



Native and invasive bunchgrasses have different responses to trail disturbance on California coastal prairies

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Abstract Ecosystems often experience small-scale disturbances through recreational foot and bike traffic. The intermediate disturbance hypothesis predicts that frequent disturbances in grasslands can negatively impact native species and lead to invasion by disturbance-adapted, non-native species. Disturbance studies often examine intentional or unintended larger scale disturbances, but do not commonly focus on common small-scale disturbances such as those caused by trampling along trails. As such, we were interested in how trail disturbance affects the vegetative growth and reproductive output of *in situ* native (*Danthonia californica* Bol. and *Stipa pulchra* Hitchc.) and invasive (*Dactylis glomerata* L. and

Holcus lanatus L.) perennial bunchgrasses commonly found on California coastal prairies. We measured the basal circumference and seed production of plants located on-trail and off-trail on five coastal prairies in Santa Cruz, CA, USA. We hypothesized that native grasses located on-trail would have lower growth and reproductive output and non-native grasses would be unaffected. We found that native and non-native plants had differences in growth and reproductive output on-trail and off-trail. *S. pulchra* had lower reproductive potential (via culm sterility) with trail disturbance, whereas both native grasses showed evidence of compensatory growth on-trail. Invasive non-native *D. glomerata* and *H. lanatus* growth was unaffected by trail disturbance, but *H. lanatus* had lower reproductive output on-trail. Results suggest that it may be prudent to restore trails with disturbance tolerant species like *D. californica* and use less tolerant species like *S. pulchra* further into the central habitat space.

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Introduction

California coastal prairies range across a thin sliver of land along the coastline in the California Floristic Province from southwest California to southwest

Oregon. California is a biodiversity hotspot, and coastal prairies are important conservation areas with high species richness. Coastal prairies are often considered the most diverse grassland type in North America, supporting over 400 endemic plant species as well as numerous animal and invertebrate species, many of which are endemic, rare, or endangered (Stromberg et al. 2001; Ford and Hayes 2007; Cornelisse et al. 2013; Eviner 2016). Historically, these native grasslands were highly productive and optimal for grazing (Ford and Hayes 2007; Huntsinger et al. 2007), but overgrazing in the early 1900s has degraded and reduced the extent of remnant prairies. Coastal prairie habitats are also impacted by species invasion, fragmentation, and development (Bartolome et al. 2004; Stromberg et al. 2001). Most annual species senesce and produce seed in late spring to early summer to avoid dry and stressful conditions. In contrast, native perennial grasses persist and grow later into the summer using tap roots to access groundwater (Corbin et al. 2005; Eviner 2016; Parker and Schimel 2010). In summer, these native perennial bunchgrasses senesce aboveground and then break dormancy and reemerge from the root tussock when rains resume in fall when there are sufficient resources for growth (Eviner 2016; Morghan et al. 2007). However, when perennial grasses such as *Stipa pulchra* Hitch. (Poaceae) and *Danthonia californica* Bol. (Poaceae) are outcompeted for light, they are less able to develop sufficient root structures to access deeper soil moisture, thereby reducing their ability to withstand summer drought (Buisson et al. 2006).

California native grasslands have been reduced in habitat size due to high levels of disturbance and intensified novel competition resulting from non-native species invasion (Corbin and D'Antonio 2010; Foin and Hektner 1986). Invasion by non-native species can alter biotic interactions (Green et al. 2011) and make it more difficult for native species to establish propagules (Pedrini et al. 2020). Abundance of native bunchgrasses in California such as *S. pulchra* and *D. californica* have been declining over time (Dasmann 1965; Schiffman 2007). Although native bunchgrasses can withstand competition when they are established (Corbin and D'Antonio 2004), they are sensitive to competition during seedling growth phases or when facing additional environmental stressors such as drought or physical disturbance (Jutila and Grace 2002). *D. glomerata* L. (Poaceae)

and *H. lanatus* L. (Poaceae) are opportunistic, non-native perennial species well-adapted to a variety of environmental conditions. These non-native species are especially invasive in California coastal prairies due to their affinity for coastal Mediterranean climates that experience fog (Foin and Hektner 1986; D'Antonio et al. 2007). For example, Corbin and D'Antonio (2005) found that *H. lanatus* was able to take advantage of summer fog. Further, *D. glomerata* and *H. lanatus* have likely been released from natural enemies and diseases that limit productivity in their native range (D'Antonio et al. 2007; Malmstrom et al. 2005; Liu and Stiling 2006).

The intermediate disturbance hypothesis suggests that the level of highest diversity is maintained at intermediate levels of disturbance (Connell 1978). Moderate levels of disturbances, including anthropogenic disturbances, trampling, and grazing are necessary to maximize species richness and maintain grassland biodiversity (Connell 1978; Hayes and Holl 2003; Yuan et al. 2016). Small and infrequent disturbances do not create enough impact to maintain ecosystem dynamics while extreme disturbances can result in succession from grassland habitat into woodland habitats or facilitate plant invasion (Zavaleta and Kettley 2006; Luong 2022; Haan and Landis 2019; Van Auken 2009).

California grasslands were historically maintained with periodic disturbance regimes through grazing and prescribed indigenous burns (Anderson 2007; Ford and Hayes 2007). However, neither non-periodic nor frequent disturbances are functionally similar to intermediate disturbance, and they can facilitate species invasion by altering the competitive dynamics within a plant community (Luong 2022; Haan and Landis 2019; Van Auken 2009; Peltzer and Wilson 2006). Frequent trampling could reduce the growth of a particular species that was able to previously preclude invaders (Graff 1983; Jutila and Grace 2002). For example, *S. pulchra* reproduction and recruitment decreased after frequent herbivory disturbances from small mammals (Eviner 2016). Reduced recruitment of foundational species like *S. pulchra* can leave the system vulnerable for shifts in dominance and allow for species invasion (Corbin and D'Antonio 2004; Schiffman 2007; D'Antonio et al. 2016). Intermediate levels of trampling, soil compaction, and soil crust disruption can help maintain grassland communities, while high levels of trampling can cause grassland

degradation (Graff 1983; Xiao et al. 2018). For example, trampling related disturbance disrupts soil crusts and can improve germination by improving seed-to-soil contact. In another example, Xiao et al. (2018) found that trampling by grazers reduced the seed production and photosynthetic rates of grassland plants in China. Trail disturbances may also cause reproductive failure and increased seed sterility in plants through direct (Graff 1983; Fernández Alés et al. 1993), or indirect effects like pollinator limitation (Wilcock and Neiland 2002). For example, Conradi et al. (2015) and Xiao et al. (2018) found that plants had reduced reproductive output along trails or after trampling.

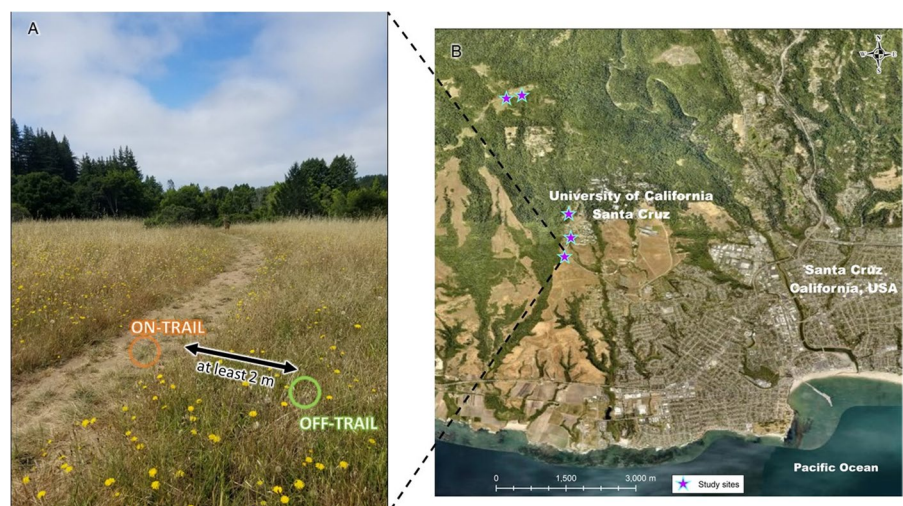
Disturbances such as trampling, soil compaction, development, and grazing can be concerning for restoration managers because they can contribute to species invasion (Bartolome et al. 2004; Luong 2022). Invasive species can overwhelm native ecosystems with high propagule pressure (Byun et al. 2015) leading to overcrowding and intense competition and eventually cause extirpation of rare and sensitive plant species (Holl et al. 2022). Human foot traffic and bike traffic are common disturbance types at restoration and conservation areas, but their effects on plant communities are not often examined. Our study aims to provide insight on the impacts of trail disturbances on the vegetative growth and reproductive capabilities of four ubiquitous coastal California bunchgrasses: native *S. pulchra* and *D. californica*, and invasive non-native *H. lanatus* and *D. glomerata*. We focused on these four species because they

are dominant across coastal prairies in California. We assessed the growth (basal circumference) and reproductive output (flowering culms and proportion of sterile culms) of the four species across five remnant coastal prairies in Santa Cruz, CA, USA. We expected that native bunchgrasses would be more negatively affected in overall size and reproduction compared to the non-native plant species.

Methods

Our study was completed at five remnant coastal prairie sites that were physically separated by a forest edge or paved roads located at the University of California, Santa Cruz, USA, ranging from three to six kilometers from the Pacific Ocean (Fig. 1). The climate across the study area is Mediterranean with hot, dry summers, cool, wet winters, and peak plant biomass in late spring. Plants in this system regularly experience summer fog, which can contribute to a plant's usable water during the dry season (Corbin et al. 2005) and reduce heat stress through shading (Baguskas et al. 2018). Our study sites are located on the unceded territories of the Awaswas-speaking Uypi Tribe, where their descendants the Amah Mutsun Tribal Band, are working towards restoring traditional stewardship practices and heal from historical trauma; historically these sites were previously stewarded with prescribed fire and harvest practices prior to Spanish colonization.

Fig. 1 **A** A photo of one of the study sites with an example of the study design and **B** a map depicting the five study sites located on the University of California, Santa Cruz



The dominant native vegetation in these coastal prairies consists of *Bromus carinatus* Hook. & Am. (Poaceae), *D. californica*, *Lupinus nanus* Benth. (Fabaceae), *Sidalcea malviflora* (DC.) A. Gray (Malvaceae), *Sisyrinchium bellum* S. Watson (Iridaceae), and *S. pulchra*. Non-native species such as *Avena barbata* Pott ex Link (Poaceae), *Bromus diandrus* Roth (Poaceae), *D. glomerata*, *Festuca bromoides* L. (Poaceae), *H. lanatus*, and *Hypochaeris radicata* L. (Asteraceae) also have high cover in these areas.

At each site, we marked 10 individuals from each species on-trail and 10 plants off-trail that were measured throughout the experiment. Trail disturbance was classified as areas that experienced periodic disturbance from walking, jogging, or biking along designated dirt trails. On-trail plants were directly on the trail path, selected haphazardly and were at least five meters apart. Off-trail plant selection was randomized by flipping a coin into the grassland and choosing an individual of the targeted species closest to where the coin landed at least two or more meters away from the trail towards the interior of the area of the habitat (Fig. 1). We consider the level of the disturbance on the trail as intermediate, as they were still vegetated and irregularly received periodic disturbance. Off-trail areas were considered low or infrequent disturbance areas. In 2019 and 2020 we quantified the basal circumference, number of flowering culms, and number of sterile flowering culms for perennial native grasses *D. californica* and *S. pulchra*, and non-native grasses *D. glomerata* and *H. lanatus*. Sterile flowering culms were identified as culms that (1) were absent of chlorophyll, (2) had discolored seeds, and (3) had seeds that were visibly smaller than seeds on nearby stalks (Abdullah et al. 2001). Sterile culm proportion was calculated for each individual as the proportion of sterile culms out of total flowering culms multiplied by 100.

We used an analysis of variance (ANOVA) to compare species specific differences and t-tests to evaluate the paired effects of on- and off-trail positioning. Pairwise differences from ANOVAs were tested with Tukey's honest significant difference. Our study was not focused on site effects, so we conducted an ANOVA to confirm that there were no site effects on basal circumference, flowering culms, or proportion of sterile flowering culms ($p > 0.05$) before conducting our analyses. Similarly, t tests were used to determine that there were

no significant year effects ($df = 14.20$, $t = 1.099$, $p = 0.290$). Data were tested for parametric assumptions such as normality and homogeneity of variances prior to using parametric analyses. To meet parametric requirements of normality and homoscedasticity we took the square root of natural log transformed metrics ($[\ln(x)]^{1/2}$) for growth, flowering culms, and sterile culm proportion. Sterile flowering culms were only compared for individuals that produced flowering culms. All data were back transformed for visualization. Analyses were completed using R studio (V3.6.1; R Core Team 2020) and maps were created with ArcMap (V10.8.2).

Results

We found that native and non-native perennial bunchgrasses had differences in basal circumference ($df = 3$, $F = 8.75$, $p < 0.001$) and proportion of sterile flowering culms ($df = 3$, $F = 22.56$, $p < 0.001$), but not average total flowering culms ($df = 3$, $F = 0.498$, $p = 0.688$). Post-hoc comparisons indicated that *Danthonia californica* had greater average basal circumference compared to *Holcus lanatus* ($p < 0.001$; Fig. 2) and *Stipa pulchra* ($p < 0.001$), but not *Dactylis glomerata* ($p = 0.129$). There were no other species differences in basal circumference. *S. pulchra* had more sterile flowering culms compared to *D. californica* ($p < 0.001$) and non-native grasses *D. glomerata* ($p < 0.001$) and *H. lanatus* ($p < 0.001$). The two non-native bunchgrasses had no observed sterile flowering culms.

On-trail individuals of *S. pulchra* had greater basal circumference compared to off-trail individuals ($df = 243$, $t = -2.304$; Fig. 3). The basal circumferences of *D. californica* ($df = 251$, $t = -0.296$) and the two invasive non-native species, *D. glomerata* ($df = 88$, $t = 0.710$) and *H. lanatus* ($df = 126$, $t = 0.749$) were not affected by trail disturbance (Fig. 3).

Flower culm production for native *D. californica* ($df = 251$, $t = 0.011$, $p = 0.991$) and *S. pulchra* ($df = 250$, $t = -0.332$, $p = 0.741$), and non-native, *D. glomerata* ($df = 79$, $t = 1.056$, $p = 0.292$) was not affected by trail disturbance. Flower culm production was lower for on-trail *H. lanatus* individuals ($df = 118$, $t = 3.465$, $p < 0.001$; Fig. 4).

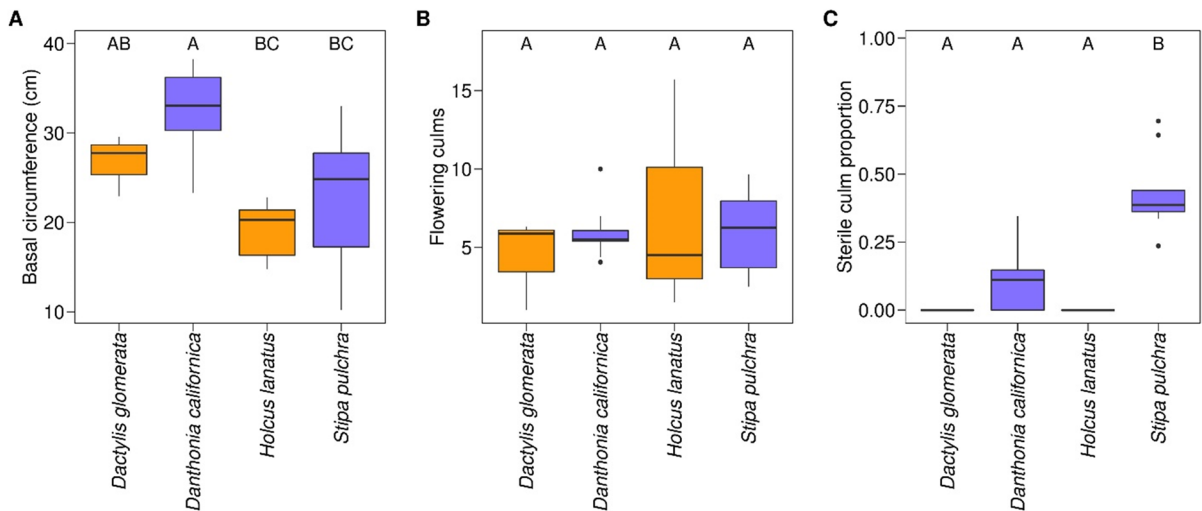


Fig. 2 **A** average basal circumference, **B** average flower culms, and **C** proportion of flowering culms that were sterile for four perennial bunchgrasses. Letters represent statistical groups of each species and non-overlapping letters represent significant differences ($p < 0.05$) between species. Sterile culm proportion was calculated as the proportion of culms that were

sterile. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers. Native species are in purple and non-native species are in orange

Fig. 3 Basal circumference for individuals off-trail (green) and on-trail (brown) of perennial bunchgrasses that are native: **A** *D. californica*, **B** *S. pulchra* or non-native **C** *D. glomerata*, **D** *H. lanatus*. Data were sqrt ln-transformed for analyses but back-transformed for representation. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers

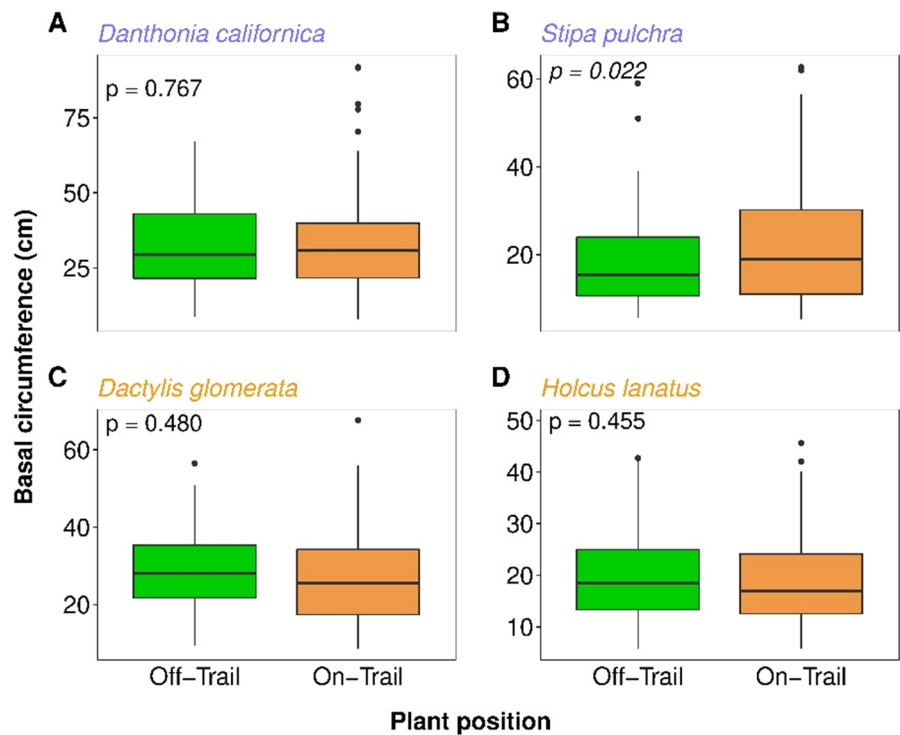


Fig. 4 Flower culm production for individuals off-trail (green) and on-trail (brown) of perennial bunchgrasses that are native: **A** *D. californica*, **B** *S. pulchra* or non-native **C** *D. glomerata*, **D** *H. lanatus*. Data were sqrt ln-transformed for analyses but back-transformed for representation. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers

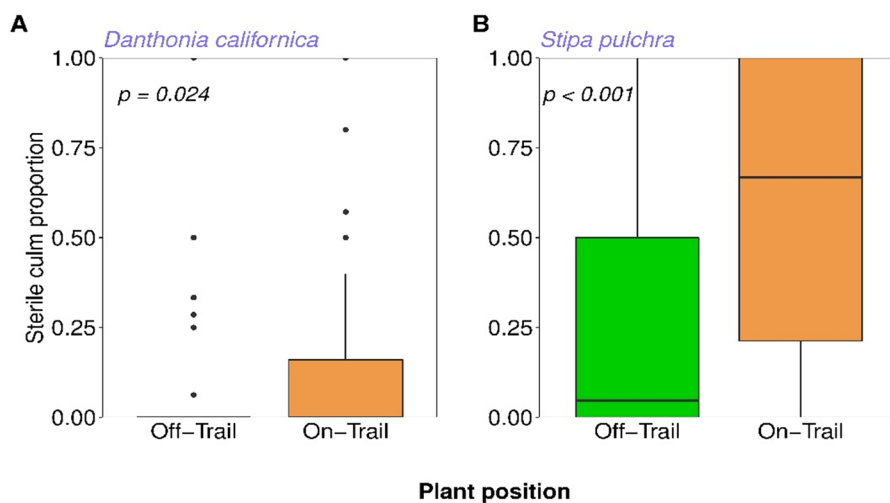
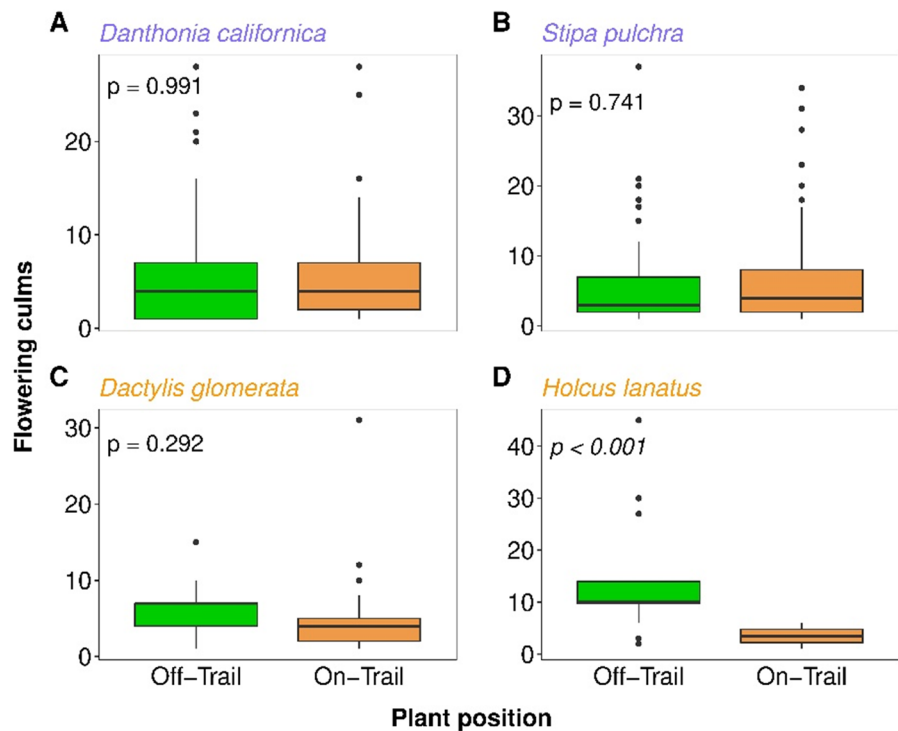


Fig. 5 Sterile flower culm proportion of native perennial bunchgrasses **A** *D. californica* and **B** *S. pulchra* for individuals off-trail (green) and on-trail (brown). Non-native grasses were not observed producing any sterile flowering culms. Sterile culm proportion was calculated as the proportion of culms that

were sterile. Data were sqrt ln-transformed for analyses but back-transformed for representation. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers

Although *S. pulchra* had a higher proportion of sterile flowering culms (under-developed seed culms) produced compared to *D. californica* (Fig. 2), both *S.*

pulchra (df = 91, $t = -3.373$, $p < 0.001$) and *D. californica* (df = 128, $t = -2.282$, $p = 0.024$; Fig. 5) had a higher proportion of sterile flowering culms for

on-compared to off-trail individuals. Non-native *D. glomerata* and *H. lanatus* did not produce any sterile seed culms.

Discussion

Our study is one of the first to explore the role of trail disturbance on plant community dynamics and demonstrates that human trail disturbance affects native and non-native bunchgrass species differently in remnant coastal prairies. Our work demonstrates that the intermediate disturbance hypothesis can be useful in informing community dynamics and management implications. We found that trail disturbance benefited basal growth for *Stipa pulchra* but negatively impacted reproduction for native *S. pulchra* and *H. lanatus*. *D. glomerata* and *D. californica* were mostly unaffected by trail disturbance, suggesting that interspecies differences may result in different disturbance adaptation strategies. As a result, interspecies differences may influence competitive dynamics between native and non-native perennial grasses leading to decreased dominance of *S. pulchra* on-trail. Based on our findings, we suggest that California coastal prairies may need additional management in areas that face high levels of human foot and bike disturbance, and that adaptive management can take advantage of differential species responses to trail disturbance to optimize conservation efforts.

Trail disturbance and reproduction

Trail disturbance significantly increased the proportion of sterile flower culms produced by *Stipa pulchra*, and we observed more sterile flowering culms for *S. pulchra* compared to non-native *D. glomerata* and *H. lanatus*, which both had no observed sterile flowering culms. While *D. californica* did produce sterile flowering culms, it was sporadic and significantly less compared to the other native, *S. pulchra*. Increased sterility of flowering culms for *S. pulchra* is supported by Conradi et al. (2015) and Xiao et al. (2018), in which they found that only plants located near trampling disturbance had significantly decreased responses in seed dispersal and regeneration (Graff 1983). *H. lanatus* had reduced flower culm production on trails, which suggests this species may be of less concern for targeted management along

disturbance corridors compared to invasive species that are unaffected by trail disturbance like *D. glomerata*.

Competitive dynamics with non-native species may also be influencing sterile flowering culm production of *S. pulchra*. Hamilton et al. (1999) found that non-native annual species competitively suppressed the seed output of mature *S. pulchra* individuals through a reduction in the number of inflorescences per plant. Furthermore, Ikeda (2003) found that in the short-term trampling decreases species richness and that some species are more tolerant to trampling than others. Over longer temporal spans, Ikeda (2003) found that competition had a greater influence over species composition compared to trampling. Similarly, we speculate that trail disturbance in our study may be directly and indirectly affecting competitive dynamics between native and non-native bunchgrasses and community composition. Therefore, there is a possibility that disturbance is enhancing the ability of unaffected *D. glomerata* to compound sterile culm production by *S. pulchra* observed on trails. Corbin and D'Antonio (2010) provide further support for this explanation, as they found that the presence of invasive non-native perennials reduces native grass growth, productivity, and seed production, whereas non-native perennial grass productivity is unaffected by native grasses. Trail disturbance may not be a severe enough disturbance to create shifts that impact the community (Graff 1983; Ikeda 2003), while invasive competition has been documented to strongly alter community dynamics (Green et al. 2011; Drenovsky et al. 2012; D'Antonio et al. 2016). To further enhance the growth of *D. californica*, Buisson et al. (2006) found that removing topsoil and the existing invasive seedbank maximized the survival of *D. californica* transplants and increased their biomass regardless of grazing treatment, which demonstrates that reducing competition from the seedbank was more effective in promoting *D. californica* compared to intermediate disturbances like grazing. Buisson et al. (2006) results also indicate that *D. californica* is tolerant of intermediate disturbance and, again, that competitive dynamics were more important than disturbance. Similarly, Graff (1983) found lower seedling emergence where competition was not reduced regardless of grazing treatment, but seedling density was higher where competition was reduced. However, timing of rainfall, rather

than total annual rainfall, is the most limiting factor in seed production, germination, and grassland diversity (Loik et al. 2004; Graff 1983; Groves et al. 2020), suggesting that a combination of regimes along with seasonality are prominent influences.

Compensatory growth

Although there is extensive research on the impacts of certain disturbances on coastal grasslands (Li et al. 2007; Haan and Landis 2019; Luong 2022; Bartolome et al. 2004), smaller facets of disturbance such as human trail disturbance are largely unexplored. Contrary to our predictions that both native species would have reduced basal circumference on-trail, *D. californica* was unaffected and *S. pulchra* had increased growth. Our results indicate that productivity and vegetative growth of *S. pulchra* benefit from intermediate trail disturbance through strong compensatory growth that results in higher basal circumference on trails. Other studies also found that disturbance from moderate grazing can improve *S. pulchra* growth (Larios and Hallett 2022; Valliere et al. 2019), although frequent overgrazing can be detrimental (Ford and Hayes 2007; Xiao et al. 2018; Dasmann 1965). Our results suggest that the benefit and harm that can come from intermediate trail disturbance are dependent on which plant characteristic is evaluated because we found on-trail individuals had higher basal circumference but greater culm sterility.

In contrast to *S. pulchra*, the basal circumferences of *D. californica* and the two non-native species were found to be unaffected by trail disturbance. This suggests the productivity (via basal circumference) of these species is less responsive to trail disturbance compared to *S. pulchra*. One reason *D. glomerata* growth may not respond negatively to trail disturbance is because it may be adapted to high levels of disturbance since it has been commonly used as grazing forage for many years (Etherington 1984). *D. californica* may not have been affected by trail disturbance through compensatory growth in response to defoliation from on-trail human activity and disturbance (Buisson et al. 2006). Certain plants under defoliation stress can exhibit compensatory growth through their ability to increase uptake and allocate resources for new and accelerated leaf growth (Venter et al. 2020). This is especially true regarding native perennial grasses' ability to use fog water

inputs during summer drought as well (Corbin et al. 2005). Others found species differences in compensatory growth responses were dependent on water availability, which can be influenced by trampling via soil compaction (van Staalduinen and Anten 2005), thereby reducing water infiltration for plant water use (Morghen et al. 2007). When plants are faced with disturbance, they may respond by optimizing survival and shifting resources away from reproduction and redirecting them toward growth instead. This would then result in plants producing fewer seeds or a greater proportion of sterile seeds, as observed in our study for both *S. pulchra* and *H. lanatus*. Plants that produced sterile flowering culms could be exhibiting a trade-off between reproduction and some other trait, such as growth or stress tolerance (Abdullah et al. 2001). This was true for natives, *S. pulchra* and *D. californica*, which showed evidence of compensatory growth for basal circumference and more sterile seed culms. Reduced reproductive potential (via increased sterility) is a concern for restoration practices and management because the ability of native species to reproduce and establish elsewhere is critical in enhancing declining populations (Pedrini et al. 2020; Luong et al. 2019). Therefore, where climatically feasible, use of *D. californica* instead of *S. pulchra* for restoration where trail disturbance is high may be more efficient since *D. californica* did not exhibit reduced reproductive output on-trails.

In terms of species differences, there may be differences in our study species' ability to store and reallocate resources and grow new tissue to increase photosynthetic capacities (Hamerlynck et al. 2016). Understanding species differences for stress tolerance to trampling and other trail disturbances is important for restoration management as these disturbances are typically widespread and unpreventable. According to Caldwell et al. (1981), differences in stress tolerance may be explained by differences in species characteristics such as amounts of carbon and nitrogen in foliage and reserves, photosynthetic rates, leaf water-use efficiency, replacement rates of photosynthetic tissues following defoliation, amount of soluble carbon and nitrogen reserves, allocation of plant resources in the event of defoliation, and provision of meristematic tissues for regrowth. Both *D. californica* and *D. glomerata* were relatively unaffected by trail disturbance, and interestingly, they both had higher basal circumference compared to affected species which could

have increased the plant's ability to access available water during the warmer season (Hamilton et al. 1999). Thus, it is possible that *D. californica* and *D. glomerata* have other adaptations (not assessed within our study) that allow them to resist disturbance from trail trampling.

Native coastal prairie management and trail disturbance

Results indicate that coastal prairie habitats may benefit from intermediate trail disturbance because trail disturbance did not negatively affect the growth of *D. californica* or *S. pulchra* albeit increasing sterility for *S. pulchra*, while reducing the reproductive output of the invasive *H. lanatus*. Increased sterility of flowering culms on-trail for *S. pulchra*, a commonly restored species, may indicate that it will be most effective to reintroduce and manage this species off-trail where there is less frequent disturbance. On the other hand, *D. californica* was largely unaffected by trail disturbance in our study, suggesting that this species is more resilient in establishing self-sustaining populations along trails. As such, *D. californica* could be used strategically to restore trails and increase native species in on-trail community composition, reducing establishment space for invasive non-native species like *H. lanatus* that exhibit reduced flowering production on trails. Furthermore, when resources are limited, it may be best to focus limited management efforts on species less affected by trail disturbance. For example, because we found *H. lanatus* had reduced flower culm production on trails, invasive species control may be more useful for unaffected species like *D. glomerata*.

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Author contributions JL conceived the research question and experimental design, analyzed the data and standardized writing styles in the manuscript. JL and TB collected the data. EV led writing with contributions from TB and JL.

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Data Availability Data are available at <https://doi.org/10.1594/PANGAEA.950233> (Luong et al. 2022)

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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