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Disturbance decreases genotypic diversity by reducing colonization: Implications for disturbance–diversity feedbacks

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Abstract

One objective of eco-evolutionary dynamics is to understand how the interplay between ecology and evolution on contemporary timescales contributes to the maintenance of biodiversity. Disturbance is an ecological process that can alter species diversity through both ecological and evolutionary effects on colonization and extinction dynamics. While analogous mechanisms likely operate among genotypes within a population, empirical evidence demonstrating the relationship between disturbance and genotypic diversity remains limited. We experimentally tested how disturbance altered the colonization (gain) and extinction (loss) of genets within a population of the marine angiosperm *Zostera marina* (eelgrass). In a 2-year field experiment conducted in northern California, we mimicked grazing disturbance by migratory geese by clipping leaves at varying frequencies during the winter months. Surprisingly, we found the greatest rates of new colonization in the absence of disturbance and that clipping had negligible effects on extinction. We hypothesize that genet extinction was not driven by selective mortality from clipping or from any stochastic loss resulting from the reduced shoot densities in clipped plots. We also hypothesize that increased flowering effort and facilitation within and among clones drove the increased colonization of new genets in the undisturbed treatment. This balance between colonization and extinction resulted in a negative relationship between clipping frequency and net changes in genotypic richness. We interpret our results in light of prior work showing that genotypic diversity increased resistance to grazing disturbance. We suggest that both directions of a feedback between disturbance and diversity occur in this system with consequences for the maintenance of eelgrass genotypic diversity.

KEYWORDS
colonization, disturbance, eelgrass, feedback, genotypic diversity, grazing

INTRODUCTION

The field of eco-evolutionary dynamics asks how the "evolutionary play acts within the ecological theater" (Hutchinson, 1965) on contemporary timescales (Schoener, 2011). Current work largely focuses on how natural selection drives phenotypic change that then simultaneously feeds back to alter the selection agent (reviewed in Hendry, 2017). However, this framework may be limiting our understanding of feedbacks given that relationships between particular trait states and ecological function can be complex, indirect, and contingent on other traits. Furthermore, selection is not the only mechanism of evolution in natural populations. Rapid changes in allele frequencies can also occur through ecological processes driving stochastic loss (e.g., overhunting increased genetic drift in Northern elephant seals) (Bonnell & Selander, 1974), gene flow (e.g., a hurricane caused admixture of a brooding isopod) (Pagán et al., 2020), mutation (e.g., starvation led to mutagenesis in *Escherichia coli* bacteria) (Bjedov et al., 2003), and nonrandom mating (e.g., parasite infection influenced mate choice in red jungle fowl) (Zuk et al., 1990). Broadening the framework beyond studies with eco-to-evo pathways centered on selection or systems where trait–function relationships are well defined will expand our understanding of how the interplay between ecology and evolution on contemporary timescales operates in natural systems.

In addition to influencing the allelic composition of a population, ecological processes, such as disturbance (sensu Sousa [1979]), can alter evolutionary processes that influence the diversity of genotypes in a population. Community ecology posits multiple hypotheses for predicting how disturbance should affect biodiversity. For example, the intermediate disturbance hypothesis suggests that moderate levels of disturbance increase richness by delaying extinction from competitive exclusion and facilitating colonization (sensu Connell [1978], Chesson & Huntly [1997], and Sousa [1979]). However, disturbance can reduce diversity under conditions of limited colonization where disturbance-driven extinctions dominate, such that only species tolerant of or resistant to the disturbance persist (e.g., Tilman & El Haddi, 1992). Disturbance can also decrease diversity if it reduces habitat complexity or otherwise weakens facilitative interactions within or among species (Bruno et al., 2003). Conversely, disturbance can enhance diversity if successful colonization is limited by resource availability and disturbance opens space for the successful establishment of migrants (e.g., Goodsell & Connell [2005] and references therein). Finally, multiple studies in community ecology reveal no effect of disturbance on richness (reviewed in Hughes et al., [2007] and Mackey & Currie [2001]), especially in systems not structured by competitive hierarchies (Chesson & Huntly, 1997) or where several of the aforementioned mechanisms counteract each other.

The shape of the relationship between disturbance and genotypic diversity also varies considerably among systems. For example, correlative studies show that sites with intensive disturbance histories can have higher (Foster et al., 2021; Hunter, 1993; McMahon et al., 2017), lower (Hangelbroek et al., 2002; Rusterholz et al., 2009), or indistinguishable (Diaz-Almela et al., 2007) genotypic richness values relative to undisturbed sites. Manipulative experiments also show mixed results. Though some studies demonstrate that variation in the strength of selection drives diversity differences between disturbed and undisturbed plots (Herrera & Bazaga, 2011; Whitney et al., 2019), other studies show no effect (Hidding et al., 2014; Larkin et al., 2010; Reusch, 2006) or increased richness under moderately disturbed regimes (Peng et al., 2015). The variable nature of disturbance may be better explained by focusing on how it separately affects colonization (the gain of new genets) and extinction (the loss of established genets). Just as for species diversity, disturbance can have variable effects on genotypic colonization and extinction beyond net changes in richness alone.

Here, we used a manipulative field experiment to test the effects of a simulated disturbance (grazing by migratory waterfowl) on genotypic diversity in a wild population of eelgrass, *Zostera marina* (hereafter *Zostera*). *Zostera* is a marine flowering plant that reproduces sexually via seeds and asexually via the vegetative propagation of shoots (i.e., clonal ramets) along a rhizome. *Zostera* forms monospecific stands with patchy distributions of genetic diversity both within and among populations (Furman et al., 2015; Hughes & Stachowicz, 2009; Kamel et al., 2012; Olsen et al., 2004; Reusch, Stam, et al., 1999; Ruckelshaus, 1998). The maintenance of variation in genetic diversity is, at least in part, driven by its interaction with seagrass life history characteristics (Kendrick et al., 2012). In perennial meadows, the clonal propagation of competitively dominant genotypes can result in long-lived genets spread across large spatial scales and low local diversity (Reusch, Boström, et al., 1999). Within a localized area in the meadow, the colonization of new genets may arise from seedling recruitment (reviewed in Kendrick et al., 2012), clonal encroachment from genets outside the patch, the reestablishment of vegetative ramets dislodged from other locations (present study), and potentially somatic mutations (Yu et al., 2020). Previous studies predicted that disturbance, such as grazing by waterfowl, could alter *Zostera* genetic diversity via effects on sexual reproduction (Kollars et al., 2017; Shaughnessy et al., 2021), but the magnitude of this influence depends on the disturbance intensity. For example, clipping vegetative shoots to a height of 45 cm in the late winter increased the production of flowering shoots the following spring (Shaughnessy et al., 2021), but severe disturbances that dislodge rhizomes, such as grazing by Canada geese (*Branta canadensis*), can drive perennial populations to extinction in the absence of adequate seedling recruitment (Rivers & Short, 2007).

Over 2 years, we simulated grazing by migratory waterfowl via a field-based clipping manipulation and monitored net change in genotypic richness over time. We further separated net change in richness into colonization and extinction events to deduce how different clipping scenarios affected genet loss (because of selection or stochasticity) or gain (resulting from clonal propagation or sexual recruitment). We recognize that the combined effects of multiple, and potentially contrasting, processes operating in our experiment would ultimately determine the net change in genotypic richness over time. We first considered that grazing was most intense in the intertidal zone (Moore & Black, 2006) and genotypic richness within populations was often highest in these areas (Kamel et al., 2012). This observation, coupled with research showing increased sexual recruitment of *Zostera* in areas of reduced standing biomass (Johnson et al., 2020; Reusch, 2006; Robertson & Mann, 1984), suggests that clipping disturbance may enhance genotypic diversity. However, clipping could reduce diversity if it created population bottlenecks that drive the stochastic loss of genets or if it acted as a selective agent by favoring more tolerant genotypes (Kollars et al., 2021). Therefore, we expected that clipping disturbance would increase both the colonization of new genets and the extinction of established genets, but we did not make an a priori prediction about how the combined effects of these two processes would drive net change in richness. We interpret our results in light of previous research establishing that genotypic diversity positively influences assemblage resistance to and resilience from grazing (Hughes & Stachowicz, 2004) in order to assess the potential for a disturbance–diversity feedback in this system that is driven by both ecological and evolutionary processes.

METHODS

Study system

We conducted our experiment within a perennial, natural assemblage of intertidal *Zostera* in Bodega Harbor, Bodega Bay, California. Within Bodega Harbor, the number of genotypes in a 1-m^2 area can range from 1 to more than 15 (Hughes & Stachowicz, 2009), and diversity and differentiation among sites have been stable for at least a decade (Reynolds et al., 2017). Genotypes collected from the harbor also show variation in functionally important traits (Abbott et al., 2018; DuBois et al., 2019; Hughes et al., 2009), including tolerance to simulated waterfowl grazing (Kollars et al., 2021). Waterfowl known to graze eelgrass in northern California include the Pacific Black Brant goose (*Branta bernicla nigricans*), the American coot (*Fulica americana*), and Canada geese (*Branta canadensis*) (Kollars et al., 2017). These birds are seasonal migrants and are only present in Bodega Harbor from November through May of each year, with peak abundances occurring in February (C. Dunford, unpublished data from 1986 to 2015). We choose to focus our efforts on simulating Brant grazing because they are the dominant grazers of *Zostera* along the western coast of North America (Kollars et al., 2017), grazing by Canada geese in Bodega Harbor is rare (N. M. Kollars, J. J. Staachowicz, personal observation), and the resilience of eelgrass plots to grazing by Brant is demonstrably increased by genotypic diversity (Hughes & Stachowicz, 2004). Grazing by Brant does not damage the basal meristem (and so does not directly cause shoot mortality), and we mimicked grazing by using scissors to remove all leaf tissue above the sheath for any individual shoot. We manipulated within-season clipping frequency to mimic varying grazing scenarios, accounting for the observation that Brant will visit previously grazed meadows to target nutritionally rich regrowth (Ganter, 2000; Moore & Black, 2006). The density of *Zostera* in Bodega Harbor typically peaks between May and August (Olyarnik & Stachowicz, 2012), and flowering peaks toward the latter half of this period (N. M. Kollars, J. J. Staachowicz, personal observations).

Experimental design

In fall of 2016, we set up a manipulative field experiment along an approximately 50-m continuous stretch of intertidal *Zostera* meadow on the west side of Bodega Harbor (tidal height: approximately −0.1 m mean lower low water; GPS: 38.318222° N and −123.0536° E to 38.317432° N and −123.05308° E). Along this transect, we delineated nine experimental blocks parallel to the shore with space of 3 m between each block. A block consisted of four 1 × 1 m plots positioned in a square layout separated by 1 m in all directions (Figure 1). At the beginning of the experiment, we used a spade to sever the rhizomes along the perimeter of each plot so that connections to ramets outside of the plot boundary would not affect the initial performance of ramets inside the plot. We did not continue to sever rhizome connections throughout the experiment to allow for the vegetative propagation of neighboring genets into the plots.

FIGURE 1 Photographs of experiment testing the effects of simulated grazing disturbance (clipping) on changes in genotypic richness in an intertidal *Zostera marina* meadow. Left: Photograph at block level highlighting placement of seed trap and design of waterfowl exclosures. Right: Close-up of each plot taken in March 2017. Clockwise from top left corner: 0X (not clipped), 1X (clipped once in February), 2X (clipped once in February and once in March), and 4X (clipped once in January, February, and March; note this photograph was taken before the fourth application of clipping in April)

We controlled the amount of disturbance imposed in each treatment by designing detachable exclosures to prevent natural grazing by waterfowl in any of the experimental plots (Figure 1). We constructed exclosures using PVC (diameter: 2.54 cm) to create posts consisting of two parts: a 1.5-m-high aboveground portion that connected to a 1-m belowground portion pounded into the sediment. We attached exclosures in October prior to bird arrival and removed them after the birds migrated the following spring to avoid entanglement of the exclosures with macroalgae that bloom over the summer (primarily *Ulva* spp. and *Agarophyton vermiculophllum*). The PVC posts alone were adequate to prevent grazing by Brant, but not coots (N. M. Kollars, J. J. Staachowicz, personal observation). Therefore, we strung orange nylon line (commonly used in landscaping as trimmer line) around the perimeter of the posts every ~40 cm to discourage coots from swimming into the plot area. Shore observations confirmed the effectiveness of the exclosures. We removed detritus from the nylon lines at least once a month.

We implemented four levels of disturbance: clipped zero times per season (0×, a control treatment representing the absence of grazing), clipped once per season (1×), clipped twice per season (2×), and clipped four times per season (4×). We clipped the 1× treatment in February, the 2× treatment in both February and March, and the 4× treatment in January, February, March, and April. We repeated the 1× and 2× treatments for two grazing seasons (2017 and 2018) but applied the 4× treatment only in 2017. We did not repeat 4× for a second grazing season because this clipping frequency severely reduced shoot densities (see the "Results" section), and we wanted to document recovery from such a severe disturbance regime. We randomly assigned one replicate of each treatment to one of the four plots within each experimental block ($n = 9$ plots per clipping frequency).

We genotyped samples collected from each plot at the beginning and end of the 2-year experimental period (December 2016 and October 2018, respectively) using nine microsatellite loci we had previously used at this location (Abbott et al., 2018) (see Appendices S2 and S3 for full genotyping and DNA extraction methods, respectively). We collected tissue using a 0.6 × 0.6 m quadrat of 36 evenly spaced points (Appendix S1: Figure S1), and we removed the inner leaf of the shoot closest to each point. We did not collect a sample at a grid position if there was not a shoot present within a radius of ~4 cm of the point. We recorded the location of the collected tissue along the grid and transported all samples to the lab where we dissected ~5 cm of the greenest tissue of the leaf, rinsed it with ultrapure water, placed the sample in a 1.7-ml tube, and stored the sample at −80°C until extraction.

We counted vegetative and flowering shoots in a 20 × 20 cm quadrat placed in the center of each plot at approximately monthly intervals. We counted a shoot as flowering if it exhibited characteristics of any flowering stage (sensu von Staats et al. [2021]). We also quantified seedling recruitment at the block level using containers of unvegetated sediment (seedling traps) placed in the center of each block (Figure 1). Traps consisted of plastic containers (19.5 cm long × 14.5 cm wide × 12.5 cm high) lined with a 2-mm-diameter mesh, filled with bare sediment, and placed flush with the sediment surface. When we noticed shoots in the trap, we removed the shoots and genotyped tissue from each putative genet.

Analysis

We separated our analysis into two parts to avoid confusing the effects of clipping frequency within versus among years: we compared the control (0×) to treatments clipped in (1) both years of the experiment (1× and 2× treatments) or (2) only in the first year (4×). For both sets of analyses, we assessed the effect of clipping treatment, initial richness, and the interaction between treatment and initial richness on each response variable using generalized linear models (GLMs), calculated in the *lme4* package (Bates et al. [2007], public communication); we conducted this and all subsequent analyses in R version 4.0.0 (R Core Team, 2013). We chose to include initial richness in the model in lieu of experimental block because of the unexpectedly high variation in the initial number of genotypes among plots within each block (Appendix S1: Figure S2), which rendered the "block" designation less meaningful. For count data that merited a Poisson family distribution, we tested for overdispersion using the dispersiontest function in the *AER* package (Kleiber et al. [2020], public communication). We followed the GLM with an analysis of deviance (χ^2 test and F-test for Poisson and Gaussian distributions, respectively) using the Anova function in the *car* package (Fox & Weisberg, 2018) to assess the importance of each factor in the model. When the model showed a treatment effect with a p-value < 0.05, we performed among-level comparisons using a post hoc Tukey's test with the *multcomp* package (Hothorn et al. [2016], public communication).

We first assessed the response of genotypic richness to clipping treatments. Though genotypic richness in clonal populations is often calculated as $G - 1/N - 1$ (where G = number of genotypes and N = number of samples) (Dorken & Eckert, 2001), we considered G alone to be an appropriate metric of richness given that our sampling effort was consistent across plots. Furthermore, any reduction in sample size due to treatment could affect colonization and extinction dynamics, which may be lost by standardization. We focused our analysis on net change in richness over time (final number of genotypes − initial number of genotypes) using the methods described previously because of high variability in the initial richness among plots and a strong effect of initial richness on final richness (see *Results* and Appendix S1: Figure S2).

Next, we decomposed net richness changes into the number of colonization and extinction events that occurred in each plot during the experiment. Our sampling design of collecting shoots in approximately the same position across time allowed us to classify the appearance of a genotype as a colonization event when a genotype was absent within a plot at the beginning of the experiment but present at the end. Similarly, we classified an extinction event as a genotype that was present within a plot at the beginning of the experiment but absent at the final time point.

Finally, we asked how clipping treatment affected shoot density, flowering effort, and site-level sexual recruitment through time. We qualitatively assessed changes in shoot densities and results from the seedling traps. We analyzed flowering effort by considering the proportion of flowering shoots relative to the total number of shoots in each plot, which yielded a proportional variable bounded between 0 and 1. Instead of using linear models that require a specified error distribution, we used nonparametric permutation tests with 1000 permutations within an analysis of variance framework (sensu Anderson [2001]) with initial richness, clipping treatment, and their interaction as the main factors of interest and time as a blocking factor to account for repeated measures. We permuted the F-statistic and calculated a p-value using one-tailed tests of the null hypothesis that the observed and simulated F-statistics come from the same distribution.

RESULTS

Clipping acted as a disturbance agent by reducing canopy height (Figure 1) and shoot density (Figure 2). During the first year, all clipped plots had fewer shoots than the unclipped plots. The 2× treatment appeared to recover by the end of the growing season and did not appear affected by clipping during the second year. In contrast, the 1× treatment recovered more slowly and did not reach densities similar to those of the control treatment until the summer after the second clipping season. On average, the 4× treatment, which was only clipped in the first year, recovered to close to control densities during the second year of the experiment, but with high variation among plots.

Contrary to predictions that disturbance would increase genotypic richness by increasing colonization, two consecutive seasons of clipping (1× and 2× treatments) resulted in a net loss of genotypes, whereas the absence of disturbance (0× treatment) resulted in a net increase in genotypes (Figure 3, Table 1, Appendix S1: Table S1). Separate analysis of the 4× treatment showed

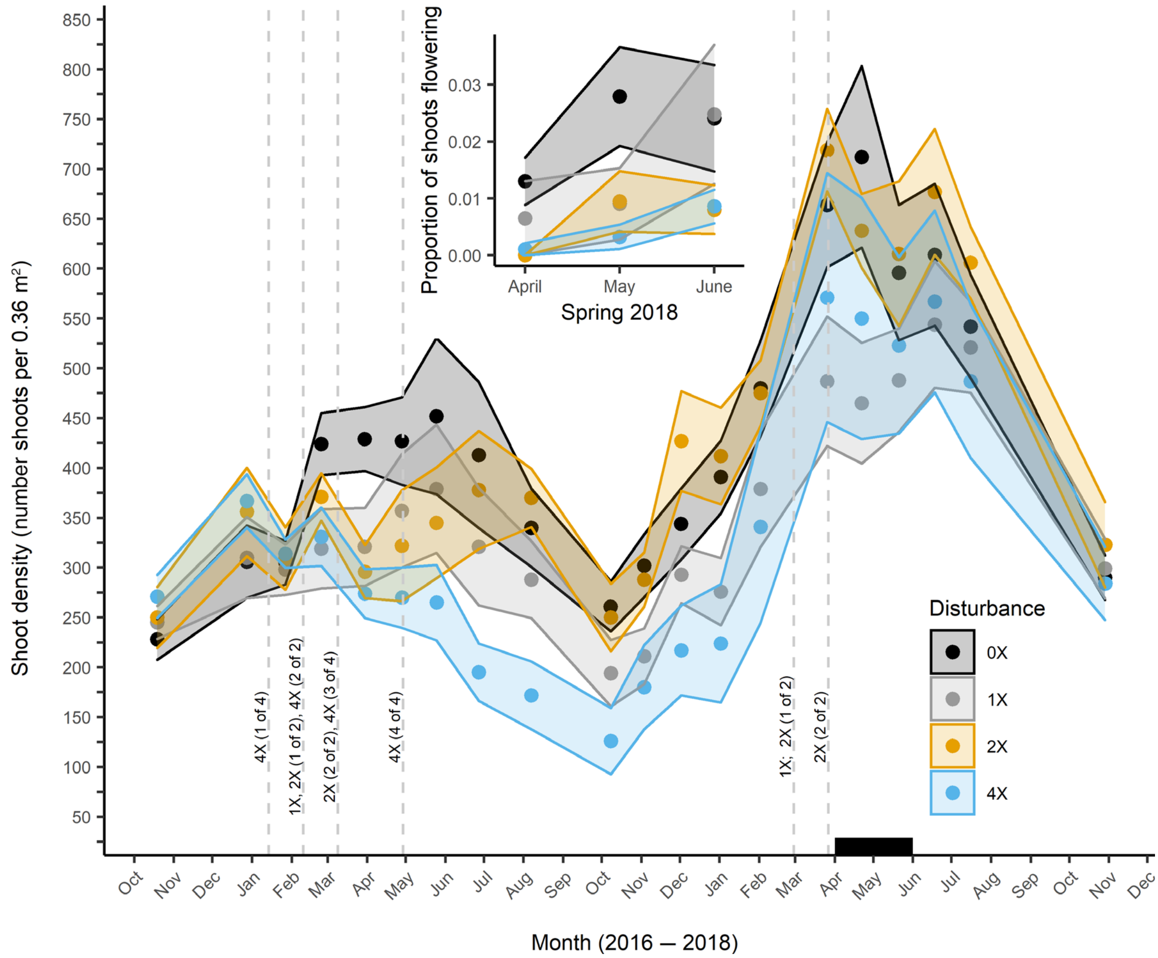

FIGURE 2 Mean total shoot densities (vegetative + flowering) of *Zostera marina* through time in response to clipping treatments in natural assemblages of genotypes in the field. Dashed gray lines indicate timing of clipping application. Inset: Mean proportion of flowering shoots during the second year of the experiment (April–June 2018, indicated on *x*-axis by black box). Shaded ribbons are ±1 standard error of the mean

that despite severe biomass loss during the first year (Figure 2), shoot density mostly recovered in the second year, and there was no residual effect of clipping frequency (0× versus 4×) on the net change in genotypic richness by the experiment's end (Figure 3, Table 1).

Separating net richness change into colonization and extinction showed that differences among clipping treatments were primarily driven by treatment effects on colonization rather than extinction. Clipping reduced colonization in the 1× and 2× treatments (Figure 4a, Table 1, Appendix S1: Table S1) such that the mean number of new genets gained in the 0× treatment was greater than in the 2× treatment (mean ± SE: 0× = 1.22 ± 0.36 vs. 2× = 0.11 ± 0.33). Clipping did not result in differences in the number of genotypes gained between the 0× and 4× treatments by the experiment's end (Figure 4a, Table 1). Overall, we observed a total of 36 colonization events (i.e., unique genotypes that were present across the plots at the end of the experiment but not at the beginning), and colonization occurred in a higher number of replicates in the 0× treatment relative to the 1× and 2× clipped treatments ($X^2 = 8.31$, df = 2, $p = 0.02$; Appendix S1: Table S2), but not the 4× treatment ($X^2 = 0.4$, df = 1, $p = 0.53$; Appendix S1: Table S2).

In contrast to colonization, clipping frequency did not alter the number of genotypes lost from a plot (Figure 4b, Table 1). We observed a total of 41 extinction events during the experiment, and extinctions occurred in a similar number of plots across the 0×, 1×, 2×, and 4× treatments ($X^2 = 4.0$, df = 3, $p = 0.26$) (Appendix S1: Table S2).

We next examined whether reduced colonization in the clipped plots was connected to the effects of clipping on flowering effort. Clipping decreased the proportion of flowering shoots produced in the spring of 2018 (see inset in Figure 2, Appendix S1: Table S3). In May of

2018, the mean proportion of flowering shoots in the 0× treatment was three times higher than in the 1× or 2× treatments. However, by June of 2018, the mean proportion of flowering shoots for both the 0× and 1× plots was similar (~2% of all shoots and three times higher than the 2× plots), further suggesting that clipping delayed flowering effort. Strikingly, the density of flowering shoots in the recovering 4× plots (Spring 2018) was still lower than in the undisturbed (0×) plots, despite the fact that a year had passed since the last application of the 4× treatment (Figure 2, Appendix S1: Table S3). Overall, the percentage of plots in which we observed flowering was similar across all treatments ($X^2 = 1.33$, df $= 3$, $p = 0.72$) (Appendix S1: Table S2).

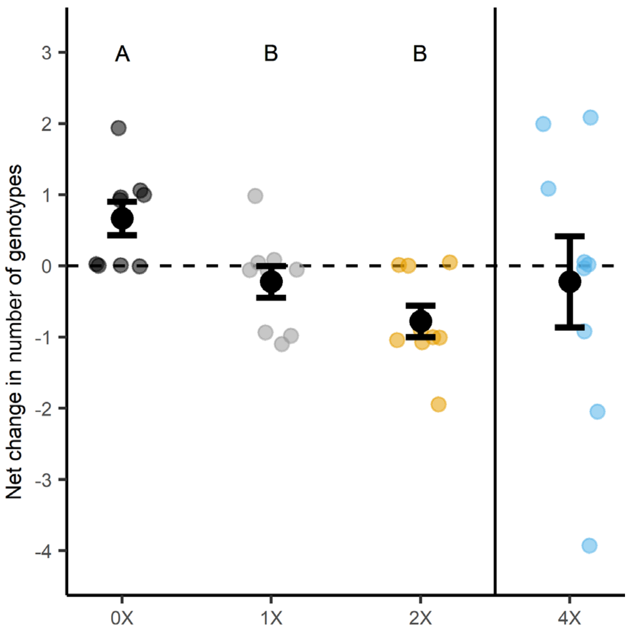

FIGURE 3 Net change in number of genotypes in response to clipping treatments in natural assemblages of *Zostera marina*. Colored points: individual replicates; black points: treatment mean. Y-bars are standard error of mean. The vertical black line reminds readers that we analyzed the results of the 4X treatment separately. Post hoc Tukey's comparison tests with a *p*-value equal to or less than 0.05 are indicated by capital letters

Some of the colonization events were due to vegetative spread or rafting of detached shoots into plots. Seven of the 36 colonization events ($n = 2$ plots in 0×, $n = 2$ plots in 1×, and $n = 3$ plots in 4×) were genetically identical to a rooted shoot that we genotyped in a neighboring plot located no further than 3 m away. Data from seed traps also provided evidence that rafting ramets had become established. We observed three cases of shoots being present in the seedling traps. We could not determine the genotypic identity of the sample in one of the three cases due to polymerase chain reaction (PCR) amplification failure, but the multilocus genotype of the shoots in the remaining two cases matched a genet within the block in which the trap was located, even though there were no rhizomal connections between shoots across the trap boundary. In both cases, the distance between the seedling trap to which the fragment dispersed and the nearest shoot of the parental genotype was less than 1 m. We never observed the recruitment of a seedling into our traps ($n = 9$ traps and 24 months of surveying).

TABLE 1 Statistical effects of initial richness and clipping treatment on response variables characterizing changes in genotypic richness in *Zostera marina*

			Clipping both seasons (Comparison: 0X, 1X, 2X)				Recovery of 4X (Comparison: 0X, 4X)			
Response	**Distribution (link)**	**Factor tested**	**Δ df**	**Δ Res dev**	***F* or X^2 (df)**	***p*-value**	**Δ df**	**Δ Res dev**	***F* or X^2 (df)**	***p*-value**
Net change in no. genotypes	Gaussian (identity)	Initial	1	0.86	2.06 (1, 21)	0.17	1	12.51	10.50 (1,14)	**<0.01**
		Treatment	2	8.74	10.41 (2, 21)	**<0.01**	1	0.60	0.50 (1,14)	0.49
		Interaction	2	1.44	1.71 (2, 21)	0.21	1	4.36	3.66 (1,14)	0.08
No. genotypes gained	Poisson (log)	Initial	1	14.93	14.93 (1)	**<0.01**	1	2.34	2.34 (1)	0.13
		Treatment	2	11.73	11.73 (2)	**<0.01**	1	0.13	0.13 (1)	0.72
		Interaction	2	3.03	3.03 (2)	0.22	1	2.09	2.09 (1)	0.15
No. genotypes lost	Poisson (log)	Initial	1	14.70	14.70 (1)	**<0.01**	1	19.17	19.17 (1)	**<0.01**
		Treatment	2	0.83	0.83 (2)	0.66	1	−0.01	−0.01 (1)	0.94
		Interaction	2	1.53	1.53 (2)	0.47	1	0.49	0.49 (1)	0.49

Note: Model selection is presented as analysis of deviance (test statistic: *F*-test and X² test for Gaussian and Poisson distributions, respectively). *p*-values less than or equal to 0.05 are in bold.

Abbreviations: df, degrees of freedom; initial, initial richness; Res dev, residual deviance.

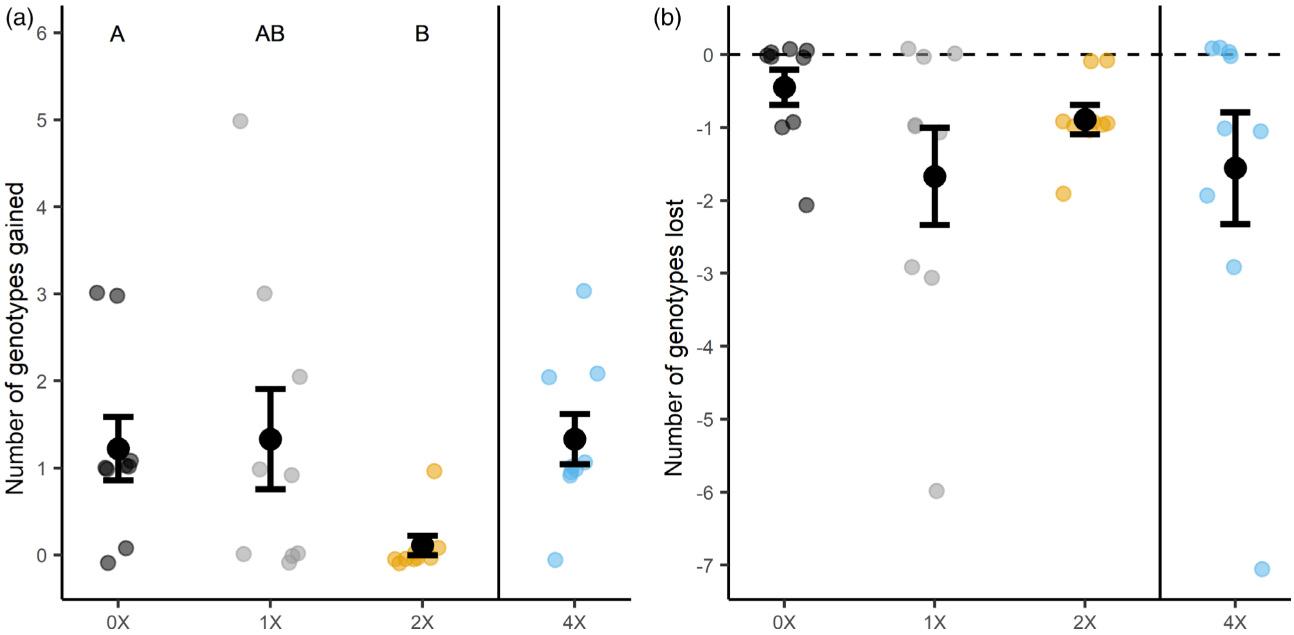

FIGURE 4 Effects of clipping treatments on number of genotypes (a) gained or (b) lost over time in natural assemblages of *Zostera marina*. Colored points: individual replicates; black points: treatment mean. Y-bars are standard error of mean. The vertical black line reminds readers that we analyzed the results of the 4X treatment separately. Post hoc Tukey's comparison tests with a *p*-value equal to or less than 0.05 are indicated by capital letters

DISCUSSION

We found that disturbance caused by simulating grazing across two seasons reduced genotypic richness. By deconstructing net changes in richness over time into the number of colonization and extinction events, we inferred that clipping did not drive genet mortality through the evolutionary mechanisms of selection or stochasticity (or, alternatively, that clipping-induced effects on these processes were too weak to result in differential extinction). This is surprising because we expected that clipping would select for more tolerant genotypes (Kollars et al., 2021), or that clipping-induced reductions in shoot density would increase stochastic loss. Rather than reducing richness through the mortality of genotypes already established in the population, we found that disturbance reduced the number of new genotypes that colonized clipped plots. This is also surprising given that disturbance both in *Zostera* meadows (Johnson et al., 2020; Reusch, 2006; Robertson & Mann, 1984) and within macrophyte populations more generally (e.g., Kimmerer & Allen, 1982) often facilitates sexual recruitment by reducing the competition-induced mortality of seedlings/sporelings. Interestingly, genotypic diversity recovered in the 4× treatment (a season of intense simulated grazing proceeded by a season of no simulated grazing) despite prolonged reductions in flowering effort, suggesting alternative mechanisms of colonization beyond localized seedling recruitment. We discuss several potential mechanisms underlying these unexpected results and interpret their implications for a feedback between disturbance, genotypic diversity, and resilience to that same disturbance agent.

We were particularly surprised that clipping did not increase genet extinction in our experiment. Indeed, our results contrast previous experiments demonstrating disturbance-driven loss of genets due to population bottlenecks (e.g., Whitney et al., 2019) or selection (e.g., Agrawal et al., 2012). Instead, most extinctions we observed across all treatments were of genets whose initial sampling abundance was less than 5% (data not shown). The more abundant genotypes typically persisted, even in the 4× treatment, where we observed severe reductions in shoot density after the first year. This high temporal stability of dominant genets is consistent with previous studies in *Zostera* showing greater turnover of rarer genets and that initial genotype richness strongly predicts final richness (Becheler et al., 2014; Reusch, 2006; Reynolds et al., 2017). The extinction of rare genotypes, regardless of treatment, is not surprising given that genets with few ramets likely have fewer reserves that can be shared intraclonally via belowground connections (reviewed in Song et al. [2013]). What is unexpected is that clipping did not act as a selection agent, especially given previous research showing genotypic variation for tolerance to clipping among genotypes collected from this site (Kollars et al., 2021). One possible explanation for the lack of discernible selection, despite genotypic variation for tolerance, is fluctuating selection generated by the temporally concentrated nature of the selective agent (e.g., Tiffin & Rausher, 1999). Grazing is seasonal and other selective agents may dominate during different times of the year. For example, heat tolerance may be important during the late summer, and we found in our previous work that warming and clipping favored distinct trait combinations (Kollars et al., 2021).

The observation of enhanced colonization in the absence of disturbance was also surprising, especially given that disturbance facilitating colonization is the cornerstone of multiple hypotheses predicting the relationship between disturbance and diversity (Connell, 1978; Goodsell & Connell, 2005; Sousa, 1979). This result also contrasts with previous studies suggesting that physical disturbance increases eelgrass genotypic diversity by facilitating seedling recruitment (Foster et al., 2021; Reusch, 2006; Zipperle et al., 2010). The reductions in flowering effort we observed in clipped treatments (see also Shaughnessy et al. [2021]) might partially explain reductions in colonization if the colonizing genets are new seedlings, especially given that contributions to the seed bank come from both local and distant sources (Furman et al., 2015; Harwell & Orth, 2002; Ruckelshaus, 1998; Zipperle et al., 2010). However, the magnitude of local seed production is likely not the only process influencing the number of genets gained in our experiment. Colonization in the 4× and 0× treatments was equivalent by the end of the experiment despite significant differences in local flowering effort. One possible explanation for this is that the 4× treatment was the only treatment severe enough to sufficiently reduce competition by reducing shoot densities and, thus, facilitate the survival of new seedlings. Indeed, previous studies showing the importance of disturbance-mediated seedling recruitment to diversity involved severe reductions in shoot densities due to whole-shoot mortality (Reusch, 2006; Rivers & Short, 2007). Another possibility is that the 4× treatment was more prone to invasion by the asexual spread of genets from outside of the plots. We can confirm that at least seven colonization events were from vegetative spread or rafting of detached shoots, but this number is likely higher because we did not sample all the genets that bordered a plot at the beginning of the experiment.

Though we cannot conclusively explain why we observed higher colonization in the 0× plots, we propose multiple possibilities. Increased flowering effort in the 0× treatment may have increased the density of seedlings due to localized seed dispersal (reviewed in Kendrick et al., [2012]). However, the observation of flowering in plots in which we did not record colonization, and the high level of colonization despite low flowering effort in the 4× treatment means this cannot be the sole explanation. Another possibility is that clipping an emerging seedling could directly increase mortality, thereby reducing the number of successful sexual recruits (but not affecting the arrival of colonists per se). This could explain why colonization did not differ between the 0× and 4× treatments given that we did not clip the 4× plots during the second year of the experiment. A final alternative is that clipping decreases facilitative interactions among shoots that buffer environmental stress above ground (e.g., desiccation) or below ground (e.g., sulfide toxicity) (Dooley et al., 2013). Lack of facilitation could, for example, explain the absence of seedlings in our experimental traps, despite evidence of colonization in adjacent plots.

Though our results deviated from our initial expectations, the conditions that led to these outcomes occur in a wide range of macrophyte and sessile animal populations and communities. For example, disturbance will often have minimal effects on extinction if individuals can regenerate biomass lost to disturbance (Hulme, 1996), directional selection for tolerance to biomass loss is weak or fluctuating (e.g., Kollars et al., 2021; Tiffin & Rausher, 1999), or intraclonal resource sharing buffers against genet extinction (reviewed in Song et al. [2013]). We also predicted that disturbance would decrease colonization in systems in which there is temporal overlap of the establishment of colonists and the disturbance event or if colonists are more vulnerable to disturbance than established individuals. Reduced colonization with disturbance will also be common when adult plants facilitate localized seed trapping and increase seedling survival via environmental buffering (reviewed by Filazzola & Lortie [2014]). In contrast, if colonization and disturbance are temporally separated, disturbance may be more likely to increase diversity (e.g., Sousa, 1979). Importantly, however, we only detected effects of disturbance on diversity by explicitly quantifying net change in richness and deconstructing those changes into colonization and extinction effects. As suggested by Hughes et al. (2007), we would not have discovered a relationship between disturbance and diversity if we had examined the effects of clipping on final richness alone. Though it is possible to alleviate this problem by experimentally controlling for initial richness, such a design comes at the cost of ecological relevance, especially in systems composed of mosaic patches of differing levels of diversity.

Our experiment investigated the effects of disturbance over a 2-year period. Developing projections for the long-term consequences of disturbance on the maintenance of genotypic diversity requires understanding how genotypic diversity reciprocally influences the realized impact of disturbance (Hughes et al., 2007). In synthesizing our work with Hughes and Stachowicz (2004) specifically, we suggest the potential for feedback between grazing disturbance by Brant geese and genotypic diversity such that standing diversity increases resilience to grazing but grazing modestly reduces diversity by decreasing or delaying seed production. This feedback could result in lower resilience to future disturbance in the absence of other ecological or evolutionary processes that counteract the modest reductions in genotypic diversity due to grazing. The consequences of this feedback for naturally grazed *Zostera* populations requires further investigation, including documenting the spatial extent of grazing impact on *Zostera* life history. We also encourage future researchers to broaden the framework for the study of eco-evolutionary dynamics by recognizing that feedbacks between ecology and evolution extend beyond the effects of ecological processes on selection alone. Disentangling the complexities of multiple eco-evo processes operating in natural populations is essential to understanding the maintenance of genotypic diversity.

AUTHOR CONTRIBUTIONS

Nicole M. Kollars and John J. Stachowicz conceived the study. Nicole M. Kollars conducted the experiment, performed statistical analysis, and wrote the manuscript with significant input from John J. Stachowicz.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Kollars, 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.6011003.

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SUPPORTING INFORMATION

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