

Reconstructing the worldwide colonization history of the world's most widespread marine plant

Using population genomics, we reveal the global dispersal history of eelgrass (*Zostera marina*) from its origin in the Northwest Pacific Ocean, across to the East Pacific, Atlantic and the Mediterranean Sea. Striking differences in genetic diversity among the locations reflect past glaciations and repeated bottlenecks during *Z. marina*'s worldwide colonization.

This is a summary of:

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The project

Marine flowering plants, or seagrasses, have recently experienced a surge in scientific and public interest¹ owing to the many ecosystem services they provide, such as sequestration of 'blue carbon', the enhancement of associated biodiversity and improvements to water quality. The most widely distributed species of seagrass, *Zostera marina*, occurs circumglobally in the northern parts of the Pacific and Atlantic Oceans between 35° and 70° latitude (Fig. 1a). However, it remains unclear how and when *Z. marina* (or eelgrass) expanded across two major ocean basins from its origin in the Northwest Pacific. It has previously been assumed that eelgrass reached the Atlantic through the Canadian Arctic some 3 million years ago following the opening of the Bering Strait², but a time-calibrated phylogeny is lacking thus far.

The discovery

To find out whether *Z. marina* did reach the Atlantic millions of years ago, we re-sequenced the nuclear and chloroplast genomes of 190 individuals across 16 locations. Leveraging the chromosome-level reference genome^{3,4} and a dated whole-genome duplication (WGD) event³, we applied the multi-species coalescent model and a strict molecular clock calibrated against the divergence between *Z. japonica* and *Z. marina*. We discovered that there were at least two trans-Pacific colonization events. Subsequent population exchange along the East Pacific coastline led to admixture of gene pools that complicated our analysis; we accounted for this effect by constructing split networks and by removing identified admixed populations based on *D*-statistics. Along with a molecular calibration point based on the WGD event, the major divergence events could be dated in absolute time. Reassuringly, chloroplast (cp)-haplotype networks (Fig. 1b) in combination with a general cpDNA molecular clock yielded similar results.

We found that the arrival of eelgrass in the Atlantic through the Canadian Arctic occurred around

243 thousand years ago (ka), which is much more recent than previously assumed. We also estimate that divergence happened more recently in the Atlantic than the Pacific, and populations in the Mediterranean were founded around 44 ka (Fig. 1b). The effects of the Last Glacial Maximum (LGM) 19 ka reveal a major Atlantic refugium along the North Carolina and Virginia coast, from which the East Atlantic was rapidly recolonized.

We also identified striking differences in genome-level diversity: Atlantic populations featured 5–7-fold lower genetic diversity than Pacific populations and the least genetically diverse population in the East Atlantic featured 35-fold lower heterozygosity and nucleotide diversity (Fig. 1c) than the most diverse population in the West Pacific.

The implications

Our findings indicate that eelgrass beds have only existed for a relatively short time in the Northwest and Northeast Atlantic. These beds are the foundation of diverse and productive ecosystems, and there are no other extant species that could fill their niche above approximately 50° N. This short time span is also reflected in specific associated fauna that are rare in Atlantic eelgrass beds but more abundant in those found in the Pacific⁵.

While we can now explain how striking gradients in neutral genetic diversity came about, it is still unclear whether this translates to adaptive genetic diversity – that is, whether genetically depauperate populations in the Atlantic will be able to adapt to climate change.

The obvious next step is to focus on adaptive variation, for example, variation that correlates with the broad latitudinal cline spanning 35° latitude of the distribution range of eelgrass. Development of the *Zostera* pangenome is underway and is expected to capture the adaptive genetic diversity across *Zostera*'s range of habitats.

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EXPERT OPINION

"The authors present a manuscript that uses thorough interrogation of the nuclear genome to unravel the global phylogeographic history of *Z. marina*, an ecologically important seagrass. The authors have assembled an impressive

genomic dataset and push the boundaries of the geographic extent that can be encompassed in phylogeographic studies."

Richard Hodel, Smithsonian Institution, Washington, DC, USA.

FIGURE

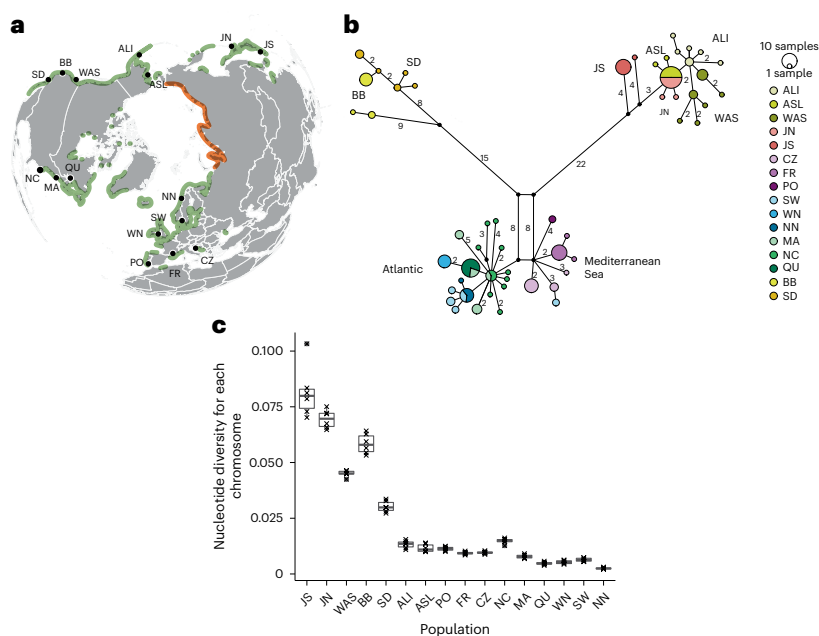


Fig. 1 | Sampling locations, nucleotide diversity and population structure of *Z. marina*. a, Extant distribution of *Z. marina* in green and documented absence in orange. b, Network of cpDNA genome haplotypes showing three deeply divergent clades. Numbers indicate mutation steps. c, Box plots (median, 25th and 75th percentiles, outliers) showing nucleotide diversity, averaged over the 6 chromosomes of all 16 sampled populations from west to east. San Diego, SD; Bodega Bay, BB; Washington state, WAS; Alaska-Izembek, ALI; Alaska-Safety Lagoon, ASL; Japan North, JN; Japan South, JS; North Carolina, NC; Massachusetts, MA; Quebec, QU; Northern Norway, NN; Sweden, SW; Wales North, WN; Portugal, PO; Mediterranean France, FR; Croatia, CZ. © 2023, Yu, L. et al., [CCBY 4.0](#).

BEHIND THE PAPER

This work is the result of more than 12 years of worldwide collaboration within the *Zostera* Experimental Network (ZEN) to understand the drivers of eelgrass's global ecology. This collaboration enabled us to obtain necessary high-quality tissue samples from across *Z. marina*'s entire distribution range. Another key prerequisite was a chromosome-scale reference genome^{3,4}. Given that most seagrass researchers are ecologists, we brought together computational biologists to

carry out a variety of different population genomic and coalescent approaches. We were initially struck by the recency of the trans-oceanic events and were thus relieved when additional independent phylogenetic analyses yielded similar time estimates. Our results also support another finding: that phylogeographic legacies can affect the community structure of animals within eelgrass ecosystems more than current environmental forcing⁵. **J.L.O.**

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FROM THE EDITOR

"The seagrass *Z. marina* has the widest distribution amongst marine angiosperms, exceeding that of most land plants. An evolutionary path for *Z. marina* colonization reconstructed using genetic factors is in good agreement with climatic and geographic factors (such as ocean currents). *Z. marina* is significant for fisheries as a spawning ground, and the methods developed could be used to investigate the phylogeographic distribution of other plant species." **Chris Surridge, Chief Editor, Nature Plants.**