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REVIEW

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Genetic diversity and resilience in benthic marine populations

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Abstract

Background Understanding the mechanisms behind resilience has become more relevant in the last decades, due to the increasing and intensifying disturbances from natural and anthropogenic sources that threaten biodiversity. Evidence from terrestrial populations suggests that resilience increases with genetic diversity. Few studies, however, have evaluated the relationship between genetics and resilience in benthic marine populations.

Methods and results For this review, we gathered studies where genetic diversity was the predictor variable, and resilience was the response variable. Twenty-five publications between 2001 and 2018 were included. Thirteen benthic marine species were identified, mainly sea-grass species, among which *Zostera marina* was the most frequently studied. The relationship between genetic diversity and resilience was variable-dependent. Considering all the analyses ($N = 150$) in the studies reviewed, 44% reported positive relationships between genetic diversity and resilience capacity. Negative relationships were found in 6%, and no relationship was found in 50%. Positive relationships indicated that genetic diversity increased resistance and recovery capacity after different types of disturbances. Dominance and complementarity were suggested as the underlying mechanism explaining these findings in the few studies that conducted this type of evaluation.

Conclusions The results of this review suggest that the relationship between genetic diversity and resilience is mainly positive. However, this relationship relies on how genetic diversity and resiliency were measured, as well as on the biological characteristics of the species under study. This reinforces the importance of acknowledging and maintaining genetic diversity for the conservation of benthic populations in marine ecosystems.

Keywords Disturbances, Genetic diversity, Resilience, Resistance, Recovery

Background

Given that the frequency and intensity of disturbances are increasing in marine ecosystems due to anthropogenic activity and climate change, it is important to evaluate underlying mechanisms that increase population resilience capacity [1, 2]. There is supporting evidence for the hypothesis that greater genetic diversity in natural populations would maximize resistance and adaptive potency when facing biotic and abiotic environmental changes. However, recent studies have demonstrated that populations may be able to adapt by means of a few large-effect variants despite low overall genetic diversity [3]. Accordingly, questions have arisen regarding the

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importance of neutral genetic diversity versus functional genetic diversity [4].

Genetic diversity has important consequences, to which all organizational levels of biodiversity are connected. It affects individual biological fitness, population viability, adaptability of species to environmental changes, evolutionary potential, as well as the structure and functioning of communities and ecosystems, particularly during periods of environmental stress, providing higher resilience capacity [5–7]. At the individual level, heterozygosity has been positively related to fitness (heterosis), and is associated with higher adaptive phenotype plasticity [8–12]. Genetic variation among individuals within a population provides a base mechanism for plasticity and adaptability. This allows for a greater range of possible functional responses (physiological versatility), occupying different niches, promoting population diversity, and hence, higher resilience under environmental stress or disturbances [5, 7].

Genetic variation among populations and subpopulations may be evaluated based on degrees of relatedness among individuals. Greater endogamy increases homozygosity in the genome and can decrease biological fitness by inbreeding depression and the expression of lethal recessive alleles. On the contrary, extreme exogamy may diminish biological fitness due to heterozygote disadvantage, and the breaking up of complex co-adapted advantageous genes, or because of low adaptation [13].

Under a regime of frequent and expectable disturbances, some organisms, through their evolutionary history and selective processes, have been able to develop local adaptations that reduce the risk of mortality and maximize fitness in temporally unstable environments [14, 15]. However, the capacity to develop adaptations and survive extreme conditions becomes difficult when the frequency and severity of natural and anthropogenic disturbances escalate.

Several studies have evaluated population resilience (*e.g.*, [1, 7]). However, the concept of resilience is quite controversial, given that it involves many definitions that have accumulated over time, producing confusion and the synonymous or complementary use of terms such as *persistence*, *resistance*, *recovery*, and *stability*. The word *resilience* was coined by Elton in 1958. He defined it as "the possibility for communities to resist some disturbance and not suffer structural changes" [16]. In 1973, Holling defined *resilience* as "the measure of the persistence of systems and their capacity to absorb changes and disturbances, keeping the same relations between populations or variable states" [17]. Later in 1996, this author distinguished between *engineering resilience* and *ecological resilience*, where the former refers to the capacity to resist a disturbance and the speed with which the previous equilibrium state is recovered, and the latter indicates the magnitude of the disturbance absorbed before a system changes to a subsequent state [18]. Other authors have defined *ecological resilience* as the capacity of a system to resist and recover from a disturbance [19]. Despite these potential confusions in terminology, the use of the term *resilience* has significantly increased in recent decades, with an average rise of 7.46% per year between 1984 and 2014. Contrary to this, the frequency of use of the words *resistance* and *recovery* decreased by 1.01% and 0.86% during the same period [19].

Studies on marine species have accumulated evidence that genetic diversity increases resistance, resilience, and productivity. However, studies regarding benthic species are scarce [5, 7, 20, 21]. The objective of this review is to synthetize results from scientific studies related to benthic marine species that have evaluated the existence of a relationship between genetic diversity and resilience capacity.

Method

This review presents results from studies that evaluated the existence of relationships or effects between genetic diversity and resilience capacity in populations of marine benthic species. In this review, the term *resilience* refers to "the capacity of a system to resist and to recover from a disturbance", as recommended by Hodgson (2015) [19]. Studies included are only those in which genetic diversity was the variable or independent factor or predictor variable, and resilience was the dependent response variable. Empirical studies included laboratory and field experiments. The analysis excluded theoretical studies and those that did not use molecular analyses of genetic diversity. References from previous reviews were considered, as well as articles complying with the above-mentioned criteria.

Studies were searched using the web sites Science Direct, Web of Knowledge, Scopus and Mendeley. The key words employed were resilience, resistance, recovery, genetic diversity, population, benthic, marine and disturbance. The articles extracted from the search underwent three evaluation stages to be selected or eliminated. Main titles and summaries were assessed in the first stage; methodologies and results from the first stage selection were assessed in second stage; and studies selected in the third stage were subject to complete revision.

From the selected articles, we extracted methodological information on type of research (experiment, field experiment or field study), duration of the study, molecular genetic marker used, species studied, unit of measurement for genetic diversity (variable or predictor factor), type of disturbance (treatment), and unit of measurement for *resilience* (response variable). The relationships or effects of genetic diversity on resilience capacity after disturbances were classified as positive, negative, or without relation. By aggregating the information from all the studies, we estimated the percentages of results showing positive, negative, or no relation between genetic diversity and resilience, and highlighted the types of measurements used the most. Finally, we described an underlying mechanism that could explain the findings, as commonly outlined by the studies that considered this type of analysis.

Results

The search and selection of studies regarding the existence of a relationship or an effect between genetic diversity and resilience capacity in benthic marine species unearthed twenty-five publications between 2001 and 2018, six of which were published in the last year. The publications included 13 species as follows: Eight sea-grass species (*Zostera marina*, *Z. muelleri* and *Z. noltii*, *Posidonia australis*, *P. oceanica*, *Vallisneria americana*, *Phragmites australis* and *Spartina alterniflora*); three sea-weed species (*Gracilaria chilensis*, *G. vermiculophylla* and *Ecklonia radiata*); one oyster (*Crassostrea virginica*), and one crustacean (*Americamysis bahia*). 84% of the publications were related to seagrass species, among which *Z. marina* was the most studied (32% of publications) (Fig. 1, See also Table 1 Add file). The methodologies included 12 laboratory experiments (48%), 9 field experiments (36%), and 4 field studies (16%) (Fig. 1). The duration of the studies varied between three weeks and three years, and only one lasted more than two years (Fig. 1). The genetic markers used for genetic diversity analyses were microsatellites (SSR) in 88% of the studies; alloenzymes in 4%, Amplified Fragment Length Polymorphism (AFLP) in 4%, and Single Nucleotide Polymorphism (SNP) in 4% (Fig. 1). All studies included 22 measures of genetic diversity that are detailed in Table 1. Resilience was evaluated with nearly 50 different direct and indirect measures for resistance and recovery. The types of disturbances that were studied the most were variations in temperature, light, nutrients, and herbivores, as well as the effects of transplantation and/or relocation. Survival, growth, biomass, density and recruitment were

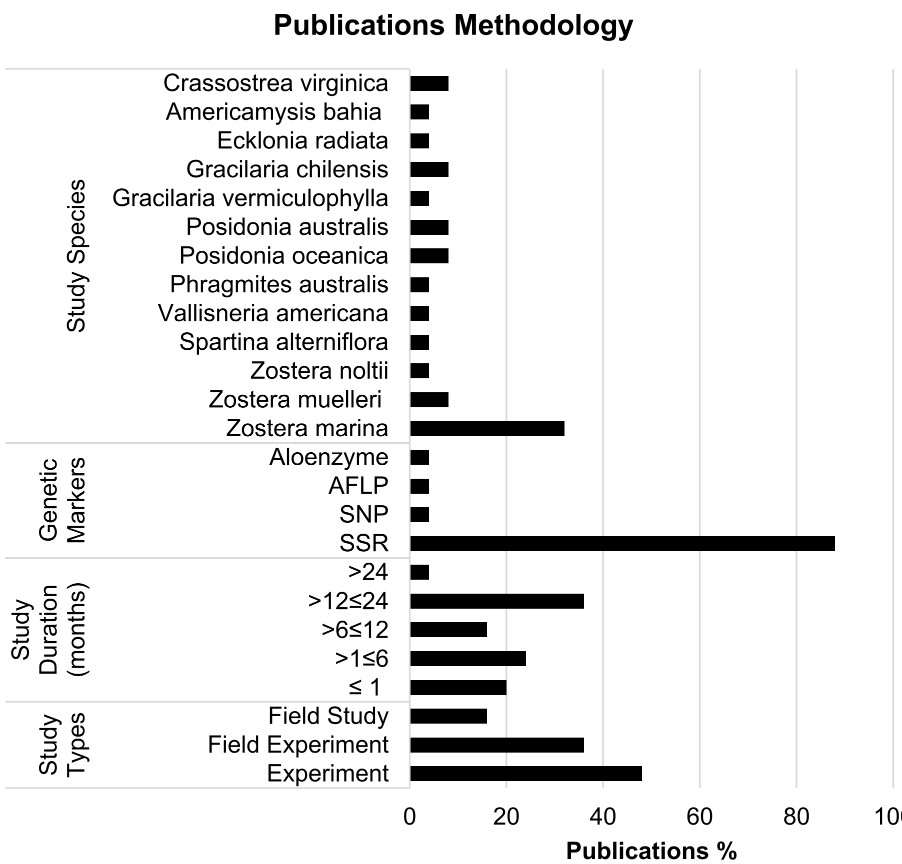

Fig. 1 Publications Methodology: Percentage of publications according to study type (experiment, field experiment, field study), study duration (in months), genetic marker (SSR, SNP, AFLP, alloenzymes) and species studied

Table 1 Measures of genetic diversity used to evaluate resilience capacity in the studies included in this review

Sigla	Name	Definition
MLG	Multi-locus genotype	Number of unique multi-locus genotypes
R	Genotypic diversity	Number of unique multi-locus genotypes relative to the number of samples collected
PLP	Percentage of polymorphic loci	Fraction of polymorphic loci within the sample
NHL	Number of heterozygous loci	Number of heterozygous loci for each unique multi-locus genotype
H	Heterozygosity	The proportion of heterozygous loci at the individual level
Ho	Observed heterozygosity	The proportion of N samples that are heterozygous at a given locus
He	Expected heterozygosity	The proportion of heterozygosity expected under random mating
H_j	Heterozygosity	The probability that two genes, randomly drawn from population j, differ at the i^{th} locus
Hnb	Unbiased heterozygosity	Expected heterozygosity corrected; estimated on the set of MLL defined after removing ramets derived from the same zygote ancestor according to psex(fis)
Diploide	Diploide	Organisms have two alleles per locus (identified by the presence of at least one heterozygous locus)
Heterozygous (MDH and GPI-2)	Heterozygote at the MDH and GPI-2	Individuals that have two different alleles at the malate dehydrogenase (MDH) and glucose-6-phosphate isomerase (GPI)
Heterozygous (MDH)	Heterozygote at the MDH	Individuals that have two different alleles at the malate dehydrogenase (MDH)
Heterozygous (GPI-2)	Heterozygote at the GPI-2	Individuals that have two different alleles at the glucose-6-phosphate isomerase (GPI-2)
AR	Allele richness	Number of alleles per locus and population, corrected for sample size
D. Cohorte	Cohort diversity	The number of independent juvenile cohorts created from different adult source populations or parents
GR	Genetic relatedness	Genetic similarity among individuals within and across cohorts
Fis	Inbreeding coefficient	The correlation between genes on uniting gametes relative to the total array of those in random derivatives of the foundation stock
Pareto B	Pareto B	β is derived from the slope of Pareto distributions
Pareto Max	Pareto Max	Maximum number of clonal replicates
D	Simpson's genotype diversity index	The probability of encountering distinct Multi-Locus Genotypes (MLG) when randomly taking two sample units
CR	Clonal sub range	The maximum distance in meters between two identical genotypes belonging to the same clone
Set	MLG, R, AR, Na, Ho and He	Set of diversity measures that include MLG, AR, Na, Ho and He

the most frequently resilience measures found (See Table 1, Add file).

The number of tests used to evaluate the relationship or effect between genetic diversity and resilience capacity ranged from 1 to 23. Consequently, many studies presented results with more than one type of relationship between genetic diversity and resilience capacity, depending on how genetic diversity and resilience were measure (Fig. 2). In total, the studies included 150 analyses, using different combinations of measures for genetic diversity (predictor variable) and resilience (response variable). Among the analyses, 44% found positive relationships between genetic diversity and resilience capacity, 6% found negative relationships, and 50% found no relation (Fig. 3). The genetic diversity measure that was used the most to evaluate resilience was multi-locus genotype (MLG), where 60% of studies that used this measure found positive relations, 2% found negative relations, and 38% found no relation. Allele richness (AR) was the second most used measure, resulting in 42% positive relationships, 11% negative, and 47% no relationship with resilience. Genotypic diversity (R) was the third most used measure, yielding 20% positive relationships, 20% negative, and 60% no relationship with resilience (Fig. 4).

The measure that was used the most to analyze resilience with respect to genetic diversity was population density, where there were positive relationships 61% of the time, and no relationship 39% of the time. Daily growth rate was the second most used measure for resilience, for which 33% of the results were positive, 7% negative, and 60% found no relation with genetic diversity. Finally, survivability was the third most used measure, which resulted in 62% positive relationships, 23% negative, and 15% no relation with genetic diversity (Fig. 5).

There were seven studies (39%) that examined the mechanism underlying the relationship between genetic diversity and resilience capacity, all of which used Microsatellites (SSR) to evaluate genetic diversity.

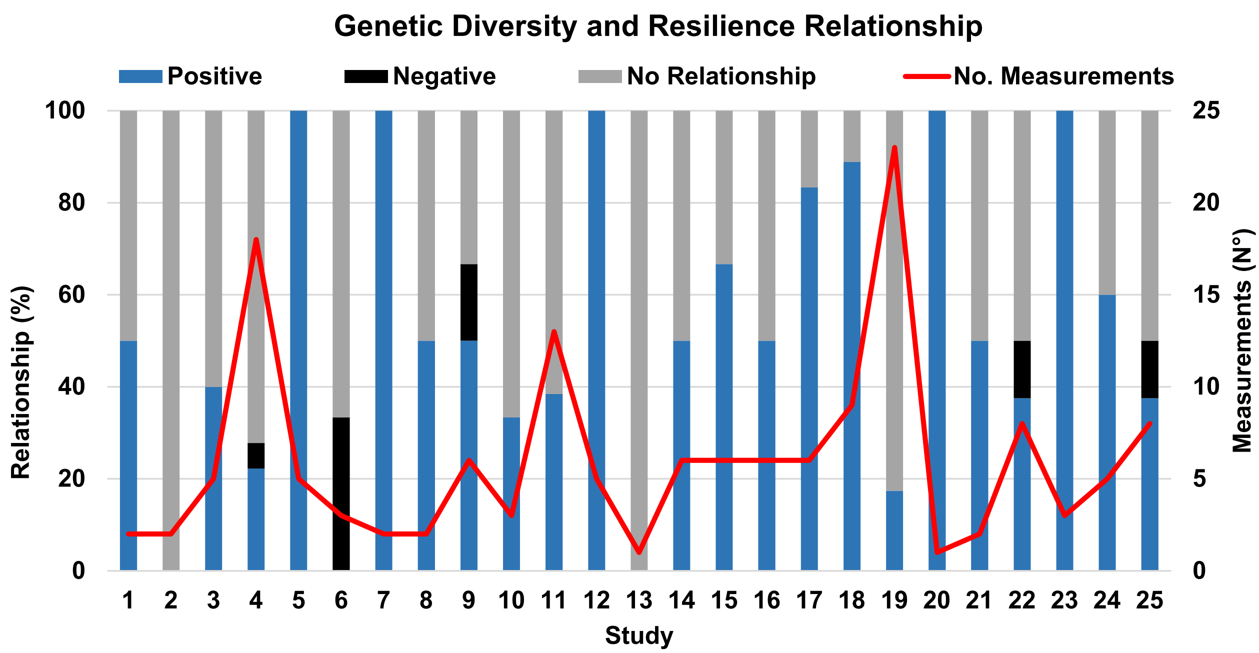

Fig. 2 Genetic Diversity and Resilience Relationship: Percentages (%) of the type of relationship or effect between genetic diversity and resilience; Positive (blue), Negative (black) and No Relationship (grey) with the number of measurements (red line) for each study

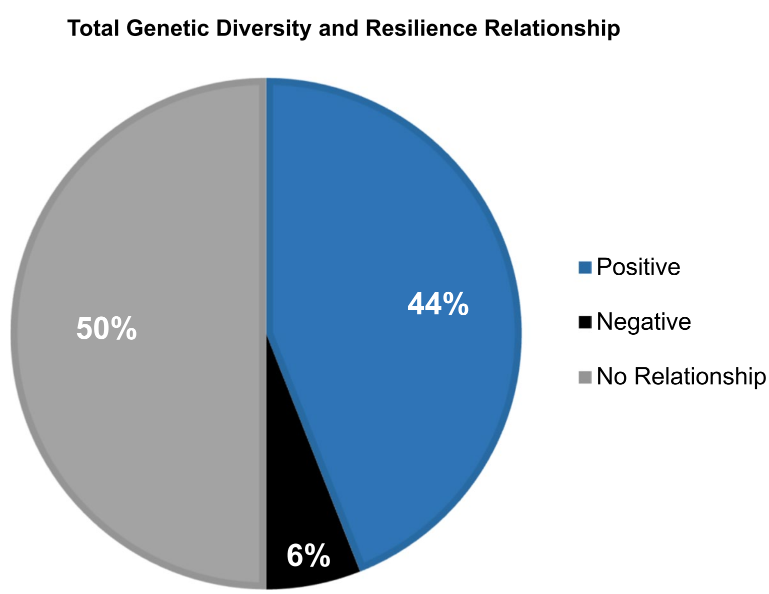

Fig. 3 Total Genetic Diversity and Resilience Relationship: Percentages (%) of the type of relationship or effect between genetic diversity and resilience; Positive (blue), Negative (black) and No Relationship (grey) out of all measures ($N = 150$)

Six studies emphasized on a mechanism that combined the effect of natural selection (dominance) and complementarity, and one study only highlighted complementarity.

Discussion and conclusions

Despite evidence suggesting the importance of genetic diversity for individual survival, population persistence and the functioning of communities and ecosystems,

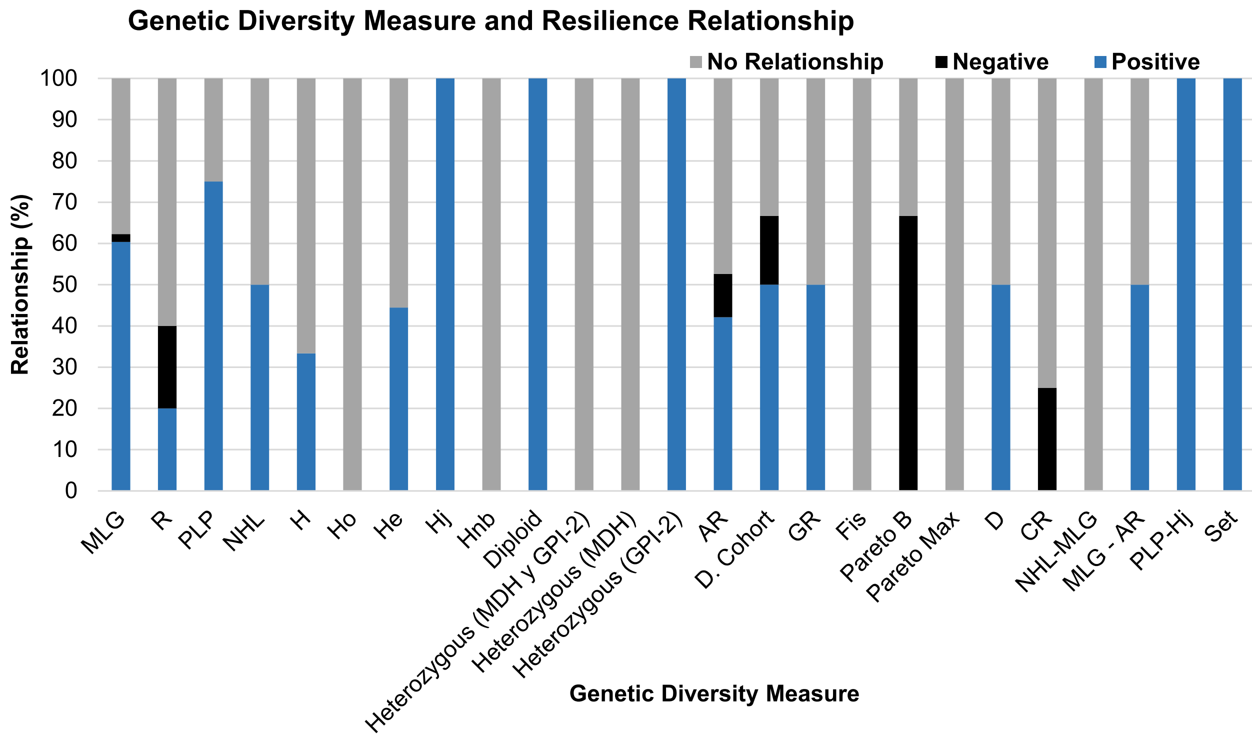

Fig. 4 Genetic Diversity Measure and Resilience Relationship: Percentage (%) of relationship or effect between genetic diversity and resilience capacity; Positive (blue), Negative (black) and No Relationship (grey). MLG = Multi-locus genotype, R = Genotypic diversity, PLP = Percentage of polymorphic loci, NHL = Number of heterozygous loci, H = Heterozygosity, Ho = Observed heterozygosity, He = Expected heterozygosity, Hj = Heterozygosity, Hnb = Unbiased heterozygosity, Diploid, Heterozygous (MDH y GPI-2), Heterozygous (MDH), Heterozygous (GPI-2), AR = Allele richness, D. Cohort = Cohort diversity, GR = Genetic relatedness, Fis = Inbreeding coefficient, Pareto B, Pareto Max, D = Simpson's genotype diversity index, CR = Clonal sub range, NHL-MLG, MLG-AR, PLP-Hj and Set = MLG, R, AR, Na, Ho and He. See also Table 1 for definitions

few studies were found regarding benthic marine species (N = 25). These studies gradually increased between 2001 and 2018 (nearly two decades), although there were 6 publications in the last year. There were clearly more studies on sea-grass and marine sea-weed species (84%), particularly on the species *Zostera marina* (32%).

The effects of genetic diversity on resilience were variable dependent. Most of the studies found more than one relationship, depending on the resilience measure and the measure of genetic diversity employed. When analyzing the results by variable, independent of the study, more positive relationships between genetic diversity and resilience were found (44%) compared to negative relationships, which were few (6%). No relationship between genetic diversity and resilience was found in 50% of the analyzed cases.

Positive relationships between genetic diversity and resilience were associated with greater survival, growth and physiological versatility under disturbances such as number of contaminators, salinity, alterations in temperature, and so forth. For instance, genetic diversity was related to increases in resistance to transplantation and herbivores in *Z. marina* [5], as well as to better recovery rates, densities and biomass after temperature changes [7, 21, 22]. Populations of the alga *Ecklonia radiata* with greater genetic diversity had more growth and physiological versatility under heat waves [23]. The crustacean *Americamys bahia* showed higher fitness and adaptation capacities with changes in salinity, presenting higher genetic diversity [24]. One recent experiment on the marine plant *Cymodocea nodosa* showed that resistance to lack of light increased significantly with genetic diversity, and that recovery was conditioned by this resistance [42].

Negative relationships between diversity and resilience were associated with mortality, net growth, biomass and survivability. Sea-grass beds of *Posidonia oceanica* with low genetic diversity were more resistant to pisciculture [44]. Although the mechanism was not evaluated, the authors related these results to the existence of large and dominant clones that would have been selected over a long period of time due to phenotypic plasticity, thus causing low genetic diversity and/or exclusion by competition. Any of these processes should provide resistance advantages under short-term environmental disturbances such as fish farming. However, the authors also

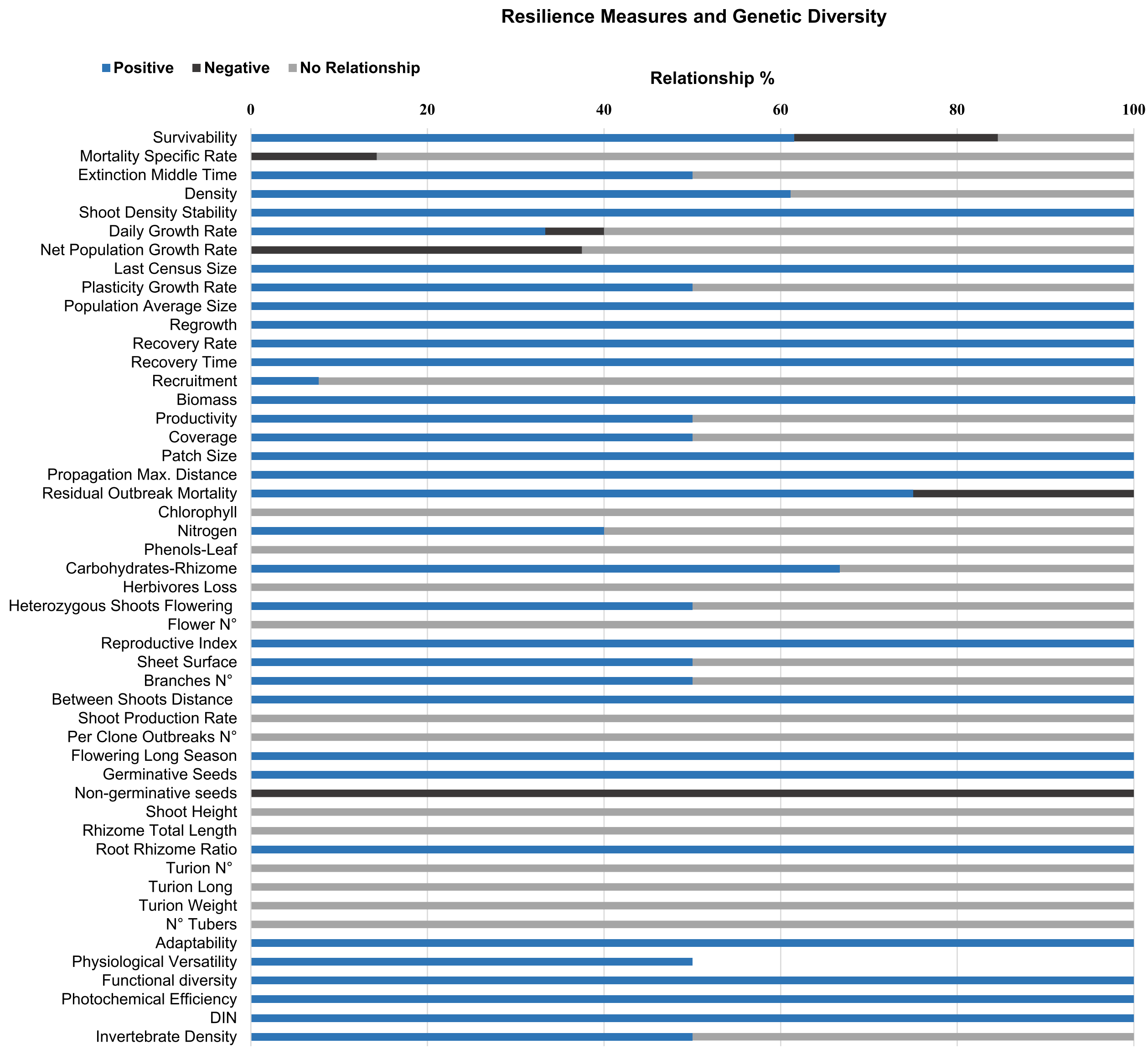

Fig. 5 Resilience Measures and Genetic Diversity**:** Percentages (%) of the types of relationship or effect between genetic diversity and resilience capacity: Positive (blue), Negative (black) and No Relationship (grey) for each measure or resilience. For details of these resilience measures, see also references number [5–7, 20–44]

recognized a potential bias due to the absence of genetic data prior to the disturbance, thus suggesting more laboratory experiments. This study [44] conducted the highest number of evaluations ($N=23$) on measures for genetic diversity and resilience. Only four of these evaluations found negative effects or relationships, whereas no relationship or effects were found in the others. Regarding *Posidonia australis*, a negative relationship was also found between genetic diversity and two of the seven measures for resilience employed (area and leaf growth rate) [25].

One of the studies where no relationship was found between genetic diversity and resilience was conducted by Macreadie et al. (2014) [26] on populations of *Z. muelleri*. They concluded that population recovery for this species after small-scale disturbances would depend on the growth of the clones, and that sexual reproduction would have little or no relevance. In *Z. marina*, recovery after an extreme disturbance initially would have been by sexual reproduction via germination of a seed bank. However, later recovery was accompanied by vegetative growth, decreasing genotype diversity. Despite this, genetic diversity among new sea-grass beds remained high. This proves the importance of sexual reproduction in the recovery and persistence of these beds [43].

Sexual reproduction provides genetic variation by segregation and recombination, while asexual reproduction provides genetic variation only by recombination. Consequently, populations with sexual reproduction show more genetic variation than asexual populations. However, there is evidence that sexual reproduction can also cause a decrease in genetic variation [45]. The mixture of reproductive modes can produce flexibility, allowing genotypes locally adapted to favorable environments to multiply rapidly by clonal propagules. Alternatively, the mixture of gametes may provide the genetic novelties necessary for the colonization of new habitats [46, 47]. The maintenance of alternative reproductive methods allows for the persistence of populations in unpredictable environments or highly fluctuating conditions [48]. The classic model of clonal propagation dynamics suggests a relationship between genetic diversity and physical disturbances, where genotype richness is low (high clonality) in stable environments and high (low clonality) in disturbed environments [43, 46, 49].

No effects of heterozygosity were found on growth or physiological responses in populations of *Gracilaria chilensis*. These results are likely to be connected to historical domestication, which would have limited genetic diversity in these cultivated populations. However, no evaluations of these proposed mechanisms were found [27]. The relationship between genetic diversity and resilience depends on the environmental conditions. The magnitude and direction of these effects vary depending on the measure of genetic diversity used [28] and on the biological characteristics of the species, as well as the methodology used. The absence of a relationship in some studies may be due to methodological design, the selection of measures for genetic diversity and resilience, the type and number of genetic markers, the duration of the study or other reasons. For example, the observed heterozygosity, the Simpson index of genotypic diversity, and the fixation indices found no relationship with any of the measures for resilience. Chlorophyll and phenol concentration and structures, like the turion, reflected no relations with any of the measures of genetic diversity. Capdevilla et al. (2021) recommended using common and comparable resilience measures [50]. This recommendation has not yet been accepted, since there is currently a dispute about which definition is to be used, and new definitions continue to appear [51].

Only 39% of the reviewed studies evaluated the underlying mechanisms of the relationship between genetic diversity and resilience capacity. These results mainly highlighted a combined effect of natural selection and complementarity. Microsatellites were used in all studies that analyzed genetic diversity. The use of neutral molecular markers has been a constant topic of discussion in evaluating the effect of genetic diversity on resilience, given that neutral variation by definition does not have ecological consequences, which is why this type of marker has no adaptive potential [22, 26, 29, 52, 53]. Nevertheless, the theory of biological heterozygosity-fitness, inferred from neutral markers, can be interpreted as a result of a general effect on the genome ("the general effect hypothesis") or as a local effect in a unique locus ("the local effect hypothesis") [54]. New tools, such as Next-Generation Sequencing (NGS), are more appropriate for the study of gene expression with adaptive importance [52]. Differentiating between the underlying mechanisms related to diversity effects, such as complementarity and selection, is fundamental, given that these effects help identify the processes that connect genetic diversity and demographic traits [28, 55].

The results of this review demonstrate that the relationship between genetic diversity and resilience is mainly positive. Genetic diversity tended to increase the resistance and recovery capacity of benthic marine populations after natural perturbations such as heat waves and algal blooms, as well as after anthropic disturbances such as marine eutrophication. This reinforces the importance of acknowledging and maintaining genetic diversity for the conservation of populations in marine ecosystems. Its loss might lead to decreases in physiological versatility and in resilience capacity, while also causing a cascading effect towards lower biodiversity levels, which could become critical and cause potentially irreversible changes in the structure and functioning of ecosystems [23]. Maintaining resilience and the adaptive capacity of marine ecosystems by conserving genetic diversity must be a central component of efforts in the current decade, which the United Nations has declared the Decade of the Oceanographic Sciences for Sustainable Development [56].

Abbreviation

DIN Dissolved Inorganic Nitrogen

Supplementary Information

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Additional file 1: Table 1. Comparative synthesis of scientific studies included in this review.

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Authors' contributions
CV: Conceptualization, Methodology, Formal analysis, Investigation, Writing Original Draft. RQ: Writing—Review & Editing. AB: Writing—Review & Editing. EHM: Conceptualization, Methodology, Writing—Review & Editing. All authors read and approved the final manuscript.

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Availability of data and materials
The datasets used in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors have declared that no competing interests exist.

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