East Basin. Therefore, it can be called a proper ocean basin. A shallow threshold (350 m deep) in the Strait of Sicily divides it into two entities, the Eastern and Western Mediterranean. The Bosphorus-Dardanelles Strait (40-70 m) separates the Black Sea from the Mediterranean Sea. The Pelagosa sill (160 m) separates the central Adriatic from the eastern Mediterranean. The man-made Suez Canal (opened in 1869) in the southeastern Mediterranean provides a steady influx of saltwater (and biota) from the subtropical Red Sea. The Mediterranean has ranged from near-total aridity during the 'Messinian Salinity Crisis' (MSC) (up to 5.33 Ma) to cycles of cold glacial periods followed by warm interglacial periods in the Quaternary over the past million years. Most of today's biota is the result of colonization, primarily from the Atlantic Ocean

(Almada et al., 2001), with less significant influence from the Red Sea. Indeed, after a period of isolation and aridity lasting about 500,000 years, the influx of Atlantic waters through the newly opened Strait of Gibraltar could lead to renewed flooding of the Mediterranean Basin. MSCs have wiped out the existing Indo-Pacific biota with the few exceptions of taxa of Miocene origin that survived in shallow-water refuges such as Aphanius (Hrbek & Meyer, 2003).

Hypotheses of biogeographic scenarios to explain genetic patterns between the Mediterranean and the Atlantic. There are myriad biogeographic hypotheses concerning the current spatial genetic patterns observed in the Atlantic-Mediterranean boundary. In this class, we will address four main scenarios (Castilho et al., 2017): (1) panmixia, whereby there is no discernible geographic or otherwise genetic structure corresponding effectively to a random distribution of haplotypes; (2) isolation-by-distance (IBD) pattern by which genetic and geographic distances are positively, and therefore alleles will show a frequency cline pattern between the Atlantic and the Mediterranean; (3) secondary contact between populations of the two regions, where alleles will transiently show a cline pattern at the contact zone between the two areas, and (4) genetic phylogeographic break between adjacent regions, wherein a sharp change of allele frequencies is observed between the Atlantic and the Mediterranean.

Case studies. The class will be exposed to examples showing strict divergence or no differentiation at the AOF level. Species such as *Dicentrarchus labrax*, *Diplodus puntazzo* and *Coryphoblennius galerita* have shown high genetic divergence between populations inhabiting both sides of the AOF (Bargelloni et al., 2005; Domingues et al., 2007; Lemaire, Versini & Bonhomme, 2005), while others display evidence of strong genetic flow (e.g., *Thalassoma pavo*, *Chromis chromis* and *Diplodus sargus* — Bargelloni et al., 2005; Costagliola et al., 2004; Domingues et al., 2005). Other species display clear asymmetric migration from the Mediterranean to the Atlantic but only marginally support the isolation-by-distance model (e.g. *Salaria pavo*) (Castilho et al., 2017). Assigning the observed differences promoted by the AOF to specific environmental or biological parameters has proven quite difficult. The work of Patarnello et al. (2007) and Galarza et al. (2009) will be used to illustrate this difficulty. Students will be prompted to critically evaluate the range of case studies presented in terms of the number of samples, locations of samples, molecular markers used, and known basic biology of the species.

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Class 10

Summary: Marine Island evolution: what makes islands so interesting? The North Atlantic archipelagos. Evolution of marine organisms. Case studies: molluscs and fish, differences and similarities in colonization and differentiation.

Ever since Darwin visited the Galapagos Islands and observed their great biodiversity, the marine archipelagos have been considered a natural laboratory for studying evolution and biodiversity (Cunha et al., 2005). In that context, isolation is key to understanding the evolutionary biology of islands; oceanic island biota has led to high levels of endemism and ecomorphological specialization through several colonization events followed by rapid radiation. Moreover, ancient marine archipelagos of similar geological ages are expected to have comparable numbers of endemic lineages with identical life history strategies, especially if the islands share similar habitats. We will discuss four case studies regarding the speciation of marine organisms in the North Atlantic archipelagos.
In the North Atlantic, the traditionally called Macaronesia includes the Azores, Madeira, Canaries and Cabo Verde, which have distinct origins and geological timelines. While Sal and Maio from Cabo Verde and Selvagens emerged more than 20 million years (Myr) ago, Gran Canaria, Porto Santo and Boavista emerged around 15 Myr, Santo Antão, S. Nicolau, and S. Vicente have ca. 5 Myr, while El Hierro and some islands of Azores appeared less than 1.5 Myr (Torres et al., 2002). Macaronesian archipelagos were never connected to the continental mainland, they are all of volcanic origin, and therefore their biota is the result of dispersal from external geographic sources and in situ diversification. These archipelagos provide an ideal yet understudied system to investigate evolution and phylogeography in marine benthic organisms with limited dispersal capacity.

The first case study deals with contrasting diversification patterns of *Conus* observed in Cape Verde, Canary Islands, Azores and Madeira archipelagos, combining molecular phylogenetic and geometric morphometry data with bathymetric and paleoclimate reconstructions (Cunha et al., 2014). The second case study focuses on keyhole limpets (*Fissurella* and *Diodora*) from Cape Verde Islands, and through an integrative approach combining molecular phylogenetics with ocean transport simulations, we will infer species distribution patterns and analyze connectivity (Cunha et al., 2017). The third case-study focus on a benthic fish, the Madeira rockfish, *Scorpaena maderensis*, which displays genetic hyper-diversity relatively uncommon in rocky coastal species, whose dispersal capability is limited by local oceanographic patterns (Francisco et al., 2021). Finally, a fourth case study deals with the common two-banded seabream (*Diplodus vulgaris*). The species is presently relatively common along the coast of the Azores archipelago, but it was virtually non-existent before the 1990s. Genetic results for the North-Atlantic archipelagos suggest that this species has probably lived in the Azores for about 40 generations, equivalent to about 80-150 years. This may suggest roughly contemporaneous colonization followed by more recent population growth driven by changing climatic conditions. Moreover, the lack of previous records for this species, along with the lack of lineage segregation and the presence of relatively few private alleles, does not rule out the possibility of an even more recent colonization event (Stefanni et al., 2015).

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Computer Laboratory classes

In these computer lab classes, students are also asked to enter an online session besides being present in the classroom. The online session allows the students to share their screens once they have questions or a particular methodological problem. Moreover, students are encouraged to implement the “Pomodoro timer” method. With this method, students working individually can adjust their focus capacity to time slices with the individual-tailored duration. Students are encouraged to clearly identify their specific tasks and break the 4-hour classes into 25-45 minute chunks separated by five-minute breaks. After four of these work-break cycles, they will take a longer break of about 15 to 20 minutes. This way, students with different attention and focus spans do not depend on a fit-all break. However, there are three “discussion” periods where all the students stop their tasks and engage in the discussion that I will promote.

All the materials and links to introductory guides are available in the dedicated webpage.

Sessions 1-3

The first-course project will span 1 to 3 weeks and has a central goal: to understand similarities of fish community composition of geographic regions of the Northeastern Atlantic Ocean. To that end, students will be given a presence/absence database of over 800 continental shelf fish species from 13 different regions, including the Lusitania Province, Bay of Biscay, Atlantic Iberia, western Mediterranean Sea, eastern Mediterranean Sea, Atlantic Morocco, West Sahara, archipelagoes of the Azores, Madeira and the Canary Islands, the tropical eastern Atlantic, Cape Verde and São Tomé and Principe. Students will curate the database and use similarity ecological indexes to investigate biogeographical relationships of fish composition among those geographic areas. A main part of the work will be to summarise species richness and level of endemism and get data ready to produce tables and graphs. Students will work individually. Although the goal seems achievable through trivial tasks such as excel manipulation, the fact is that most students find the work challenging. That is mostly because their base knowledge of simple Excel functions and R-scripts is rudimentary. In these classes, we want also students to experience facing and resolving small problems for which solutions are readily available at their fingertips. The final result of this project is a selection of graphs representing species richness, endemicity and area-cladograms based on cluster and multi-dimensional scaling analysis. A reference list is available on the website to support this work, but students are encouraged to go beyond this list and find other relevant information. We will also explore principles of graph choice and design for more effective communication. As a final result, students must write an A4 page (500 words) explaining their results. This work contributes to 10% of the evaluation.

Resources.

Link for data
Starting with R
Short-R-Intro
The R Guide
RStudio primer “The Basics”

script for cluster analysis
script for MDS analysis

References

Almada, V. C., Toledo, J. F., Brito, A., Levy, A., Robalo, J. I., Martins, J., & Almada, F. (2013). Complex origins of the Lusitania biogeographic province and northeastern Atlantic fishes. Frontiers of Biogeography, 5, 9.

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Sessions 4-6

The second project consists of three sessions. Each session begins with an instructional lecture on a niche modelling topic which is followed by hands-on model development and a group discussion on the applications and consequences of the findings. Although these sessions are not a deep dive into niche modelling, the starting introductory lectures will cover the theoretical and conceptual foundations of modelling approaches and the most simple statistical algorithms, assumptions, and data requirements. In modelling sessions, the students will choose a marine species they will work on. Some choice criteria are given; namely, the species should not be an endemic or a cosmopolitan species, and there must be possible to access online presence geo-referenced data. Students will practice loading and viewing example data, then use pre-developed code to execute the modelling steps, troubleshoot as needed, and develop models. The emphasis of these computer labs is on understanding the steps and code rather than on replicating or developing code. The results should be included in an A4 page (500 words) explaining their results. This work contributes to 10% of the evaluation.

All the materials and links to introductory guides are available in the dedicated webpage.

Resources.

script for retrieving occurrences
script for modelling

References

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Annexe 1 - Evaluation criteria for written assignments

Evaluation criteria for written assignments

adapted from MELAB (L. Hamp-Lyons, 1992)

GRADE	Task Compliance/ Format	Topic Development	Organization	Vocabulary	Discourse Control	Sentence structure	Mechanics
A **18-20**	• Fully addresses all aspects of the writing assignment (topic), including in-text citations and frames. • Stays on task throughout.	• Full and rich development (*focus, relevance, explanations, support*) • shows knowledge of subject matter through effective use of topic-related concepts to support argument • shows sophistication in fluency of expression.	• Organization fully appropriate and effective for topic (*point of view, unity, paragraphing*) • very strong introduction & conclusion, thesis statement, topic sentences.	• Broad and fluent range of vocabulary • elaboration and detail achieved through full use of topic-related terms • concise and appropriate use of vocabulary (formal English) • correct use of word forms and word choice.	• Full control (*logical coherence*) and excellent use of *cohesive devices* (key words, pronouns, references, transitions, etc.) • presentation of ideas extremely clear and coherent.	• Full range of sentence patterns (*simple, compound, complex*), effectively used • error-free sentence-level grammar.	• Correct use of in-text citations & references • spelling, capitalization, and punctuation **error-free.**
B **16-<18**	• Addresses the writing assignment (topic) but may not fully develop or include all parts of the assignment (topic). May digress in parts of the writing.	• Clear and complete development of content high level of fluency in expression (clarity) • evidence of logical progression of ideas • mostly effective use of topic-related concepts to show knowledge of subject matter to support argument.	• Organization controlled generally appropriate to topic appropriate paragraphing introduction & conclusion, thesis statement, topic sentences evident and appropriate.	• Flexibility in range • appropriate use of topic-related terms and other vocabulary in a variety of situations • mostly correct use of word forms and word choice • occasional wordiness or colloquialisms (informal English)	• good control of cohesive devices (key words, pronouns, references, transitions, etc.) used successfully in a range of situations • coherence apparent.	• Mastery of sentence patterns demonstrated may have occasional grammatical errors on the sentence level.	• Spelling, form, indentations, capitalization, punctuation, and citation errors **few and not distracting**.
C **13-<16**	• May address a part of the writing assignment (topic), but generally writes about the topic and does not address the assignment (topic) directly • Obviously digresses throughout the writing. Several omissions in the assignment (topic).	• Development of content **adequate**, but **lacks** clearly stated positions or supporting information • some use of topic-related concepts to show knowledge of subject matter and to support argument • fluency of expression may be halting of awkward.	• Organization **controlled but limited** • some paragraphing problems • adequate introduction & conclusion • limited thesis statement & use of topic sentences.	• Adequate range (*word choice*) • no precise use of subtle meanings displayed • vocabulary sometimes used inappropriately • often incorrect use of *word forms* • few instances of wordiness or colloquialisms	• Generally **adequately** connected • presentation of ideas generally **clear** and coherent • cohesive devices could be used more often and more effectively.	• Sentence patterns most often successfully used • several grammatical errors on the sentence level.	• **Occasional** errors in spelling, form, indentations, capitalization, punctuation, and citation sometimes distracting.
D **10-<13**	• May write within the topic, but no evidence of addressing the writing assignment (topic) itself • Major omissions in the assignment (topic).	• Development of content **restricted** may be incomplete or unclear lack of fluency in expression.	• **Little** or **poorly** controlled organization • incorrect paragraphing or sequencing • purpose statement/thesis, conclusion, topic sentences may be **missing or incomplete.**	• Narrow range (*word choice*) • many *word form* errors • vocabulary often used inappropriately • only basic and elementary meanings are conveyed • many instances of wordiness or colloquialisms	• Connections **awkward**; cohesive devices (key words, pronouns, references, transitions, etc.) may be missing or are used inaccurately • **lack** of logical sequencing of ideas.	• Many sentence structure problems • Simple and complex sentences attempted but often unsuccessful **grammatical errors distract from meaning**.	• Spelling, capitalization, punctuation, and citation errors are **frequent and distracting**.
E **<9.5**	• Does not address the writing assignment (topic) • off-topic throughout the writing • required assignment (topic) instructions not included.	• Simplistic statement of content • often copied from sources or lists of information • no argument no use of topic-related concepts to support argument.	• Minimal attempt at paragraphing, often unsuccessful strings of sentences no introduction or conclusion, thesis statement, topic sentences.	• Simple vocabulary, often inappropriately used • no control of word choice and word forms • no attempt to use topic-related terms • many instances of wordiness or colloquialisms	• Connections **not present** or unsuccessful presentation of ideas unclear and confusing.	• **Replete** with errors in sentence structure and sentence grammar	• Spelling, form, indentation, capitalization, punctuation, and citation errors **throughout**.

Annexe 2 - Poster instructions

The main characteristics of a scientific poster are:

1. Organized, clean, simple design.
2. Focused on one specific research topic that can be explained in 3 minutes.
3. Contains a Title, Authors, Abstract, Introduction, Materials & Methods, Results, Discussion, References and Acknowledgements. However, because students will not be presenting their own data, the poster can also contain the explanation and application of concepts related to biogeography.
4. Has high-resolution figures and/or tables that describe the research in detail. The most important parts of a scientific poster will likely be its figures and/or tables because these are what an audience will naturally focus their attention on.
5. It should contain minimal text, with figures and tables being the main focus.
6. Pay attention to fonts used in the poster: the largest fonts (e.g., 40-120 point font) will be used for the title, author list and institutions. Section headings will use 30-40 point font. Section text, table captions, figure captions and references will typically use 20-30 point font. Font sizes smaller than about 20 points can be difficult for an audience to read and should only be used for the References and Acknowledgements sections.

Annexe 3 - Format of flash talks - 3 minutes

Please follow the guidelines below for developing your slides:
Slide 1 · Photo of yourself with your title, name and institution. When you are presenting, there is no need to repeat this information. Instead, present the research topic - for example, “This research reports on a project which addresses the issue of ...."
Slide 2 · Context/Background: For example, "This research draws on the theory of ...., particularly the idea that ...."
Slide 3 · Methods: For example, “This study was a retrospective cohort study comparing…”
Slide 4 · Results/One major finding: For example, "The study found that X had a significant effect on Y".
Slide 5 · Key implications and wrap-up: For example, "One important implication of this study is that X should be taken into account when doing Y” and:"Overall we found that topic .... is a promising area for further investigation, with possible extensions to other areas of research, such as ..."

Hints for Creating an Engaging Flash Talk

- Create and present your Flash Talk like a story, with a beginning (catch attention), middle (explain the details) and ending (wrap up and explain the importance of the work).
- Use a 'hook' to catch everyone’s attention; something personal, emotive, and funny.
- Dive straight into the topic.
- Mention the most important details, without which we cannot understand the presentation.
- Use active language; it makes it more dynamic.
- Use shorter words, sentences and paragraphs than a scientific paper; it is easier to listen to.
- Rehearse, rehearse and rehearse again (and time each one).
- Do not (ever) presume you have this without rehearsing and timing yourself.
- Write more and then distil down. It's much easier to streamline your presentation than to plump it up.
- Take your time, speak clearly, but don’t be monotonic. Even with 3 minutes, you have time to breathe.
- Stand straight, shoulders down, head up, look at your audience, smile and make eye contact.