PNAS RESEARCH ARTICLE | ENVIRONMENTAL SCIENCES

The genetic legacy of a global marine invader

Erik E. Sotka[a,1], Ryan B. Carnegie[b], James T. Carlton[c], Lucia Couceiro[d], Jeffrey A. Crooks[e], Hikaru Endo[f,g], Hilary Hayford[h], Masakazu Hori[i], Mitsunobu Kamiya[j], Gen Kanaya[k], Judith Kochmann[l], Kun-Seop Lee[m], Lauren Lees[n], Hannah Miller[a], Masahiro Nakaoka[o], Eric Pante[p], Jennifer L. Ruesink[q], Evangelina Schwindt[r], Åsa Strand[s], Richard B. Taylor[t], Ryuta Terada[f,g], Martin Thiel[u,v,w], Takefumi Yorisue[x,y], Danielle Zacherl[z], and Allan E. Strand[a,1]

Affiliations are included on p. 8.

Edited by Daniel Simberloff, University of Tennessee at Knoxville, Knoxville, TN; received September 13, 2024; accepted February 22, 2025

The massive geographic expansion of terrestrial plant crops, livestock, and marine aquacultured species during the 19th and 20th centuries provided local economic benefits, stabilized food demands, and altered local ecosystems. The invasion history of these translocations remains uncertain for most species, limiting our understanding of their future adaptive potential and historical roles as vectors for coinvaded species. We provide a framework for filling this gap in invasion biology using the widely transplanted Pacific oyster as a case study. A two-dimensional summary of population-level variation in single nucleotide polymorphisms in native Japan reflected the geographical map of Japan and allowed identification of the source regions for the worldwide expansion. Pacific oysters proliferate in nonnative areas with environmental temperatures similar to those areas where native lineages evolved. Using Approximate Bayesian Computation, we ranked the likelihood of historical oyster or shipping vectors to explain current-day distribution of genotypes in 14 coinvaded algal and animal species. Oyster transplants were a more likely vector than shipping for six species, shipping activity was more likely for five species, and a vector was ambiguous for three species. Applying this approach to other translocated species should reveal similar legacy effects, especially for economically important foundation species that also served as vectors for nonnative species.

biological invasions | *Magallana (Crassostrea) gigas* | aquaculture

Significance

Nearly every nonnative species of economic value was intentionally transplanted, and many accidentally transported multiple hitchhiking species. These nonnative populations have signatures of their history embedded in their DNA, but we have lacked a statistical framework for using these genetic markers to assess alternative hypotheses of dispersal. We statistically distinguish between competing vector hypotheses that themselves are empirically derived. The quantitative approach confirmed vector hypotheses based on historical evidence for some but not all species. Our results also reinforce the threat that deliberate introductions of aquacultured species can represent to local nearshore ecosystems and suggest that management strategies focus on prevention.

Nearly all terrestrial plant crops and livestock occur outside their regions of origin from centuries of human migration and deliberate translocation (1–6). Many of these range expansions accelerated during the 20th century and now provide economic security and reliable sustenance for local communities while profoundly impacting the biodiversity and functioning of local ecosystems (7). The introduction histories of many domesticated species remain poorly described, yet are essential to maintaining crop diversity (8), understanding the evolutionary processes of adaptation, dedomestication, and ferality (9, 10), and predicting a species' capacity to adapt to current and future environmental conditions (2).

Deliberate translocation of species also provided potential vectors and reservoirs for a variety of diseases and pests that are accidentally introduced (5, 11, 12). Successful management of these accidental invasions depends on prevention of future invasions via these same vectors and on eradication and mitigation strategies based on knowledge of the invaders' ecological and evolutionary background in their native range (4, 13). However, for many species, it has been difficult to unambiguously identify a role for movement with transplanted species versus other vectors [e.g., long-distance natural dispersal (5)] or to identify original source populations. To date, such inference has largely depended on historical information (i.e., the timing and location of introduction) or the geographic distribution of genetic diversity in the cointroduced species alone (e.g., refs. 14–16). It is rare for population genetic patterns (which infer invasion history) of cointroduced species to be directly compared with those of a putative plant or animal vector and for alternative vector hypotheses to be statistically assessed.

Like terrestrial species, aquatic species have a centuries-long history of transplantation and aquaculture that accelerated greatly during the 20th century (1, 17), and many of these deliberate transplants accidentally introduced hitchhiking species (18). Among the most important of the deliberate transplants is the Pacific cupped oyster *Magallana gigas* (syn. *Crassostrea gigas*), which generates an estimated $1.5 billion annually in income from half a million tons of harvested biomass (19). *M. gigas* is native to China, the Korean Peninsula, Japan, and Russia and is currently harvested on all continents except Antarctica (20, 21), as a consequence of massive and deliberate introductions during the 20th century at a scale greater than any other marine or estuarine species (20). *M. gigas* became feral

The authors declare no competing interest.

This article is a PNAS Direct Submission.

[1]To whom correspondence may be addressed. Email: SotkaE@cofc.edu or StrandA@cofc.edu.

This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2418730122/-/DCSupplemental.

Published April 7, 2025.

almost everywhere (20, 22–24) and has both positive and negative impacts on biodiversity and ecosystem functioning (20, 24, 25).

The massive transport of live oysters was associated with the accidental cointroduction of dozens of species of invertebrates, seaweeds, and microbes (6, 18, 26, 27). While there are direct observations of species that occur in shipments of imported Pacific oysters (28), these observations are relatively rare. Most of the evidence for cointroduction is based on the timing and location of discovery in introduced regions (18, 27). However, there has not been statistical evaluation of the role of oysters versus other mechanisms [e.g., shipping activity (29)] as vectors for any putative coinvader species, in part because we lack an empirical description of oyster invasion history. There are population genetic studies within the native range (30–32) and the nonnative range (33–35) or both (36). Our ability to confidently identify native sources (13) has been hampered by a lack of extensive sampling across both the native and nonnative range of *M. gigas*.

To address these gaps, we genotyped 726 *M. gigas* individuals from 41 populations globally using Restriction-site associated DNA sequencing (RADseq). We assessed the population structure of native Pacific oysters from Japan and South Korea and the invasion history of nonnative Pacific oyster populations in western North America, South America, Europe, and New Zealand. We then used Approximate Bayesian Computation [ABC; (37)] to quantify the relative importance of shipping activity (29) versus Pacific oyster movement as a vector for 14 introduced species for which population genetic patterns were already published. These results have implications for future aquaculture efforts, the functioning of estuaries dominated by nonfarmed oysters, and the study of invasive species more broadly.

Results

Native Structure and Invasion History. Our single nucleotide polymorphism (SNP) survey detected geographic population structure of native *M. gigas* in Japan and South Korea. The first axis (PC1) of a principal components analysis (PCA; Fig. 1 *A* and *B*) with native individuals recapitulates a latitudinal distribution of populations along the eastern coastline of Japan. The 2nd axis (PC2) largely separates the west coast of Japan and South Korea from the Pacific shoreline of Japan. Consistent with reports of historical and ongoing movement of oysters in the native range from the Miyagi region (which includes Miyagi and Fukushima) to other locations (32), a population in southernmost Japan (YOJ) and another on the southern side of Hokkaido (AKK) had genotypes similar to Miyagi in PC space, suggesting recent admixture (Fig. 1*C* and *SI Appendix*, Figs. S4 and S5). Latitudinal variation is also revealed by an admixture analysis, which reveals latitudinal shifts in the frequency of genetic clusters assigned to individuals. This result was insensitive to the choice of the number of genetic clusters (K) and was observed at K = 3 through K = 8 (*SI Appendix*, Fig. S8). Overall magnitude of genetic differentiation among Japanese and Korean populations was low (mean F_{ST} ± SE = 0.0027 ± 0.0020; range = −0.0003 to 0.0108; *SI Appendix*, Fig. S6), and likely reflects incomplete lineage sorting coupled with elevated polymorphism that characterizes broadcast-spawning high-fecundity marine invertebrates such as *M. gigas* (38).

The population genetic structure in the native range allowed us to distinguish among three major regions of the oyster industry from where historical exports from Japan originated (39): Hokkaido, Miyagi, and Seto Inland Sea (Hiroshima). We used both PCA and unsupervised machine learning (ML) approaches trained with native populations to assign nonnative oysters. Results were broadly similar between assignment approaches (PCA: Fig. 1*C*; ML: Fig. 1*D*), an admixture analysis (*SI Appendix*, Fig. S8), and regional patterns of F_{ST} (*SI Appendix*, Fig. S6), and are organized by nonnative regions below.

First, New Zealand oysters originated from the Seto Inland Sea of southern Japan. Historical records suggest New Zealand populations were accidentally introduced from Australia where there has long been aquaculture of Pacific oysters (41). The historical record indicates that Australia imported oysters from several locations in Japan during the mid-20th century (42), our results indicate that the oysters from Seto Inland Sea persisted, given the strong signal of that region in feral New Zealand populations.

Second, there were two separate invasions along the west coast of North America. Pacific oysters in Canada and Washington State were aligned to the Miyagi region in PCA assignments (Fig. 1*C*) and clustered with Miyagi in F_{ST} values (*SI Appendix*, Fig. S6). The admixture-based analysis indicates that sources were approximately 50% Hokkaido and 50% Miyagi (*SI Appendix*, Fig. S8 and Table S3) while the ML-based analysis indicated 3% Hokkaido and 97% Miyagi (Fig. 1*D* and *SI Appendix*, Table S4). Thus, we infer that Miyagi oysters were the predominant source, which aligns with most accounts of shipments between the Miyagi region and western North America (43).

Oysters in southern California were visually aligned to Tokyo (OHK, BAN) in the PCA assignments (Fig. 1*C*) and clustered with Tokyo in F_{ST} values (*SI Appendix*, Fig. S6). The admixture-based analysis indicates that the sources were approximately 20% Miyagi, 40% Tokyo, 40% Seto Inland Sea (*SI Appendix*, Fig. S8 and Table S3) while the ML-based analysis indicated 49% Miyagi, 0% Tokyo, and 51% Seto Inland Sea (Fig. 1*D* and *SI Appendix*, Table S4). Our interpretation is that intermediate genotypes of Seto and Miyagi oysters in California reflect either hybridization in Tokyo before introduction, hybridization after introduction from these two regions, or both.

Third, European populations were largely sourced from Miyagi, but there were separate invasion histories between northern and southern Europe. In southern Europe (Spain and Atlantic France), oysters were likely directly imported from Miyagi or via a secondary introduction from Canada and Washington state, as suggested by the historical record (23). In contrast, oysters from northern Europe populations (Ireland, Denmark, Norway, Sweden) represent a highly divergent group of genotypes relative to genotypes collected elsewhere (*SI Appendix*, Figs. S5, S6, and S8). The most parsimonious explanation for these northern European genotypes is that Pacific oysters were bred within an aquacultural setting, deliberately released, and became feral. Walne and Helm (44) describe how "*adults of the Miyagi strain*" were imported from hatcheries in western North America to Conwy, United Kingdom, bred, and then deliberately introduced to UK estuaries, where they subsequently spread to other regions in Europe via larval dispersal and deliberate introductions (34). Our results suggest that oysters from northern Europe were then shipped to Chile and subsequently to Argentina for aquaculture where they then became feral (24).

Consistent with our results, several Pacific oyster studies indicate genetic differences between aquacultured and feral populations from which they are sourced within Europe and South America (35, 36, 45–47). Our in silico simulations demonstrate how quickly such divergence can arise (see details in *Materials and Methods*). Even a single generation of isolation with between 2 to 8 breeding pairs from Miyagi can create F_{ST} values (~0.03;

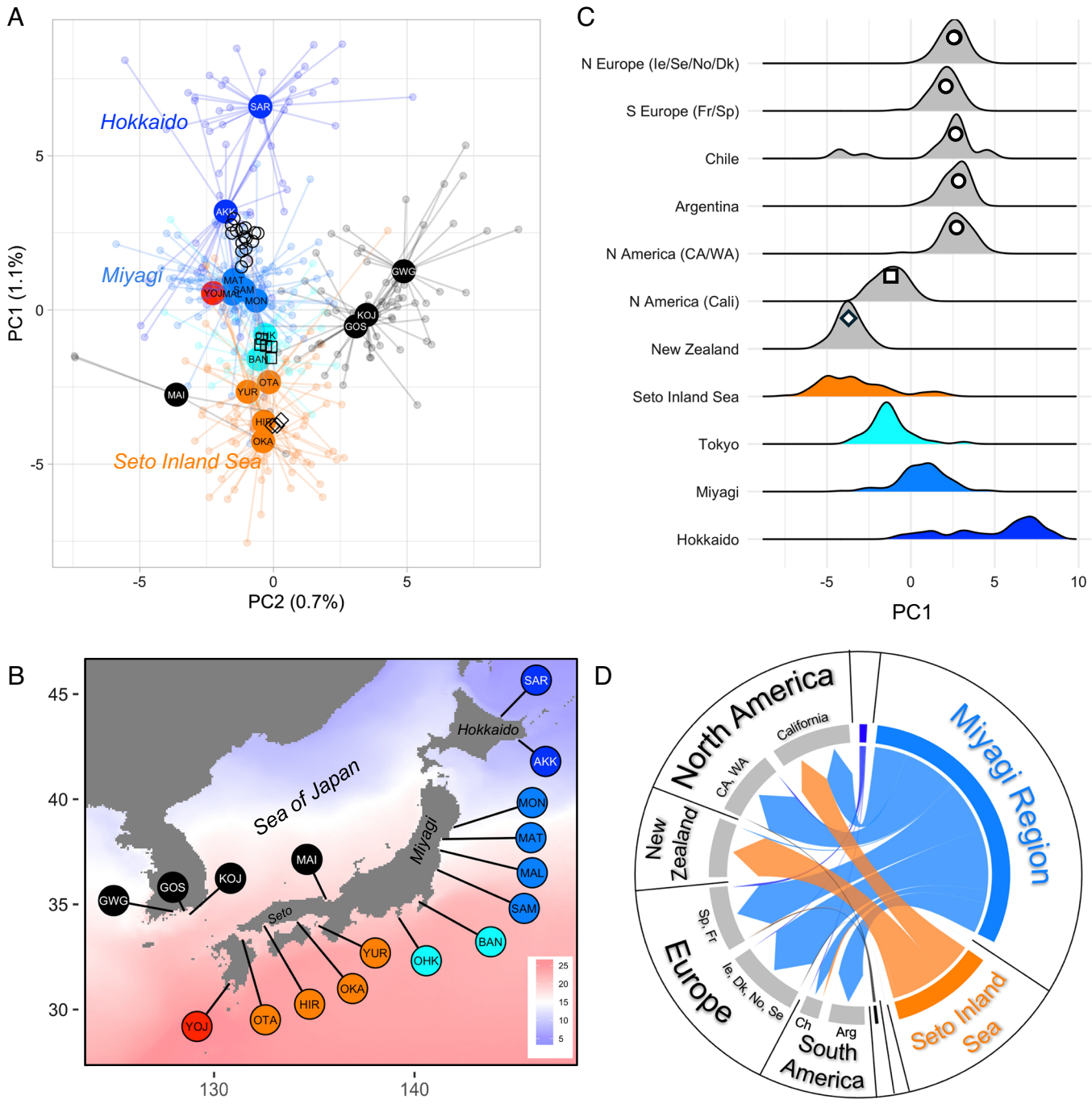

Fig. 1. Population structure of native and nonnative Pacific oysters. (*A*) PC analysis of native oysters from Japan. Open gray symbols indicate means for nonnative populations. Regional locations of three native oyster strains (39) are indicated. (*B*) Map of native populations collected, overlaid on annual mean sea surface temperature (°C). (*C*) Density plots of PC1 values from native oysters (color fill) used to train the PCA and assigned PC1 values from nonnative oysters (gray fill). (*D*) Chord diagram (40) of ML assignments of nonnative oysters to Japanese populations; color codes same as (*C*). Ie = Ireland, Se = Sweden, No = Norway, Dk = Denmark, Sp = Spain, Fr = France, CA = Canada, WA = Washington State, Ch = Chile, Arg = Argentina.

SI Appendix, Fig. S7) as great as or greater than what we detected between oysters from northern Europe and Miyagi populations (mean F_{ST} ± SE = 0.0132 ± 0.0006; n = 16).

Nonnative populations of suspected aquaculture origins (i.e., Argentina, Chile, and northern Europe) have effective population sizes (or N_e, a proxy of genetic variation; Fig. 2*A*) and expected heterozygosity (Fig. 2*B*) that were lower than native populations. N_e was significantly lower among nonnative populations with an aquaculture history than other nonnative populations (Fig. 2*A*) and heterozygosity did not differ among the two groups of nonnative populations (Fig. 2*B*). The genetic results mirrored theoretical predictions (48) and our simulations of an aquacultural bottleneck, which saw a 10% decline in heterozygosity relative to that in the original population.

Thus, despite their different invasion pathways, the ultimate source of Japanese oysters for populations in northern and southern Europe, Argentina, and Chile is the Miyagi region. Genetic and phenotypic divergence between northern and southern European oysters was noted previously (35, 49), and our results provide a global perspective on the pathway. We note that it is unlikely the lineages of northern Europe, Argentina, and Chile are confamilial hybrids (*Materials and Methods*).

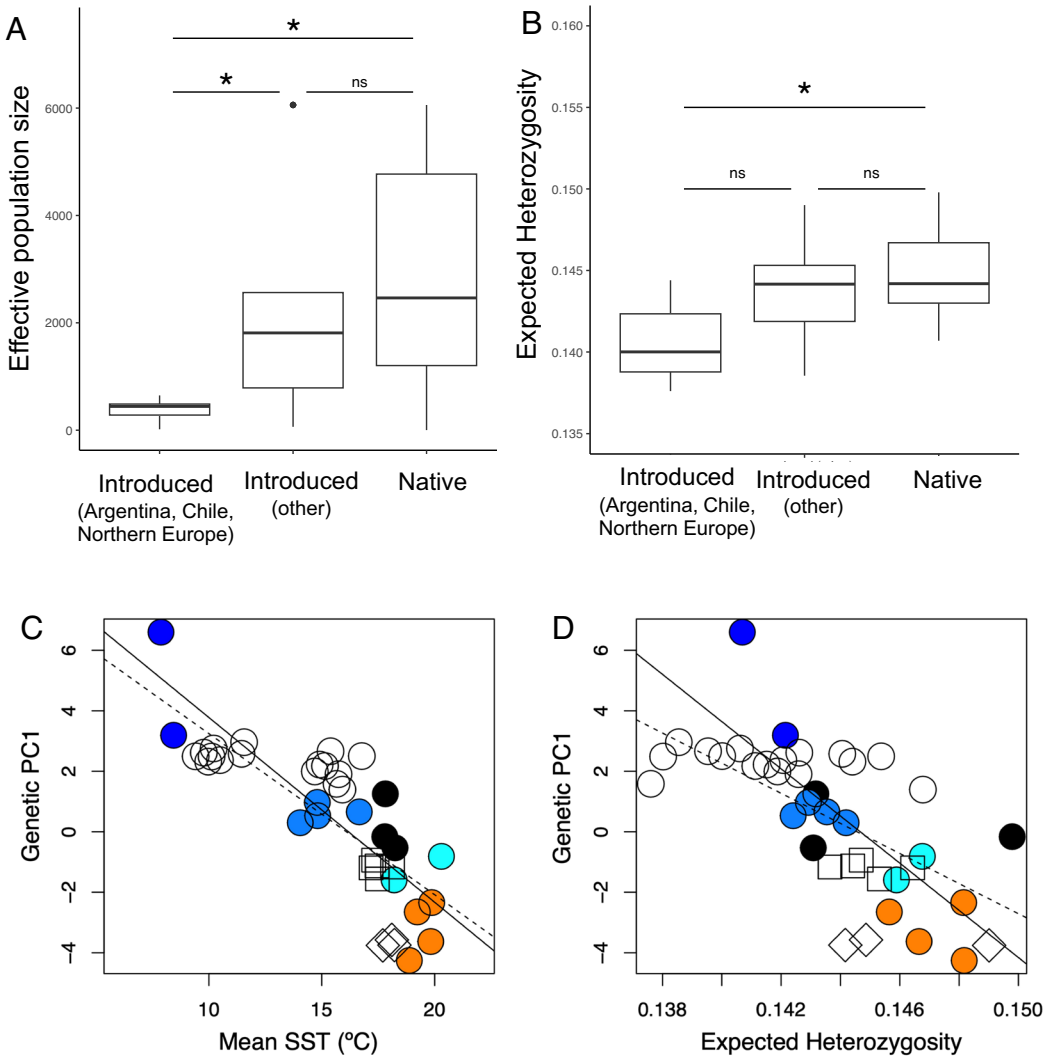

Fig. 2. Population genetics of *M. gigas*. (*A*) Effective population size (N_e) and (*B*) expected heterozygosity (H_s) for native populations versus nonnative populations from putatively aquacultured populations (Argentina, northern Europe, and Chile) versus the others. Groups were statistically distinct in N_e ($c^2 = 10.3$, df = 2 and $P = 0.006$) and H_s (F = 3.8, df = 2 and $P = 0.032$). Asterisks indicate $P < 0.05$ and "ns" indicate $P > 0.05$ from post hoc tests. (*C*) Genetic PC1 correlates with mean sea surface temperature (Native r = −0.869; df = 13; $P < 0.001$; Introduced r = −0.744; df = 22; $P < 0.001$). (*D*) PC1 correlates with expected heterozygosity (H_s; Native r = −0.755, df = 13, $P = 0.001$; Introduced r = −0.634, df = 22; $P < 0.001$). Population colors reflect native regions in Fig. 1*B*, symbols reflect nonnative regions in Fig. 1*C*. Solid and dotted lines in Fig. 2 *C* and *D* indicate correlations for native and nonnative populations, respectively.

Deliberate Environmental Matching. The relative importance of pre- and postadaptation processes in the successes of introduced species is debatable (50), and evidence has largely focused on accidentally introduced species. In contrast, the Pacific oyster was deliberately introduced by oyster biologists who frequently used experimentation to determine the appropriate native sources (39, 44) in a process similar to that for many terrestrial crop plants (2). The genetic legacy of these choices is evident today. The genetic PC1 (a proxy for native source populations) significantly correlates with mean annual sea surface temperature (SST; Fig. 2*C*) for both native and nonnative populations ($P < 0.001$ for each). Our interpretation is that Pacific oysters proliferated in nonnative areas that are environmentally similar to those areas where native lineages evolved, and thus where their fitness is likely greatest. In some cases, these oysters then expanded via secondary introduction via larval dispersal or human-mediated vectors into other regions [e.g., Sweden and Norway (34)]. Thus, the Pacific oyster represents a clear example of preadapted native genotypes proliferating in appropriate nonnative habitats after deliberate environmental matching, a term that extends the environmental matching hypothesis of Riccardi et al. (51).

In native Japan and Korea, oyster genotypes associated with colder regions had lower heterozygosity, while populations from warmer regions had higher heterozygosity. This was revealed when correlating H_s against genetic PC1 (Fig. 2*D*) or against mean annual SST (*SI Appendix*, Fig. S9). It is unclear what factor(s) generated and maintained this latitudinal decline in heterozygosity, as theoretical predictions and empirical patterns of latitudinal gradients in genetic diversity across organisms are highly variable (52). We note that one population in northern Japan (AKK) had greater heterozygosity likely because oysters have been deliberately introduced from Miyagi. When AKK is removed from this analysis, the relationship of H_s with PC1 and SST persists ($P < 0.01$).

The latitudinal declines in heterozygosity among native populations were recapitulated in the nonnative range. That is, heterozygosity correlated with genetic source (i.e., PC1) in the nonnative range (Fig. 2*D*) although the correlation with SST was weaker ($P = 0.100$; *SI Appendix*, Fig. S9). These patterns did not change when populations with bottlenecks from known aquacultural history were removed (i.e., Chile, northern Europe, and Argentina). The recapitulation of native heterozygosity patterns (especially as measured by PC1) within the nonnative range

decades after transplantation represents an important ongoing legacy.

Delineating between Vectors of Invaders. ABC coupled with the *M. gigas* vector map (Fig. 1*D*) allowed us to estimate the relative likelihood that oysters or historical shipping activity (1950 to 2010) better explains the global population genetics of 14 Japanese species introduced into western North America, Europe, or both. While there are dozens of introduced species whose origins are in Japan, we focused on the 14 species for which a published population genetic study sampled three or more regions in Japan, among other criteria (*Materials and Methods*). We included three species that were likely introduced via an oyster vector based on their ecology or the historical record, seven species that were likely introduced with shipping activity, and four species with mixed or unknown vectors (*SI Appendix*, Table S2; see *SI Appendix, Appendix 2* for compilation of historical information). We applied a statistical vector inference for this system because 1) quantitative estimates of propagule pressure were available and 2) the most important regions of Japanese shipping activity (i.e., Tokyo and Hokkaido primarily) are not colocated with the most important region of oyster export (i.e., Miyagi; Fig. 1*D*; summarized within chord diagrams of Fig. 3).

Six of the 14 species had global population structure significantly better explained by an oyster vector than by shipping activity (Fig. 3). The strongest signal (68-fold more likely) emerged with the shell-boring polychaete *Polydora hoplura*, which had previously been suggested to have been introduced by both shipping activity and oyster aquaculture (53). Its population genetics were more consistent with a Miyagi source and thus, an oyster vector (see *P. hoplura* chord diagram of Fig. 3). Three species historically ascribed to oyster introductions were also more likely to have support for an oyster vector: the Japanese bubble snail *Haminoea japonica* (54), the Japanese false cerith snail *Batillaria attramentaria,* and one of its trematode parasites (HL6) (55). The red alga *Gracilaria vermiculophylla* has been ascribed to both oyster vector (56) and other shipping activity (*SI Appendix, Appendix 2*). The Asian brush-clawed shore crab *Hemigrapsus takanoi* had strong support for the oyster vector model, despite assertions based largely on observational data that shipping may have been primarily responsible (57).

We found five species were more likely to have been introduced via shipping activity rather than oyster transport. This is consistent with the historical record for three species: the Oriental shrimp *Palaemon macrodactylus*, the ascidian *Didemnum vexillum*, and an Asian shore crab *Hemigrapsus sanguineus* (58–60). The brown alga wakame (*Undaria pinnatifida*) was deliberately introduced for local farming (61). A second trematode (HL1) of *Batillaria* may have been introduced by migratory birds as was previously hypothesized (55) because its genetic diversity was equal between native and nonnative populations. The significant signal of shipping activity in our analysis suggests that areas with high shipping activity also serve as source locations for both of these species. We also note that the contrast in vectors between the *Batillaria* snail and the trematode HL6 (oyster vector) versus the trematode HL1 (shipping vector) highlights the potential usefulness of the ABC approach to quantitatively assess vectors for hosts and their endoparasites, the latter of which may have surprisingly different vectors.

This approach could not distinguish between oyster and shipping vector models for three species: the green alga *Ulva pertusa,* the brown alga *Mutimo cylindricus,* and the goby fish *Acanthogobius flavimanus*. In cases where we are unable to choose between vectors, then both vectors or some other vector (e.g., direct import) could be important, or the single-locus (mitochondrial and/or chloroplast) datasets we used for all species (*SI Appendix*, Table S2) could have limited our ability to detect patterns of gene flow that a larger number of nuclear loci would allow. In addition, these previously published datasets could have field sampling designs that were limited in power. All species had sampling intensities and geographic representation different from our oyster sample, which could limit the power of our analysis. Further, the potential impact of shipping from outside Japan on our inference is uncertain and must await further genetic sampling and modeling efforts. Our inferences were consistent between models with uninformed prior distributions and with strong priors informed with historical information (*SI Appendix, Appendix 2*). Moreover, the results were consistent across admixture or ML-based models of oyster movement (*SI Appendix*, Fig. S13) with the exception of *Undaria,* which seemed to be highly sensitive to which oyster model was used, and its inference should be viewed with caution.

Overall, vector hypotheses based on historical information (i.e., spatial and temporal correlations and direct observations) are a reasonable predictor of vectors inferred from genetic data and ABC analyses (Fig. 3 and *SI Appendix*, Table S2). In seven of the 14 species, the historical prediction was confirmed with genetic models (weighted k = 0.51 [CI = 0.14, 0.88)]). When the three species with inconclusive vectors were excluded, predictions were confirmed in 6 of the 11 species (weighted k = 0.56 ([0.15, 0.97]).

Discussion

Using a SNP survey, we found 1) that the majority of introduced populations of *M. gigas* were originally sourced from northeastern Japan (Miyagi), followed in importance by Seto Inland Sea in the south, 2) oysters were largely preadapted for thriving in the local conditions of nonnative regions, a pattern we termed deliberate environmental matching, and 3) nonnative feral populations have intrapopulation genetic diversity that reflects historical aquacultural propagation, intrapopulation diversity of their source region, or both. We also present a framework for delineating alternative vector hypotheses for a variety of co-occurring species, which confirmed the importance of introduced foundation species such as *M. gigas* in facilitating other introduced species. We describe the implications below.

First, deliberate environmental matching of oyster sources to local environments may help explain the success of current-day populations. This mirrors the success of terrestrial crops decades after farmers chose appropriate genotypes (2). For example, soybean crops in northern, colder states of the United States are dominated by genetic strains from northern China while southern, warmer states are dominated by southern China strains (62). For the subset of locations where oyster aquaculture is absent and *M. gigas* dispersed from other nonnative regions via natural means (e.g., Scandinavia) or where the historical record indicates multiple strains were introduced (e.g., Australia and New Zealand), *M. gigas* succeeded because of pre- or postadaptation processes or both.

Second, our results demonstrate the genetic legacy effects of farming oysters on some but not all populations. Lower effective population sizes and heterozygosity in northern Europe and South America may indicate lower adaptive diversity [(63, 64) but see ref. 65], which would limit the oysters' capacity to respond genetically to new stressors, including novel pathogens and climate change. Moreover, future efforts to use traditional or genomics-guided breeding for desirable traits (e.g., growth rate, disease resistance, heat tolerance, and shell characteristics such as shape and color) may be more fruitful in other regions with higher adaptive diversity. These bottlenecks are strikingly similar to those of several terrestrial

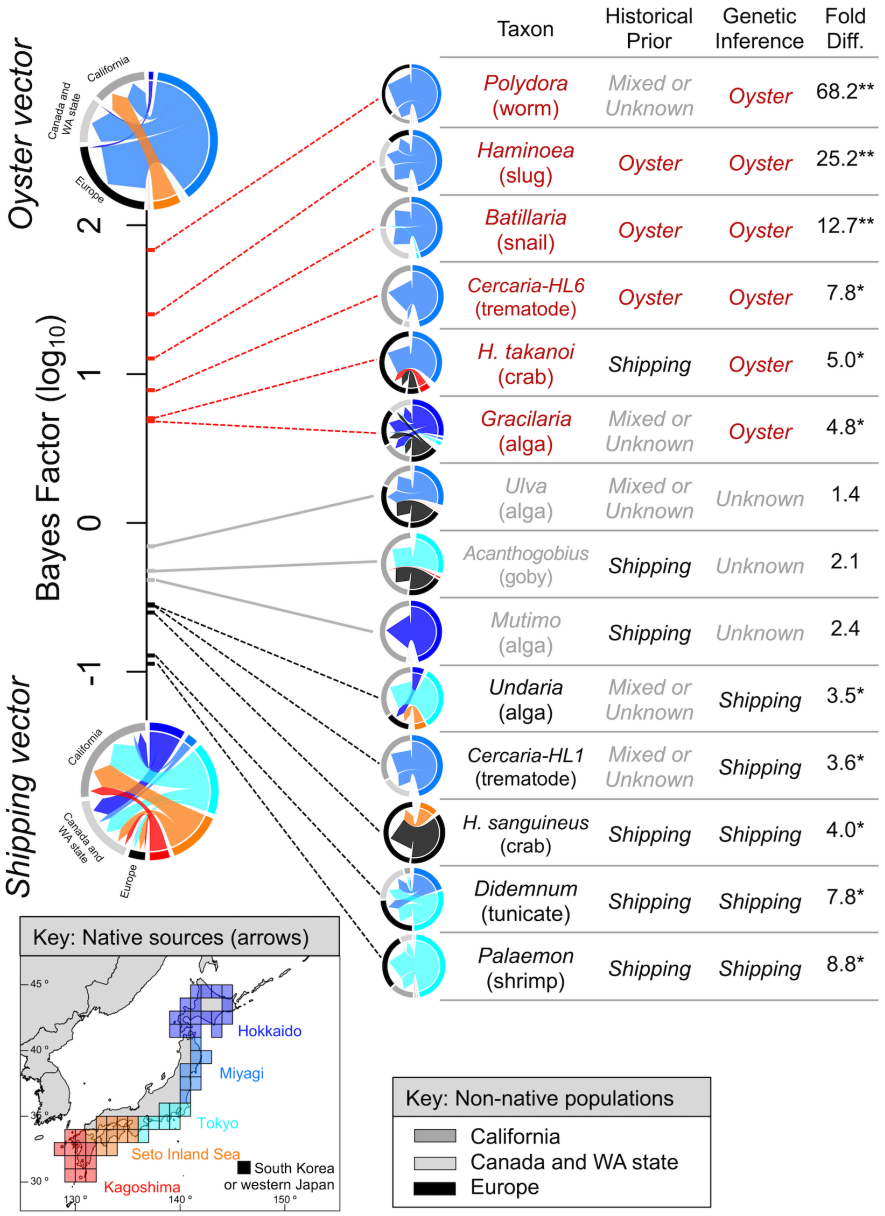

Fig. 3. Statistical vector inference of 14 nonnative species. Large chord diagrams reflect the relative importance of native source regions for two vector hypotheses (i.e., ML analysis of genetic data for oyster versus 30-d shipping model). Smaller chord diagrams represent ML analyses of genetic data for 14 coinvaders (*SI Appendix*, Table S2). Species are arrayed along the Bayes Factor (BF) support axis from ABC simulations. Historical prior comes from a summary of the literature (*SI Appendix, Appendix 2*). BF (log10-transformed) and fold difference indicate how many times more likely the inferred vector is relative to the alternative. Species with moderate (greater than 3×) to strong (greater than 10×) support for a vector are highlighted with red and black dotted lines and with asterisks. Gray lines indicate species with equal statistical support for either model. Keys for native and nonnative regions are indicated by color.

crops and animals (3, 10), and emerged likely through neutral founder effects. Supplementation of *M. gigas* diversity through new introductions from historical source locations, as already begun in the Pacific Northwest of the United States (66), may be necessary to support breeding programs.

In contrast to northern Europe and South America, populations in southern Europe, western North America, and native regions of Japan and Korea did not reveal a strong genetic bottleneck effect. This was especially notable in native Japan, where oysters have been farmed for centuries. It is tempting to conclude that the high diversity among these populations reflects historical reliance of these regions on natural settlement for aquaculture production, the use of relatively high numbers of parents for contemporary aquaculture breeding, or both.

As an aside, the Pacific oyster represents an important case study in the ongoing debate over patterns in genetic diversity within introduced populations (4). Typically, introduced populations undergo strong bottlenecks when moved from a single native population. However, when introduced populations are sourced from multiple populations, intrapopulation genetic diversity can be greater than that of native populations (e.g., ref. 67). For the Pacific oyster, genetic diversity within introduced population depended on the importance of its aquacultural history, the genetic diversity within the native source region (higher or lower), or both factors. To our knowledge, the dependence of the genetic diversity of introduced populations on the diversity of the native source region has not been emphasized in this ongoing debate.

These results provide context to the accelerating expansion of aquaculture worldwide. Aquaculture generates substantial employment and other economic benefits for coastal communities (21), produces nearly half of the fish and shellfish consumed, and will need to be expanded further in order to provide enough protein

for human populations projected for 2050 (19). Relative to the farming of fish and shrimp species, mollusk farms can be especially attractive because they can remove nitrogen and phosphorus loads from the water column, provide habitat for local biodiversity, and generate a carbon sink (1, 19). However, this expansion may come with an ecological tradeoff about which we need to be clear. On land, the deliberate translocation and domestication of animals and plants also have clear economic and societal benefits, but are also principal drivers of local declines in biodiversity largely through their effects on conversion and degradation of natural habitats (7, 68). Feral populations of mollusks have impacts outside aquacultural farms that are both positive and negative (20), and future acceleration of mollusk farming may magnify these effects (1, 17).

Third, an enduring legacy of intentional *M. gigas* introductions is the oyster's role as a vector for multiple algal and invertebrate species, many of which had tremendous impacts on the ecosystems to which they were introduced. Our analysis demonstrates that the two principal vectors that were largely responsible for marine introductions during the latter half of the 20th century, shipping and oysters, can be evaluated quantitatively. The threats posed by oysters as a vector have declined in the last few decades as oyster translocations across continental shores have declined and local hatchery production of oyster seed has increased (20, 32). In addition, laws and international standards have been implemented that greatly reduced the accidental introductions of coassociates of oysters, although the translocation of coassociates of other species continues unabated (17). In contrast, shipping activity continues to increase in frequency and magnitude in the 21st century and serves as an unrelenting vector that requires ongoing management (29). Delineating vectors will be helpful for efficient management actions (69), which our statistical vector inference made possible for 11 of the 14 introduced species we tested. It is encouraging that a priori vector inference from historical information (i.e., the timing and location of introduction) was a significant predictor of vectors inferred by genetic data, as we have such historical information for many introduced species. However, the correlation between historical and genetic inference was not perfect, indicating that future efforts to infer vectors should be confirmed with robust genetic data and ideally, simulations.

In conclusion, this study provides a multidimensional analysis of the long-term adaptive and ecological effects of aquaculture, using the Pacific oyster—a globally dominant, reef-forming foundation species, as a case study. We showcase how broader community-level impacts driven by cointroduced species associated with the oyster can be assessed by leveraging paired genetic data from the Pacific oyster (as a biological vector) and its cointroduced species to rigorously evaluate vector–source relationships. Analogues of Pacific oysters are the many terrestrial plants and animals that were deliberately transplanted and domesticated, as they also serve as vectors and reservoirs for their associated coinvaders, including insects, fungi, and bacteria (5, 12, 70). We predict that applying our quantitative approach to these systems would be fruitful, reveal similar legacy effects, and confirm vector hypotheses based on historical evidence for some but not all species.

Materials and Methods

We sampled populations of *M. gigas* from its native range of Japan and Korea and from nonnative populations of western North America, South America, western Europe, and New Zealand (*SI Appendix*, Fig. S1 and Table S1). Historical records indicate that Japan was the principal country of oyster export in the 20th century (20). It is unlikely that we missed other native sources (e.g., China or Russia) given that Chinese and Japanese *M. gigas* are strongly genetically differentiated (71, 72) and that we detected low levels of genetic differentiation between nonnative and Japanese populations (*Results*).

At each site, we collected approximately 20 individuals at least 1 m apart from natural and artificial substrata outside of obvious aquacultural infrastructure to target naturally settled spat. The two exceptions were in Chile, which were a mix of aquacultural (n = 17) and feral (n = 3) samples collected from the same estuary (Estero Tongoy) and New Zealand, where oysters were naturally settled within aquaculture farms. Whole or mantle tissue was preserved in 95% ethanol and shipped to Charleston South Carolina (USA) for DNA extraction using Macherey-Nagel Nucleospin Tissue kits, using the manufacturer's instructions. We prepared three double-digest RADseq libraries following protocols in ref. 73 (*SI Appendix, Appendix 1*). All samples used in these analyses are likely *M. gigas,* given that samples showed a 98 to 100% match to two mitochondrial loci in *M. gigas* (*SI Appendix*, Fig. S2 and *Appendix 1*) and greater than 87% of their reads mapped to a high-quality *M. gigas* genome [(74); *SI Appendix*, Fig. S3]. After filtering protocols (*SI Appendix, Appendix 1*), we generated a set of 738 individuals and approximately 298K SNPs with genotype likelihoods and 726 individuals and 7,046 loci with genotype calls.

For the admixture analysis, we implemented 50 independent replicates of K = 2 to 8 using ngsAdmix (75). We ran principal components analyses on the covariance matrix using *R::prcomp* (76) on all called genotypes and on native genotypes. We used *R::predict* to assign nonnative genotypes to the PCs trained on native genotypes. Mean annual SST was surveyed from Bio-Oracle and WorldClim datasets using *R::sdmpredictors* (77). We used *R::hierfstat* (78) to generate expected gene diversity (H_s) and pairwise F_{ST} from genotype calls on those populations with more than five individuals (i.e., we removed YOJ, MAI). Effective population size (Ne) was calculated in *R::strataG* (79) using estimates from linkage disequilibrium (80). We used ML to assign nonnative genotypes to nonnative source regions with random forests using *R::ranger* (81) and visualized results with chord diagram plots.

We assessed whether N_e or H_s differed between three regions: Introduced (Argentina, Chile, and northern Europe), Introduced (other), and Native populations. We applied Kruskal–Wallis overall and post hoc tests for N_e because groups did not have homoscedastic variances and a one-way ANOVA and Tukey multiple comparisons for H_s because all assumptions were met. The estimate of N_e was infinite at five populations (GOS - Korea; OHK - Tokyo; PES - so Cal; TJE - so Cal; WLB - PNW). The statistical results were qualitatively identical when we excluded these populations as when we set infinite N_e to the maximum N_e seen among all populations (N_e = 6,058). All correlations between PC1, H_s, and SST were implemented with a Pearson's correlation test.

We used forward-time genetic simulations [implemented in *R::Rmetasim*; (82)] to model the effects of limited broodstock size on population genetic diversity. Three factors were investigated, source of broodstock (different choices of populations from the most likely sources in Miyagi), numbers of broodstock individuals (2, 4, 8, 10, and 16), and number of years in aquaculture (1, 3, 5, 7, 10, 20) before release. For each simulation, we created an in silico source population with the same number and distribution of SNPs as potential sources. Each factorial combination was replicated five times.

We identified population genetic studies of invasive species along western North America and Europe by identifying species in review papers (4, 27, 83–85) and cross-referencing those species against Google Scholar with the terms "genus species population genetic introduction." We also did a Web-of-Science search (December 1, 2022) with the search terms "gene*" and "Introduc* or Nonnative or Native" and "Marine or Estuarine" and "Japan." We chose species based on several criteria. The population genetic study must have collected samples across three or more regions in Japan (Fig. 1*B* for a map) including the Miyagi region that we identified as the source for most of the world's *M. gigas*. We included studies with at least one population from western North America or Europe. The species must be recognized as a single species, and not a hybrid or cryptogenic species complex. When there were multiple datasets available, we chose the study that had sampled the native range most extensively.

We identified 14 species that matched these criteria: four algae, nine invertebrates, and one chordate (*SI Appendix*, Table S2 and *Appendix 2*). Five species had populations sequenced in western North America only, two species had populations sequenced in Europe only, and seven of these species were sequenced from both regions. All species were sequenced at a mitochondrial locus, with the exception of *U. pertusa*, which was also sequenced at a chloroplast locus. Observations and

anecdotal accounts ascribed the vectors for these invaders as either oyster translocations, shipping and other boat activity, deliberate introduction, or some mix of these.

We estimated pathways for which shipping could act as a vector based on data available from the International Comprehensive Ocean–Atmosphere Data Set [ICOADS r3.0.2 (86) maintained by the National Oceanic and Atmospheric Administration]. This dataset comprises the largest public collection of historical vessel log data. To estimate the relative frequencies of voyages from regions within Japan to introduced species ranges across the globe, we first restricted the data to voyages by ship (indicated in ICOADS by "platform type" = 5) over the 60 y from 1950 to 2010. We then considered a voyage origin to occur when a ship spent more than 1 d in one of the five native regions we identified in Japan. Voyage destinations were considered to occur when a ship spent more than 1 d in one of the introduced regions in the eastern Pacific or in Europe. The definitions of these regions are included as KML formatted files in the GitHub repository. Finally, we counted voyages that lasted either up to 30 d or up to 60 d. This approach yielded 206 observations for the 60-d duration voyages and 98 voyages for the 30-d duration voyages. The relative contributions of each point of origin to each introduced region were estimated from these counts and are reproduced in Tables A3-3 and A3-4.

Alternative models of introduction (30- and 60-d shipping versus ML- and admixture-based oyster movement) were compared using ABC (*SI Appendix, Appendix 3*). We simulated individual haplotypes of each of the 14 introduced species under these four alternatives using fastSimCoal 2.7 (87) and calculated population genetic summary statistics intended to capture diversity both among and within populations. We then used random forests (88, 89) to estimate the posterior probability of each introduction model after applying it to the empirical data and calculated log Bayes factors (BF) as the logarithm of the ratio of posteriors for oyster introduction models to shipping introduction models. We note our ABC approach did not tease apart primary and secondary introduction routes and instead inferred only primary introductions. We translated BFs from ABC into discrete categories of support (moderate, strong) for oysters or shipping as suggested by refs. 90 and 91. We used a weighted Cohen's Kappa to assess whether the historical prior and our inference were associated. To do this, we coded ordinal numbers (1, 2, 3) for Shipping-vector, Mixed/unknown, and Oyster-vector respectively and report the estimate and CI at alpha = 0.05.

Data, Materials, and Software Availability. Data and code are available on GitHub (92, 93). The entire vector simulation environment including the coalescent simulator, R, and R packages is containerized, and a docker image of the environment is available (94). Individual FASTQ-formatted files are archived at GenBank (95). Data are also archived at the NSF BCO-DMO database (96). Previously published data were used for this work. We re-analyze population genetic datasets from previous publications in Fig. 3. We cite all datasets in *SI Appendix*, Table S2.

ACKNOWLEDGMENTS. We thank Hannah Rothkopf, Dallas Crowder, and Emma Senf for help with DNA extraction and Emmanuel Dubillot and Thomas Lacoue-Labarthe for help with fieldwork. We thank Osamu Miura, Christophe Lejeusne, and Shotaro Hirase for haplotype frequency tables from published studies. We thank Eric Archer and Jeb Byers for discussion. We also thank the NSF (OCE-1924599 to E.E.S. and A.E.S.) for funding. We thank the reviewers for thoughtful comments that improved the manuscript.

Author affiliations: [a]Department of Biology, College of Charleston, Charleston, SC 29412; [b]Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, VA 23062; [c]Williams College-Mystic Seaport Coastal and Ocean Studies Program, Mystic, CT 06355; [d]Facultade de Ciencias, Departamento de Bioloxía, Universidade da Coruña, A Coruña 15071, Spain; [e]Tijuana River National Estuarine Research Reserve, Imperial Beach, CA 91932; [f]Faculty of Fisheries, Kagoshima University, Kagoshima 890-0056, Japan; [g]United Graduate School of Agricultural Sciences, Kagoshima University, Kagoshima 890-0065, Japan; [h]Puget Sound Restoration Fund, Bainbridge Island, WA 98110; [i]Japan Fisheries Research and Education Agency, Yokohama, Kanagawa 236-8648, Japan; [j]Department of Ocean Sciences, Tokyo University of Marine Science and Technology, Tokyo 108-8477, Japan; [k]National Institute for Environmental Studies, Tsukuba 305-8506, Japan; [l]Faculty of Biology, Institute of Organismic and Molecular Evolution, Johannes Gutenberg University, Mainz 55128, Germany; [m]Department of Biological Sciences, Pusan National University, Busan 46241, Korea; [n]Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697; [o]Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Akkeshi, Hokkaido 088-1113, Japan; [p]CNRS, IRD, Ifremer, UMR 6539, Laboratory of Environmental Marine Sciences (LEMAR), Université de Bretagne, Plouzané 29280, France; [q]Department of Biology, University of Washington, Seattle, WA 98195-1800; [r]Instituto de Biología de Organismos Marinos, Consejo Nacional de Investigaciones Científicas y Técnicas (IBIOMAR-CONICET), Puerto Madryn U9120ACD, Argentina; [s]Department of Environmental Intelligence, IVL Swedish Environmental Research Institute, Fiskebäckskil 451 78, Sweden; [t]Leigh Marine Laboratory and Institute of Marine Science, University of Auckland, 0985, New Zealand; [u]MarineGEO Program, Smithsonian Environmental Research Center, Edgewater, MD 21037; [v]Departamento de Biologia Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo 1781421, Chile; [w]Center for Ecology and Sustainable Management of Oceanic Island, Coquimbo 1781421, Chile; [x]Nature and Environment Division, Institute of Natural and Environmental Sciences, University of Hyogo, Sanda, Hyogo 669-1546, Japan; [y]Division of Nature and Environmental Management, Museum of Nature and Human Activities, Sanda, Hyogo 669-1546, Japan; and [z]Department of Biological Science, California State University, Fullerton, CA 92834-6850

Author contributions: E.E.S., R.B.C., and A.E.S. designed research; E.E.S., R.B.C., J.T.C., L.C., J.A.C., H.E., H.H., M.H., M.K., G.K., J.K., K.-S.L., L.L., H.M., M.N., E.P., J.L.R., E.S., Å.S., R.B.T., R.T., M.T., T.Y., D.Z., and A.E.S. performed research; E.E.S., R.B.C., and A.E.S. contributed new reagents/analytic tools; E.E.S. and A.E.S. analyzed data; E.E.S., R.B.C., J.T.C., L.C., J.A.C., H.E., H.H., M.K., G.K., J.K., K.-S.L., L.L., H.M., M.N., E.P., J.L.R., E.S., Å.S., R.B.T., R.T., M.T., T.Y., D.Z., and A.E.S. reviewing and editing; E.E.S., R.B.C. and A.E.S. funding acquisition; and E.E.S. and A.E.S. wrote the paper.

1. R. L. Naylor *et al.*, A 20-year retrospective review of global aquaculture. *Nature* **591**, 551–563 (2021).
2. L. T. Evans, *Crop Evolution, Adaptation and Yield* (Cambridge University Press, 1996).
3. L. A. F. Frantz, D. G. Bradley, G. Larson, L. Orlando, Animal domestication in the era of ancient genomics. *Nat. Rev. Genet.* **21**, 449–460 (2020).
4. M. Rius, X. Turon, G. Bernardi, F. A. M. Volckaert, F. Viard, Marine invasion genetics: From spatio-temporal patterns to evolutionary outcomes. *Biol. Invasions* **17**, 869–885 (2015).
5. P. Gladieux *et al.*, The population biology of fungal invasions. *Mol. Ecol.* **24**, 1969–1986 (2015).
6. C. Elton, *The Ecology of Invasions by Animals and Plants* (University of Chicago Press, 1958).
7. E. Crist, C. Mora, R. Engelman, The interaction of human population, food production, and biodiversity protection. *Science* **264**, 260–264 (2017).
8. N. P. Castañeda-Álvarez *et al.*, Global conservation priorities for crop wild relatives. *Nat. Plants* **2**, 16022 (2016).
9. E. Gering *et al.*, Getting back to nature: Feralization in animals and plants. *Trends Ecol. Evol.* **34**, 1137–1151 (2019).
10. B. S. Gaut, D. K. Seymour, Q. Liu, Y. Zhou, Demography and its effects on genomic variation in crop domestication. *Nat. Plants* **4**, 512–520 (2018).
11. R. Barrett, C. Kuzawa, T. McDade, G. Armelagos, Emerging and re-emerging infectious diseases: The third epidemiologic transition. *Annu. Rev. Anthropol.* **27**, 247–271 (1998).
12. M. P. Hill, S. Clusella-Trullas, J. S. Terblanche, D. M. Richardson, Drivers, impacts, mechanisms and adaptation in insect invasions. *Biol. Invasions* **18**, 883–891 (2016).
13. J. B. Geller, J. A. Darling, J. T. Carlton, Genetic perspectives on marine biological invasions. *Ann. Rev. Mar. Sci.* **2**, 367–393 (2010).
14. M. C. Fontaine, P. Gladieux, M. E. Hood, T. Giraud, History of the invasion of the anther smut pathogen on *Silene latifolia* in North America. *New Phytol.* **198**, 946–956 (2013).
15. P. J. P. Croucher, S. Mascheretti, M. Garbelotto, Combining field epidemiological information and genetic data to comprehensively reconstruct the invasion history and the microevolution of the sudden oak death agent *Phytophthora ramorum* (Stramenopila: Oomycetes) in California. *Biol. Invasions* **15**, 2281–2297 (2013).
16. E. M. Goss *et al.*, The Irish potato famine pathogen *Phytophthora infestans* originated in central Mexico rather than the Andes. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 8791–8796 (2014).
17. S. S. De Silva, Aquaculture: A newly emergent food production sector–and perspectives of its impacts on biodiversity and conservation. *Biodivers. Conserv.* **21**, 3187–3220 (2012).
18. J. T. Carlton, Introduced marine and estuarine mollusks of North America: An end-of-the-20th-century perspective. *J. Shellfish Res.* **11**, 489–505 (1992).
19. R. Botta, F. Asche, J. S. Borsum, E. V. Camp, A review of global oyster aquaculture production and consumption. *Mar. Policy* **117**, 103952–103952 (2020).
20. NRC, *Nonnative Oysters in the Chesapeake Bay* (National Academies Press, 2004).
21. Food and Agriculture Organization, "The state of world fisheries and aquaculture 2022 (SOFIA): Towards blue transformation" (Food & Agriculture Organization of the United Nations (FAO), 2022), vol. 2022.
22. A. Kornbluth *et al.*, Mapping oysters on the Pacific coast of North America: A coast-wide collaboration to inform enhanced conservation. *PLoS One* **17**, e0263998 (2022).
23. K. Troost, Causes and effects of a highly successful marine invasion: Case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J. Sea Res.* **64**, 145–165 (2010).
24. M. M. Mendez *et al.*, Ecological impacts of the austral-most population of *Crassostrea gigas* in South America: A matter of time? *Ecol. Res.* **30**, 979–987 (2015).
25. J. L. Ruesink *et al.*, Introduction of non-native oysters: Ecosystem effects and restoration implications. *Annu. Rev. Ecol. Evol. Syst.* **36**, 643–689 (2005).
26. G. M. Ruiz, P. W. Fofonoff, B. P. Steves, J. T. Carlton, Invasion history and vector dynamics in coastal marine ecosystems: A North American perspective. *Aquat. Ecosyst. Health Manag.* **18**, 299–311 (2015).
27. F. Mineur, A. Le Roux, C. A. Maggs, M. Verlaque, Positive feedback loop between introductions of non-native marine species and cultivation of oysters in Europe. *Conserv. Biol.* **28**, 1667–1676 (2014).
28. P. Bonnot, A recent introduction of exotic species of molluscs into California waters from Japan. *Nautilus* **49**, 1–2 (1935).

29. H. Seebens *et al.*, No saturation in the accumulation of alien species worldwide. *Nat. Commun.* **8**, 14435 (2017).
30. H. S. An *et al.*, Genetic structure and diversity of *Crassostrea gigas* in Korea revealed from microsatellite markers. *Biochem. Syst. Ecol.* **55**, 283–291 (2014).
31. L. Li *et al.*, Divergence and plasticity shape adaptive potential of the Pacific oyster. *Nat. Ecol. Evol.* **2**, 1751–1760 (2018).
32. K. Kawamura, T. Miyake, M. Obata, H. Aoki, A. Komaru, Population demography and genetic characteristics of the Pacific Oyster *Crassostrea gigas* in Japan. *Biochem. Syst. Ecol.* **70**, 211–221 (2017).
33. D. Hedgecock, F. T. C. Pan, Genetic divergence of selected and wild populations of Pacific oysters (*Crassostrea gigas*) on the West Coast of North America. *Aquaculture* **530**, 735737–735737 (2021).
34. E. Faust *et al.*, Origin and route of establishment of the invasive Pacific oyster *Crassostrea gigas* in Scandinavia. *Mar. Ecol. Prog. Ser.* **575**, 95–105 (2017).
35. D. L. J. Vendrami *et al.*, Detailed insights into pan-European population structure and inbreeding in wild and hatchery Pacific oysters (*Crassostrea gigas*) revealed by genome-wide SNP data. *Evol. Appl.* **12**, 519–534 (2019).
36. B. J. G. Sutherland *et al.*, Relative genomic impacts of translocation history, hatchery practices, and farm selection in Pacific oyster *Crassostrea gigas* throughout the Northern Hemisphere. *Evol. Appl.* **13**, 1380–1399 (2020).
37. M. A. Beaumont, W. Zhang, D. J. Balding, Approximate Bayesian computation in population genetics. *Genetics* **2035**, 2025–2035 (2002).
38. L. V. Plough, Genetic load in marine animals: A review. *Curr. Zool.* **62**, 567–579 (2016).
39. T. Imai, S. Sakai, Study of breeding of Japanese oyster, *Crassostrea gigas*. *Tohoku J. Agricult. Res.* **12**, 125–171 (1961).
40. Z. Gu *et al.*, Circlize implements and enhances circular visualization in R. *Bioinformatics* **30**, 2811–2812 (2014).
41. P. Dinamani, Occurrence of the Japanese oyster, *Crassostrea gigas* (thunberg), in northland, New Zealand. *N. Z. J. Mar. Freshwater Res.* **5**, 352–357 (1971).
42. L. J. English, G. B. Maguire, R. D. Ward, Genetic variation of wild and hatchery populations of the Pacific oyster, *Crassostrea gigas* (Thunberg), Australia. *Aquaculture* **187**, 283–298 (2000).
43. E. M. Barrett, *The California Oyster Industry* (Department of Fish and Game, Resources Agency of California, 1963).
44. P. R. Walne, M. M. Helm, "Introduction of *Crassostrea gigas* into the United Kingdom" in *Symposium on Exotic Species in Mariculture, Woods Hole Oceanographic Institution*, , R. Mann, Ed. (1978), pp. 83–105.
45. A. Rohfritsch *et al.*, Population genomics shed light on the demographic and adaptive histories of european invasion in the Pacific oyster, *Crassostrea gigas*. *Evol. Appl.* **6**, 1064–1078 (2013).
46. M. B. Anglès D'Auriac *et al.*, Rapid expansion of the invasive oyster *Crassostrea gigas* at its northern distribution limit in Europe: Naturally dispersed or introduced? *PLoS One* **12**, 1–19 (2017).
47. V. M. Stefenon, A. D. Clauman, Genetic divergence accessed with microsatellite markers reflects the time of *Crassostrea gigas* genetic breeding in Brazil. *An. Acad. Bras. Cienc.* **96**, e20230474 (2024).
48. M. Nei, T. Maruyama, R. Chakraborty, The bottleneck effect and genetic variability in populations. *Evolution* **29**, 1–10 (1975).
49. C. C. Wendling, K. M. Wegner, Adaptation to enemy shifts: Rapid resistance evolution to local *Vibrio* spp. in invasive Pacific oysters. *Proc. Biol. Sci.* **282**, 20142244 (2015).
50. R. I. Colautti, J. A. Lau, Contemporary evolution during invasion: Evidence for differentiation, natural selection, and local adaptation. *Mol. Ecol.* **24**, 1999–2017 (2015).
51. A. Ricciardi, M. F. Hoopes, M. P. Marchetti, J. L. Lockwood, Progress toward understanding the ecological impacts of nonnative species. *Ecol. Monogr.* **83**, 263–282 (2013).
52. E. R. Lawrence, D. J. Fraser, Latitudinal biodiversity gradients at three levels: Linking species richness, population richness and genetic diversity. *Glob. Ecol. Biogeogr.* **29**, 770–788 (2020).
53. V. I. Radashevsky *et al.*, Searching for a home port in a polyvectic world: Molecular analysis and global biogeography of the marine worm *Polydora hoplura* (Annelida: Spionidae). *Biology (Basel)* **12**, 780 (2023).
54. D. Hanson *et al.*, Slipping through the cracks: The taxonomic impediment conceals the origin and dispersal of *Haminoea japonica*, an invasive species with impacts to human health. *PLoS One* **8**, 1–12 (2013).
55. O. Miura, M. E. Torchin, A. M. Kuris, R. F. Hechinger, S. Chiba, Introduced cryptic species of parasites exhibit different invasion pathways. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 19818–19823 (2006).
56. S. A. Krueger-Hadfield *et al.*, Genetic identification of source and likely vector of a widespread marine invader. *Ecol. Evol.* **7**, 4432–4447 (2017).
57. W. Makino *et al.*, Evidence of multiple introductions and genetic admixture of the Asian brush-clawed shore crab *Hemigrapsus takanoi* (Decapoda: Brachyura: Varunidae) along the Northern European coast. *Biol. Invasions* **20**, 825–842 (2018).
58. C. Lejeusne *et al.*, High genetic diversity and absence of founder effects in a worldwide aquatic invader. *Sci. Rep.* **4**, 5808 (2014).
59. A. M. H. Blakeslee *et al.*, Reconstructing the Invasion History of the Asian shorecrab, *Hemigrapsus sanguineus* (De Haan 1835) in the Western Atlantic. *Mar. Biol.* **164**, 1–19 (2017).
60. G. Lambert, Adventures of a sea squirt sleuth: Unraveling the identity of *Didemnum vexillum*, a global ascidian invader. *Aquat. Invasions* **4**, 5–28 (2009).
61. S. Uwai *et al.*, Genetic diversity in *Undaria pinnatifida* (Laminariales, Phaeophyceae) deduced from mitochondria genes – origins and succession of introduced populations. *Phycologia* **45**, 687–695 (2006).
62. X. Delannay, D. M. Rodgers, R. G. Palmer, Relative genetic contributions among ancestral lines to north American soybean cultivars. *Crop Sci.* **23**, 944–949 (1983).
63. M. P. Hare *et al.*, Understanding and estimating effective population size for practical application in marine species management. *Conserv. Biol.* **25**, 438–449 (2011).
64. M. L. Pinsky, S. R. Palumbi, Meta-analysis reveals lower genetic diversity in overfished populations. *Mol. Ecol.* **23**, 29–39 (2014).
65. J. C. Teixeira, C. D. Huber, The inflated significance of neutral genetic diversity in conservation genetics. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2015096118 (2021).
66. C. M. R. de Melo *et al.*, Introduction and evaluation on the US West Coast of a new strain (Midori) of Pacific oyster (*Crassostrea gigas*) collected from the Ariake Sea, southern Japan. *Aquaculture* **531**, 735970–735970 (2021).
67. J. J. Kolbe *et al.*, Genetic variation increases during biological invasion by a Cuban lizard. *Nature* **431**, 177–181 (2004).
68. C. F. Dormann *et al.*, Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecol. Biogeog.* **16**, 774–787 (2007).
69. J. A. Darling, Genetic studies of aquatic biological invasions: Closing the gap between research and management. *Biol. Invasions* **17**, 951–971 (2015).
70. M. A. Spyrou, K. I. Bos, A. Herbig, J. Krause, Ancient pathogen genomics as an emerging tool for infectious disease research. *Nat. Rev. Genet.* **20**, 323–340 (2019).
71. M. Sekino, S. Sato, J.-S. Hong, Q. Li, Contrasting pattern of mitochondrial population diversity between an estuarine bivalve, the Kumamoto oyster *Crassostrea sikamea*, and the closely related Pacific oyster *C. gigas*. *Mar. Biol.* **159**, 2757–2776 (2012), 10.1007/s00227-012-2037-z.
72. S. Li, Q. Li, H. Yu, L. Kong, S. Liu, Genetic variation and population structure of the Pacific oyster *Crassostrea gigas* in the northwestern Pacific inferred from mitochondrial COI sequences. *Fish. Sci.* **81**, 1071–1082 (2015).
73. T. L. Parchman *et al.*, Genome-wide association genetics of an adaptive trait in lodgepole pine. *Mol. Ecol.* **21**, 2991–3005 (2012).
74. C. Peñaloza *et al.*, A chromosome-level genome assembly for the Pacific oyster (*Crassostrea gigas*). *Gigascience* **10**, 1–28 (2021).
75. L. Skotte, T. S. Korneliussen, A. Albrechtsen, Estimating individual admixture proportions from next generation sequencing data. *Genetics* **195**, 693–702 (2013).
76. R Core Team, R: A Language and Environment for Statistical Computing (Version 4.4.2. R Foundation for Statistical Computing, Vienna, Austria, 2024). https://www.R-project.org/. Deposited 31 October 2024.
77. S. Bosch, S. Fernandez, sdmpredictors: Species Distribution Modelling Predictor Datasets (Version 0.2.15, 2023). https://CRAN.R-project.org/package=sdmpredictors. Deposited 23 August 2023.
78. J. Goudet, T. Jombart, hierfstat: Estimation and Tests of Hierarchical F-Statistics (Version 0.5-11, 2022). https://CRAN.R-project.org/package=hierfstat. Deposited 5 May 2022.
79. F. I. Archer, P. E. Adams, B. B. Schneiders, stratag: An r package for manipulating, summarizing and analysing population genetic data. *Mol. Ecol. Resour.* **17**, 5–11 (2017).
80. R. K. Waples, W. A. Larson, R. S. Waples, Estimating contemporary effective population size in non-model species using linkage disequilibrium across thousands of loci. *Heredity* **117**, 233–240 (2016).
81. M. N. Wright, A. Ziegler, Ranger: A fast implementation of random forests for high dimensional data in C++ and R. *J. Stat. Softw.* **77**, 1–17 (2017).
82. A. E. Strand, Metasim 1.0: An individual-based environment for simulating population genetics of complex population dynamics. *Mol. Ecol. Notes* **2**, 373–376 (2002).
83. E. D. Grosholz *et al.*, Aquaculture as a vector for marine invasions in California. *Biol. Invasions* **17**, 1471–1484 (2015).
84. A. M. H. Blakeslee, "Parasites and genetics in marine invertebrate introductions: Signatures of diversity declines across systems" in *Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions*, J. Canning-Clode, Ed. (De Gruyter, 2016), pp. 138–182.
85. P. E. Gribben, J. E. Byers, "Comparative biogeography of marine invaders across their native and introduced ranges" in *Oceanography and Marine Biology*, C. D. Mcquaid, B. D. Russell, I. P. Smith, S. E. Swearer, P. A. Todd, Ed. (CRC Press, 2020), pp. 395–439.
86. E. Freeman *et al.*, ICOADS Release 3.0: A major update to the historical marine climate record: ICOADS R3.0: A major update. *Int. J. Climatol.* **37**, 2211–2232 (2017).
87. L. Excoffier *et al.*, Fastsimcoal2: Demographic inference under complex evolutionary scenarios. *Bioinformatics* **37**, 4882–4885 (2021).
88. P. Pudlo *et al.*, Reliable ABC model choice via random forests. *Bioinformatics* **32**, 859–866 (2016).
89. M. Sitarz, Extending F1 metric, probabilistic approach. *Adv Artif. Intell. Mach. Learn.* **3**, 1025–1038 (2022).
90. S. Andraszewicz *et al.*, An introduction to Bayesian hypothesis testing for management research. *J. Manage.* **41**, 521–543 (2015).
91. S. H. Jeffreys, *Theory of Probability* (Oxford University Press, ed. 3, 1961).
92. E. E. Sotka, A. E. Strand, gigas-popgen: 3.3.0. Zenodo. https://doi.org/10.5281/zenodo.14947816. Deposited 28 February 2025.
93. A. E. Strand, Setup tests of invasion pathways for *C. gigas* co-invaders. GitHub. https://github.com/stranda/TestInvPath. Deposited 6 May 2024.
94. A. E. Strand, Container for invasion pathways for *C. gigas* co-invaders. Docker. https://hub.docker.com/r/astrand/testinvpath. Deposited 15 May 2024.
95. E. E. Sotka, A. E. Strand, SRA Dataset: The genetic legacy of the deliberate introduction of Pacific oysters. GenBank. https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1135237. Deposited 12 July 2024.
96. E. E. Sotka, A. E. Strand, Dataset: The genetic legacy of an Asian oyster introduction and its disease-causing parasite. Biological and Chemical Oceanography Data Management Office. https://www.bco-dmo.org/project/820200. Deposited 6 February 2025.