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RESEARCH ARTICLE

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# Moisture availability and ecological restoration limit fine fuels and modelled wildfire intensity following non-native ungulate removal in Hawaii

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## Abstract

1. The removal and exclusion of non-native ungulates for conservation of biodiversity is common globally, including on tropical Pacific Islands. However, the poorly quantified effects of ungulate exclusion on fuels and wildfire may represent an important conservation trade-off.
2. We measured fuels (live and dead fuel loads, type, height and continuity) and modelled potential wildfire behaviour (flame height and rate of spread) inside and outside of 13 ungulate exclosures, three of which received active ecological restoration (e.g. planting of native shrubs and trees), across a 2,740 mm mean annual rainfall (MAR) gradient on the Island of Hawaii. Differences in fuel characteristics and modelled wildfire behaviour inside versus outside of ungulate exclosures were assessed using linear mixed effects analyses.
3. Non-native ungulate removal, in general, increased fine fuel loading (average change ranged from −0.7 to 11.3 Mg/ha), shrub fuel loading (−0.1 to 5.6 Mg/ha) and modelled flame lengths (−0.2 to 1.9 m). Post-removal fine fuel loading and modelled flame lengths increased linearly and positively with moisture availability, by as much as 56% in the wettest sites. Dead fine fuels, a key driver of fire intensity and combustion rates, also increased with ungulate removal. Sites undergoing active ecological restoration exhibited reductions in fuel loading, with greater reductions over time since ungulate removal; by the 10th year following ungulate removal, fine fuel loading was reduced at restoration sites by 41%.
4. *Synthesis and applications*. Dry and mesic environments where wildfire occurrence is more frequent are of particular concern following non-native ungulate removal, but with drought even typically wet environments can be at high risk of wildfire following ungulate removal. Given limited resources, managers in mesic and wet forests might focus first non-native ungulates in non-native grass-dominated areas that contribute disproportionately to wildfire spread and are adjacent to fenced higher value areas, while managers in dry to mesic areas might focus on removing non-native ungulates. Where possible, land managers in all situations should invest in long-term fuel management strategies such as active ecological restoration to reduce fuel loads and the occurrence and intensity of wildfires.

**KEYWORDS**
ecological restoration, mean annual rainfall gradient, non-native grass-fire cycle, Pacific Island Region, ungulate removal, wildfire management

## 1 | INTRODUCTION

Ecosystems are threatened globally by increased frequency and severity of wildfires (Krawchuk et al., 2009). Wildfire activity globally is a dynamic ecological process that in many contexts poses a significant risk to human health and safety (Bowman et al., 2017), biodiversity (D'Antonio & Vitousek, 1992), watershed conservation (Ice et al., 2004; Trauernicht et al., 2018), primary productivity (Hawbaker et al., 2017; Lecomte et al., 2019) and other ecosystem goods and services (Moritz et al., 2014). In turn, wildfires are a widely distributed natural disturbance that plays an important role in many native ecosystems and can be a net benefit to overall ecosystem services (Pausas & Keeley, 2019). Despite increased investment in wildfire management, mitigating wildfire risk and allocating limited fuel management resources remain significant challenges (Stephens & Ruth, 2005).

Non-native ungulate herbivores (also referred to as feral ungulates) are also an increasingly important management challenge globally, with important but understudied consequences for wildfire activity and management (Archibald & Hempson, 2016; Beschta et al., 2013; Krawchuk et al., 2009). Domestic and non-native ungulates can reduce fine and woody fuel loads through grazing and browsing, and increase the discontinuity of the fuel bed (Kellner et al., 2011), therefore affecting the frequency, intensity and severity of wildfires (Archibald & Hempson, 2016; Belsky, 1992; Trauernicht et al., 2013). Meanwhile, managed grazing in native and non-native grasslands by domestic livestock can reduce fuel loads and modelled wildfire intensity over temporal scales of months to several years (Blackmore & Vitousek, 2000; Diamond et al., 2010; Evans et al., 2015; Leonard et al., 2010; Velamazán et al., 2018).

The benefits of ungulate grazing and browsing for fuel reduction often conflict with conservation objectives because of the many documented negative impacts of non-native ungulates on biodiversity and other ecosystem services. Ungulates, particularly non-native ungulates introduced into ecosystems not adapted to ungulate herbivory, can cause substantial ecological degradation through the direct effects of grazing, browsing, trampling and bark stripping on individual plant species and communities of high conservation value (Parker et al., 2006; Ramirez et al., 2019; Velamazán et al., 2020; Wardle et al., 2001). Ungulate activity can also indirectly impact ecosystem processes such as hydrology and nutrient cycling and, if population densities are high enough, cause severe habitat degradation, soil erosion and native species population declines (Chynoweth et al., 2013; Cole & Litton, 2014; Hobbs, 1996; Long et al., 2017; Siemann et al., 2009; Wehr et al., 2018). In response to these negative impacts, fencing and removal of non-native ungulates is an increasingly common global strategy for conserving and restoring native biodiversity (Beever et al., 2008; Cole & Litton, 2014; Hess, 2016; Kay & Bartos, 2000; Shono et al., 2007; Spear & Chown, 2009). These efforts have been highly effective at reducing ungulate densities within management units, with important conservation benefits in most cases. However, ungulate removal can increase the cover of both native and non-native plants due to release from top-down control, especially at sites with a substantial non-native plant presence at the time of ungulate removal (Cabin et al., 2000; Cole et al., 2012; Kellner et al., 2011; Parker et al., 2006; Stone et al., 1992). Given prior observations and studies demonstrating that ungulates can reduce wildland fuels, the practice of removing non-native ungulates for conservation purposes raises important questions about the potential implications of removal for fuel accumulation and wildfires (Trauernicht et al., 2013).

The degree to which ungulate removal impacts wildland fuels and wildfire behaviour remains largely unquantified, particularly when considered in the context of climatic variability. Wildfire and herbivores are competing ‘alternative consumers’ of vegetation biomass (Archibald & Hempson, 2016; Bond & Keeley, 2005); where herbivores consume vegetation, it deprives wildfire of fuels needed to burn and vice versa. Similar to wildfire, the magnitude and direction of the effects of ungulate removal on biomass and fuels may depend on moisture availability. As competitors for fuel, it is possible that ungulate impacts are constrained in low-rainfall areas by factors such as insufficient biomass, while in high-rainfall areas they may be constrained by forage quality or availability. For example, an Australian study of managed grasslands found that 5–10 years after removing non-native cattle and sheep and native kangaroos, phytomass increased by an average of 737%, and mean annual rainfall (MAR) accounted for 42% of the observed variation in phytomass accumulation (Schultz et al., 2011). In contrast, Koppel et al. (1996) documented that in systems of high productivity in the Netherlands, there was little difference in phytomass in the presence or absence of ungulate herbivores. Moreover, Leonard et al. (2010) found that low moisture at grazing sites hindered the ability of grasslands to accumulate fuel under even relatively low grazing pressure. Clearly, moisture availability plays a key role in regulating fuel accumulation in the presence and absence of ungulates, but the exact nature of this relationship is unclear. The intermediate fire–productivity hypothesis suggests a unimodal relationship with productivity/aridity, where fire activity is highest at intermediate levels of productivity/aridity and decreases towards unproductive/arid as well as productive/wet ecosystems (Pausas & Ribeiro, 2013). Considering the complex interactions between ungulates, vegetation and wildfire, including productivity and forage palatability, the relationship between moisture availability, fuel accumulation and wildfire activity following non-native ungulate removal may follow a similar unimodal pattern, but this has not been explored previously.

Active ecological restoration (e.g. planting saplings grown from seed in a greenhouse at restoration sites, and invasive grass control around individual plants during the initial stage of planting) is a potential mechanism to reduce wildland fuels following ungulate removal. Active ecological restoration after fencing and removal of ungulates is an increasingly common management approach (Banko et al., 2014), with growing recognition that native species recovery is limited in many cases without further management (Holl & Aide, 2011; Nafus et al., 2018; Trauernicht et al., 2018; Yelenik & Levine, 2010). However, little is known about how this practice affects fuel loads or wildfire behaviour. Fencing and ungulate removal without active ecological restoration can result in a substantial increase in non-native plants that compete with the regeneration of native plants, as seen in dry, mesic and wet ecosystems in Hawaii (Cabin et al., 2000; Cole & Litton, 2014; Cole et al., 2012; Weller et al., 2011). These studies indicate that fencing without active ecological restoration is not enough, in at least many cases, to achieve the conservation objective of returning an ecosystem to a native reference state. Additionally, active ecological restoration can be effective at reducing fuel loads and wildfire risk (Ellsworth et al., 2015; Medeiros et al., 2014). Given high initial investment costs in restoration projects (Powell et al., 2017; Wada et al., 2017), understanding the impact of active ecological restoration after ungulate removal over longer time periods (e.g. >5 years) is critical to informing management decisions.

Untangling the complex interactions between non-native ungulates and wildland fuels is important for restoring native biota and protecting ecosystem services. Domesticated cattle *Bos taurus*, goats *Capra hircus* and sheep *Ovis aries*, wild populations of axis deer *Axis axis*, and Polynesian, domestic and wild European pig mixtures *Sus scrofa* have been introduced to island ecosystems globally and have subsequently established non-native populations, many over the course of centuries (Hess, 2016). Hawaii is a model case study of the impacts of such non-native ungulate introductions on island ecosystems. Over the past 30 years, as a result of the documented negative impacts of non-native ungulates, management agencies in Hawaii have fenced and removed non-native ungulates from over 750 km$^2$ of conversation areas statewide, primarily on federally managed lands (Hess, 2016). Meanwhile, the contemporary wildfire regime in the Hawaiian Islands is characterized by a substantial increase in area burned over the past 100 years, from an average of ~800 ha/yr in the first half of the 20th century to ~8,500 ha/yr in 2005–2011 (Trauernicht et al., 2015). While the current annual area burned accounts for only 0.48% of Hawaii's total land area, this is identical to the proportion of the total land area burned across 12 fire-prone, western continental states in the United States during the same time period (0.46%). Much of this substantial increase in area burned has been driven by the widespread invasion of fire-prone and fire-adapted non-native grasses and shrubs, and their associated fuel loads (Litton et al., 2006; Trauernicht et al., 2015). Long-term historical fire data are non-spatial, making it difficult to quantify changes in metrics beyond annual area burned. However, fire probability predictions based on climate and vegetation using recent decades of fire mapping indicate highly variable fire return intervals over the landscape, ranging from relatively high frequencies (e.g. 10–30 years) across the leeward, non-native grasslands in our study site to very low frequencies (e.g. 400 years) in wet, closed-canopy forests (Trauernicht, 2019).

In this study we utilized 13 previously established non-native ungulate exclosures, including three sites that underwent active ecological restoration, that span a wide moisture gradient on the Island of Hawaii to explore how ungulate removal impacts fuel loads and modelled wildfire behaviour, as well as its interactions with moisture. The primary objectives of this study were to: (a) determine the effect of non-native ungulate removal on live and dead fuel loads, type, height and modelled wildfire behaviour; (b) determine how these effects vary with moisture availability; and (c) determine the impacts of active ecological restoration on fuel characteristics after ungulate removal. We hypothesized that: (*H1*) removal of ungulates would increase fuel loads, and flame height and rate of spread of modelled wildfire behaviour, as suggested by the results of previous studies (Blackmore & Vitousek, 2000; Evans et al., 2015; Schultz et al., 2011); (*H2*) the magnitude of changes in fuel characteristics and modelled wildfire behaviour with ungulate removal would be driven by moisture availability via the 'intermediate fire–productivity hypothesis', where ecosystems with very low (<800 mm/yr) or very high (>2,000 mm/yr) rainfall (i.e. productivity) would show little difference in fuel loads and wildfire behaviour following ungulate removal, while in mesic ecosystems with intermediate levels of rainfall (800–2,000 mm/yr), ungulate removal would increase fuels and, thus, the intensity of modelled wildfire behaviour (Pausas & Ribeiro, 2013); and (*H3*) active ecological restoration in sites that have experienced ungulate removal would reduce fuel loads and the intensity of modelled wildfire behaviour (Ellsworth et al., 2015). To address these hypotheses, we analysed differences in fuel characteristics and modelled wildfire behaviour inside and outside of 13 ungulate exclosures located across a 2,740 mm MAR gradient on the Island of Hawaii.

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

This study was conducted across 13 sites spanning a 2,740 mm MAR gradient (460–3,200 mm/yr) on the Island of Hawaii, with field sampling occurring from June 2016 to June 2017 (Table 1; Figure 1). Mean annual rainfall values were obtained from the Online Rainfall Atlas of Hawaiʻi (Giambelluca et al., 2013). In addition to MAR site values, we used moisture zone classifications developed for the Hawaiian Islands by Price et al. (2012) in all analyses, where moisture zones are organized into seven classes: arid, very dry, moderately dry, seasonal mesic, moist mesic, moderately wet and very wet. Moisture zone classification represents moisture availability better than MAR alone because this classification is based on modelled moisture availability as a function of annual precipitation (e.g. including fog drip),

**TABLE 1** Site characteristics of sampled paired plots. MAP, Mean annual precipitation; MAT, mean annual temperature; MAP and MAT values from Giambelluca et al. (2013), moisture zones from Price et al. (2012) and land cover from USGS (2011)

| Plot | MAP (mm/yr) | Moisture zone | MAT (°C) | Elevation (m) | Location | Ungulates | Years since exclusion | Land cover type |
|---|---|---|---|---|---|---|---|---|
| 1. 4CNW | 460 | 2 (very dry) | 12.4 | 1691 | 19.66533, −155.68968 | Goats, Sheep | 6 | Native Shrubland/ Sparse Ohia |
| 2. 4CSW | 460 | 2 (very dry) | 12.4 | 1691 | 19.66391, −155.68906 | Goats, Sheep | 8 | Native Shrubland/ Sparse Ohia |
| 3. 4CSE | 460 | 2 (very dry) | 12.4 | 1691 | 19.66319, −155.68786 | Goats, Sheep | 15 | Native Shrubland/ Sparse Ohia |
| 4. KK | 524 | 2 (very dry) | 13.7 | 1541 | 19.74388, −155.66463 | Goats, Pigs, Sheep | 10 | Native Shrubland/ Sparse Ohia |
| 5. PL | 571 | 3 (moderately dry) | 19.8 | 614 | 19.80138, −155.85019 | Cattle, Goats, Sheep | 6 | Native Shrubland/ Sparse Ohia |
| 6. MA | 686 | 4 (seasonal mesic) | 16.4 | 799 | 19.76876, −155.83966 | Cattle, Pigs, Sheep | 4 | Closed Ohia Forest/Alien Grassland |
| 7. MU | 686 | 4 (seasonal mesic) | 16.4 | 799 | 19.77226, −155.83881 | Cattle, Pigs, Sheep | 10 | Closed Ohia Forest/Alien Grassland |
| 8. PA | 686 | 4 (seasonal mesic) | 16.4 | 799 | 19.76876, −155.83966 | Cattle, Pigs, Sheep | 6 | Closed Ohia Forest/Alien Grassland |
| 9. PN | 782 | 3 (moderately dry) | 22 | 288 | 19.73896, −155.99732 | Goats, Sheep | 5 | Native Shrubland/ Sparse Ohia |
| 10. KC | 1,300 | 3 (moderately dry) | 11 | 2,700 | 19.84828, −155.36346 | Cattle, Pigs, Sheep | 9 | Alien Grassland |
| 11. KL | 1,700 | 4 (seasonal mesic) | 13.7 | 1961 | 19.85137, −155.34126 | Cattle, Pigs, Sheep | 9 | Alien Grassland |
| 12. KA | 3,200 | 6 (moderately wet) | 17.7 | 971 | 20.14186, −155.74844 | Cattle | 4 | Alien Grassland |
| 13. KO | 3,200 | 6 (moderately wet) | 17.7 | 971 | 20.13985, −155.75306 | Cattle | 8 | Alien Grassland |

potential evapotranspiration, trade wind exposure and elevation. Data obtained from Remote Automated Weather Stations closest to sampled sites show average rainfall from the preceding year (August 2015 to July 2016) ranged from 65% to 131% of site MAR across study sites.

Sites ranged widely in moisture zone, elevation, temperature, age with respect to time since ungulate removal, type of ungulate present and land cover (Table 1). Sites were chosen based on the presence of non-native ungulates and the absence of domestic, managed ungulates. Study sites were located with the assistance of land managers and were additionally determined based on factors such as similarity of ungulate density, land use, disturbance history, slope and aspect. Exclosures (fencing > 1.5 m height) were established prior to the conception of this study for the purposes of conservation, and varied in area from 4 ha to 567 ha, with an average of 281 ha. Land cover varied from grassland to shrubland to forest, with invasion status ranging from native-dominated to mixed to non-native-dominated. Dominant native species at sites included lovegrass *Eragrostis atropioides* and ʻāweoweo *Chenopodium oahuense*, while dominant non-native species included fountain grass *Cenchrus setaceus* and fireweed *Senecio madagascariensis* at drier sites and forage grasses such as common velvet grass *Holcus lanatus* at wetter sites. At sites where there was a substantial canopy, native trees such as ʻōhiʻa *Metrosideros polymorpha*, māmane *Sophora chrysophylla* and koa *Acacia koa* were most common, along with non-native trees such as koa haole *Leucaena leucocephala*, while non-native grasses like kikuyu grass *Pennisetum clandestinum* dominated the understorey. Ownership of study sites included state land managed under different agencies, private land managed by non-profit organizations and federally owned and managed land.

Each site consisted of a pair of fenced (ungulate removal) and unfenced (ungulate present) plots. Paired plots were no more than 70 m away from each other, and each plot was at least 30 m away from the fence line. Three of the 13 sites consisted of paired plots sampled within a single large management unit (15,000 ha) in the seasonal mesic moisture zone, differing in time since ungulate removal from 4 to 10 years, to explore if active ecological restoration (i.e. planting of native trees and shrubs including *Acacia koa* and *Sophora chrysophylla*, and invasive grass control around individual

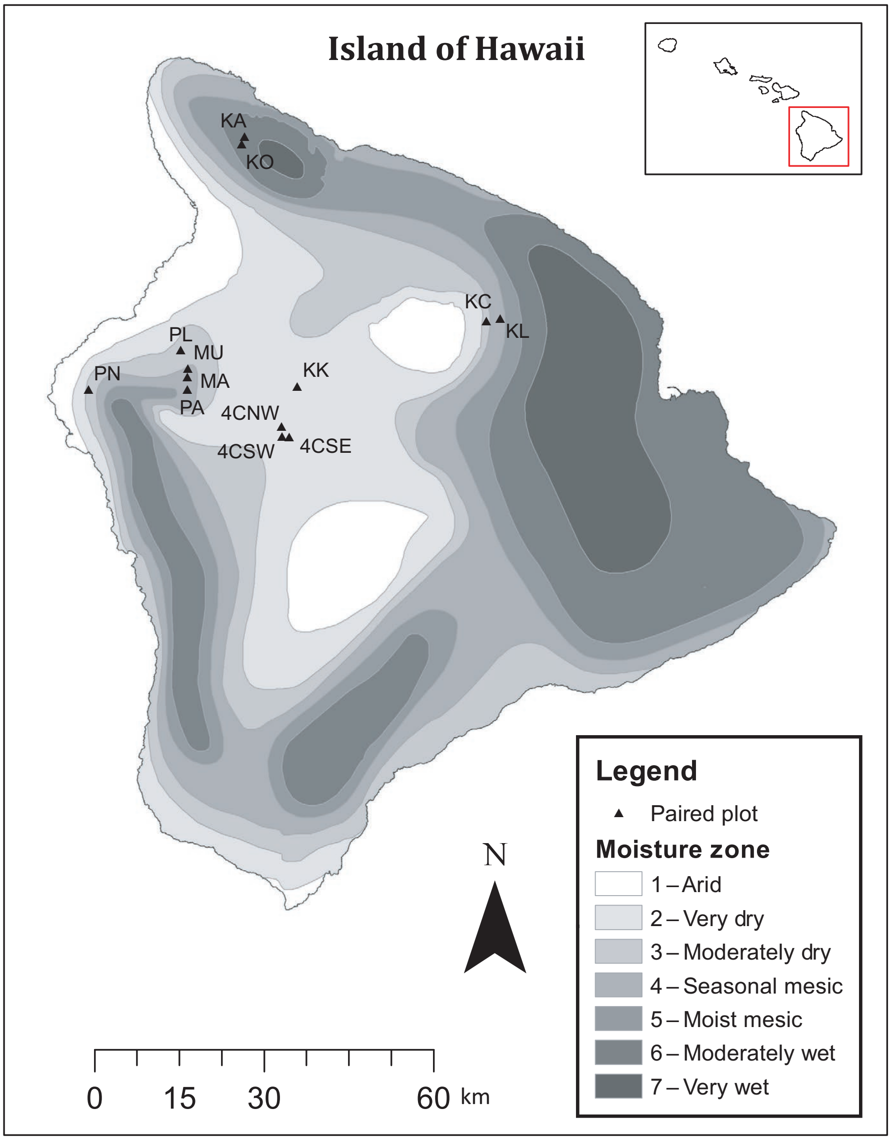

**FIGURE 1** Paired fenced and unfenced plots by moisture zone on the Island of Hawaii, Hawaii. Paired plots were located in very dry (2), moderately dry (3), seasonal mesic (4) and moderately wet (6) moisture zones

plants during the initial stages of planting) altered the impact of ungulate removal on fuel loads and wildfire behaviour.

## 2.2 | Fuel characteristics

Three 50-m transects separated by 20 m were established in plots inside and outside of each exclosure to sample fuel loads, fuel moistures, fuel continuity and fuel height. The initial transect for each plot was established parallel to the fence line with each subsequent transect placed 20 m from the first transect. The starting point for each transect placement was determined using Google Earth satellite imagery to avoid bias by identifying areas with similar canopy cover. Paired plots labelled as MA, MU and PA, and 4CNW, 4CSE and 4CSW were adjacent fenced plots that were compared with a single adjacent unfenced control plot, with all plots 70 m away from each other and ≥30 m from the fence line (Table 1). Potential lack of independence due to this design is addressed below in Statistical analysis.

Fine fuel loads were measured by collecting all litter (i.e. leaves, downed grass and herbaceous biomass and woody material <1 cm diameter) to the mineral soil surface, and clipping standing grass and herbs down to the soil surface in six 25 × 25 cm subplots along each transect at 0, 10, 20, 30, 40 and 50 m. Dominant vegetation cover (a proxy for fuel continuity) and dominant vegetation height were recorded at every metre along the transect. Samples were returned to the laboratory within 48 hr, sorted by species into live and dead biomass, oven-dried at 70°C to a constant mass and weighed to determine fine dry fuel mass. Coarse woody fuels (>1 cm diameter) were measured using a modified Brown's fuel transect (NPS, 2003). A 2-m-wide belt transect also established along each 50-m transect to quantify standing live woody fuels (i.e. shrubs and trees), where shrub basal diameter and tree DBH were measured to estimate live woody fuel loads with species-specific allometric models developed in Hawaii (Ammondt et al., 2013; Litton & Kauffman, 2008), or generalized allometry when species-specific data were not available (Chave et al., 2005).

**TABLE 2** Summary of mean fine fuel loading (±1 *SD*) and modelled flame lengths in fenced and unfenced plots

| Paired plot | Fenced fine fuel loading (Mg/ha) | Unfenced fine fuel loading (Mg/ha) | Fenced flame lengths (m) | Unfenced flame lengths (m) |
|---|---|---|---|---|
| 4CNW | 1.3 (3.3) | 0.07 (0.2) | 0.7 | 0.5 |
| 4CSE | 3.3 (5.9) | 0.07 (0.2) | 0.8 | 0.5 |
| 4CSW | 0.3 (0.6) | 0.07 (0.2) | 0.5 | 0.5 |
| KK | 4.1 (4.7) | 2.9 (5.5) | 4.1 | 4.3 |
| PL | 4.9 (5.5) | 2.6 (2.3) | 4.1 | 3.1 |
| MA | 14.6 (4.2) | 12.4 (2.7) | 5.4 | 4.8 |
| MU | 7.3 (4.8) | 12.4 (2.7) | — | — |
| PA | 11.3 (2.4) | 12.4 (2.7) | — | — |
| PN | 7.7 (6) | 4.6 (5.2) | 3.7 | 2.8 |
| KC | 7.3 (2.5) | 5.2 (4.7) | 3.7 | 3.0 |
| KL | 9.3 (3.7) | 6.5 (2.8) | 3.6 | 3.3 |
| KA | 15.1 (4) | 6.6 (3.9) | 4.8 | 3.3 |
| KO | 18 (3.5) | 11.4 (3.9) | 5.2 | 3.3 |

### 2.3 | Wildfire behaviour modelling

Potential wildfire behaviour was modelled with BehavePlus 5.0.5 (Heinsch & Andrews, 2010) using data on fuel characteristics collected in this study. Additional required parameters were obtained from relevant literature, including 1-hr surface area:volume, dead fuel moisture of extinction and live and dead fuel heat content (Scott & Burgan, 2005). To isolate the effect of ungulate removal on wildfire behaviour and assess its relationship with site moisture availability, weather (e.g. wind speed) and terrain variables (e.g. slope) were kept constant at standard BehavePlus settings in all simulations. Model output variables included maximum rate of spread (m/min) and flame length (m), both indicators of wildfire intensity.

### 2.4 | Statistical analysis

To test our hypotheses, we compared fuel characteristics (live and dead fuel loading, type, height and continuity) and modelled BehavePlus outputs (flame height and rate of spread) in unfenced ungulate present (U) versus fenced ungulate removal (F) sites. To understand the effect of moisture availability, we analysed differences in fuel characteristics and modelled wildfire behaviour between paired U and F plots along the rainfall gradient using a linear mixed effects analysis. We used R (R Core Team, 2017) and the NLME package (Pinheiro et al., 2021) to perform a linear mixed effects analysis of the relationship between potential explanatory variables and response variables at the subplot level ($n = 359$; Adams et al. (1997)). Fixed effects were MAR, MAT, moisture zone, years since ungulate removal and fencing treatment (i.e. U vs. F). Site was a random effect to account for the potential lack of independence due to the paired plot design of the study. Response variables were transformed where necessary to meet the assumptions of homogeneity of variance.

Models ($n = 44$) were constructed containing combinations of all variables, including a 'null' model that contained no fixed effects and only site as a random effect. Through multi-model inference, Akaike information criterion (AIC) was used to select the best model from multiple competing models by using a comparison of Akaike weights ($w_i$; the conditional probability that a given model is the most informative and parsimonious of those considered) and $\Delta_i$ (the difference between the AIC value of the best model and the next model under consideration; Burnham (2002)). Models with $w_i > 0.90$ and $\Delta_i < 2$ were considered to have substantial empirical support per Symonds and Moussalli (2011).

The impact of ungulate removal on fuels in active ecological restoration sites was tested with an analysis of variance (ANOVA), and Tukey's HSD test was used to test for differences in plot-level (i.e. treatment) means following significant ANOVAs'. Testing the impact of ungulate removal on wildfire behaviour in active ecological restoration sites was not performed due to limited sample size. All analyses were conducted at a significance level of $\alpha = 0.05$.

## 3 | RESULTS

### 3.1 | Fuel characteristics

Total fine fuel loads ranged widely across all fenced and unfenced plots from 0.1 to 18.0 Mg/ha (Table 2). By moisture zone, total fine fuel loads averaged (*M* ± 1 *SD*) 2.9 (±3.9) Mg/ha in the very dry moisture zone, 5.6 (±10.1) Mg/ha in the moderately dry moisture zone, 10.2 (±6.7) Mg/ha in the seasonal mesic moisture zone and 12.5 (±5.8) Mg/ha in the moderately wet moisture zone (Table 2). Overall, fine fuel loading averaged 6.6 (±6.5) Mg/ha in fenced plots and 4.4 (±10.1) Mg/ha in unfenced plots. Fine fuel load differences between paired plots averaged 2.6 Mg/ha and ranged from 0.2 to 11.3 Mg/ha, which represented an average of 46% more fine fuels with ungulate removal (Table 2). Fine fuel height averaged 0.79 (±0.29) m in fenced plots and 0.68 (±0.32) m in unfenced plots, and fine fuel height differences between paired plots averaged 0.10 m and ranged from −0.10 m to 0.28 m (see Table S1).

Moisture zone, fencing treatment and their interaction were the best predictors of fine fuel loading ($w_i = 0.91$), indicating that moisture availability and ungulate removal both increase fine fuel loading, with the magnitude of ungulate removal impacts on fine fuel loading increasing with moisture zone (Figure 2). The next closest performing model ($w_i = 0.05$) also included MAT as an explanatory variable, but this model had a low Akaike weight and high $\Delta_i$ and was not considered to have substantial empirical support (see Table S2). Fuel height was best predicted by fencing treatment, MAT, moisture zone, the interaction between moisture zone and fencing treatment and years since ungulate removal ($w_i = 0.48$). A model ($\Delta_i < 2$) that additionally excluded MAT as a predictor also had limited empirical support ($w_i = 0.18$; see Table S2).

Sites with shrubs as a major component of fuel loading were clustered on the very dry to moderately dry moisture zones (i.e. <800 mm/yr), with shrubs absent in higher moisture zones. Shrub fuel loading across paired plots averaged 0.3 to 2.1 Mg/ha. Shrub fuel loading differences between paired plots averaged a 0.8 Mg/ha increase in biomass with ungulate removal. Shrub fuel loading was best predicted by fencing treatment alone ($w_i = 0.34$). Models with $\Delta_i < 2$ that included years since removal ($w_i = 0.20$) and years since removal and moisture zone ($w_i = 0.15$) as predictors, in addition to fencing treatment, also had substantial empirical support (see Table S3).

Live fine fuel loads averaged 6.8 (±6.6) Mg/ha in fenced plots and 5.7 (±12.2) Mg/ha in unfenced plots. Dead fine fuel loads averaged 3.2 (±5.8) Mg/ha in fenced plots and 1.7 (±2.8) Mg/ha in unfenced plots. Moisture zone, fencing treatment and the interaction between fencing treatment and moisture zone were all supported as predictors of both live fine fuels ($w_i = 0.42$) and dead fine fuels, which also included years since removal ($w_i = 0.75$; see Table S4). The magnitude of the model coefficient for the fencing treatment was greater for dead fine fuels than that for live fine fuels (see Table S5). Dead fuel:total fuel ranged from 0.0 to 0.78 in fenced plots, and 0.0 to 0.86 in unfenced plots, with differences between unfenced and fenced paired plots ranging from 0.0 to 0.59.

Fine fuel loads in active ecological restoration plots ranged from 14.6 Mg/ha 4 years after ungulate removal to 7.3 Mg/ha 10 years after ungulate removal, while the unfenced plot averaged 12.4 Mg/ha (Table 2). The model ($w_i = 0.99$) including years since removal and fencing treatment performed best in predicting fine fuel loading in restoration plots. Fine fuel loads remained relatively constant 4 years after fencing (see Table S6). By year 6, fuel loads in fenced units with active ecological restoration had decreased below the level of the unfenced control, and by the 10th year after ungulate removal fine fuel loading had decreased by 5.1 Mg/ha compared to the unfenced control (12.4 Mg/ha; Figure 3).

## 3.2 | Wildfire behaviour modelling

Modelled flame length ranged from 0.5 to 5.4 m, and absolute differences in flame length between fenced and unfenced paired plots ranged from 0 to 1.9 m (Figure 4). In line with fine fuel loading, flame length was best predicted by moisture zone, fencing treatment and their interaction, indicating that flame length increases with ungulate removal and that this effect increases in magnitude with increasing moisture zone ($w_i = 0.907$; see Table S7). Modelled rate of spread ranged from 1.3 to 57.1 m/min, and absolute

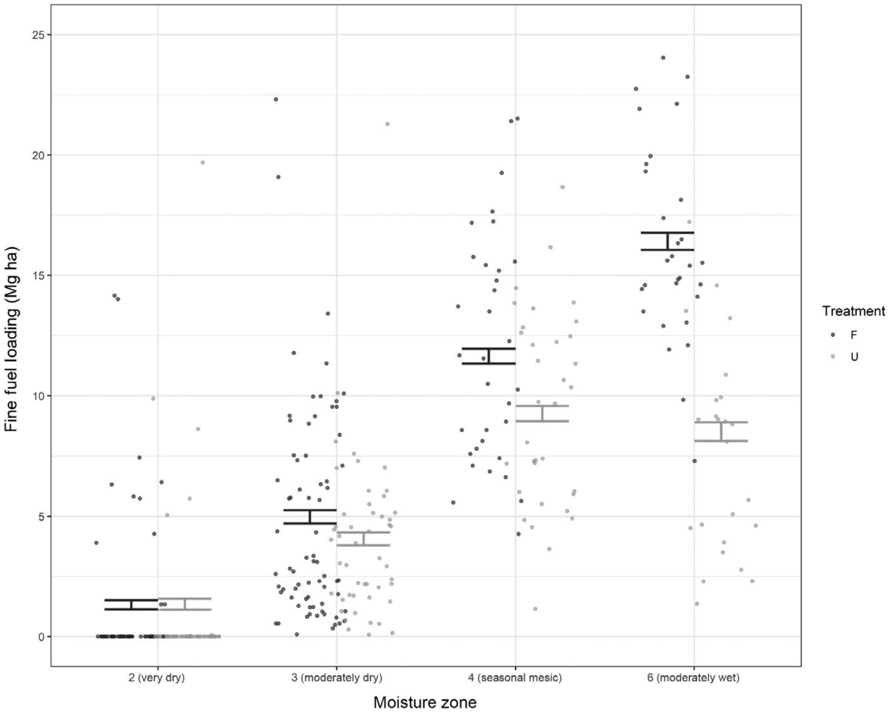

**FIGURE 2** Fine fuel loading by fencing treatment [fenced (F) and unfenced (U)], as a function of moisture zone. Fine fuel loading includes live and dead standing grass and herbaceous fuels, as well as surface litter. Points represent raw data from sampled subplots ($n = 359$). Error bars indicate 95% confidence intervals of predicted model results

differences in rate of spread between fenced and unfenced paired plots ranged from 0.3 to 2.4 m/min. None of the predictors were supported in the analyses of rate of spread. At restoration sites, modelled flame length ranged from 2.7 m 10 years after ungulate removal to 3.7 m in the unfenced plot, and rate of spread ranged from 9.6 m/min 10 years after ungulate removal to 11.2 m/min in the unfenced control plot.

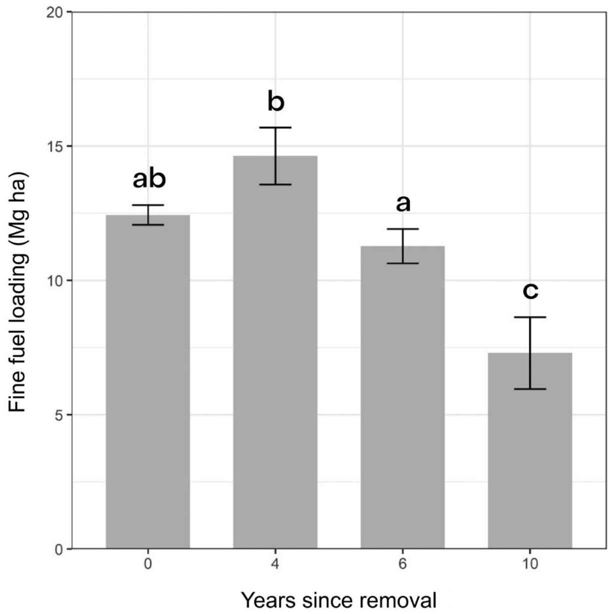

**FIGURE 3** Sampled fine fuel loading differences in seasonal mesic restoration sites by years since ungulate removal. Error bars indicate ±1 *SE*. Lowercase letters designate plots that differ significantly in fine fuel loading. Significance was set at $p < 0.05$ and determined using ANOVA and Tukey's HSD

## 4 | DISCUSSION

Wildfire management in the context of invasive species is crucial to the conservation and restoration of threatened landscapes globally (Brooks et al., 2004; Fusco et al., 2019). In this study, non-native ungulate removal increased fine fuel loading, shrub fuel loading and modelled wildfire intensity, confirming our first hypothesis (H1). These results are consistent with prior research on managed grazing where domestic ungulates reduced fuel loads and modelled wildfire intensity (Blackmore & Vitousek, 2000; Evans et al., 2015; Leonard et al., 2010).

The effect of non-native ungulate removal on fuel loads and modelled wildfire intensity increased linearly with increasing moisture zone, which does not support our second hypothesis (*H2*) that the magnitude of changes in fuel characteristics and modelled wildfire behaviour with ungulate removal would follow a unimodal relationship with moisture availability. Rather, ungulate removal impacts on fuel loading were linearly and positively related to moisture variability. Milchunas et al. (1988) suggested a generalized model for the effects of grazing by large herbivores on grasslands where the magnitude of grazing effects on biomass and species richness is a function of productivity. The results of this study demonstrate that the magnitude of fuel loading as a result of ungulate removal scales similarly on a moisture zone gradient. At the wettest sites, average fine fuel load differences increased by as much as 56% with ungulate removal, while in the driest sites average fine fuel load differences were minimal. Leonard et al. (2010) observed that at sites with low moisture availability, relatively low levels of grazing were required to maintain grasslands in a lawn-like state, in line with our results for drier sites, compared to sites with higher moisture availability that required more intensive grazing. In turn, removal of ungulates

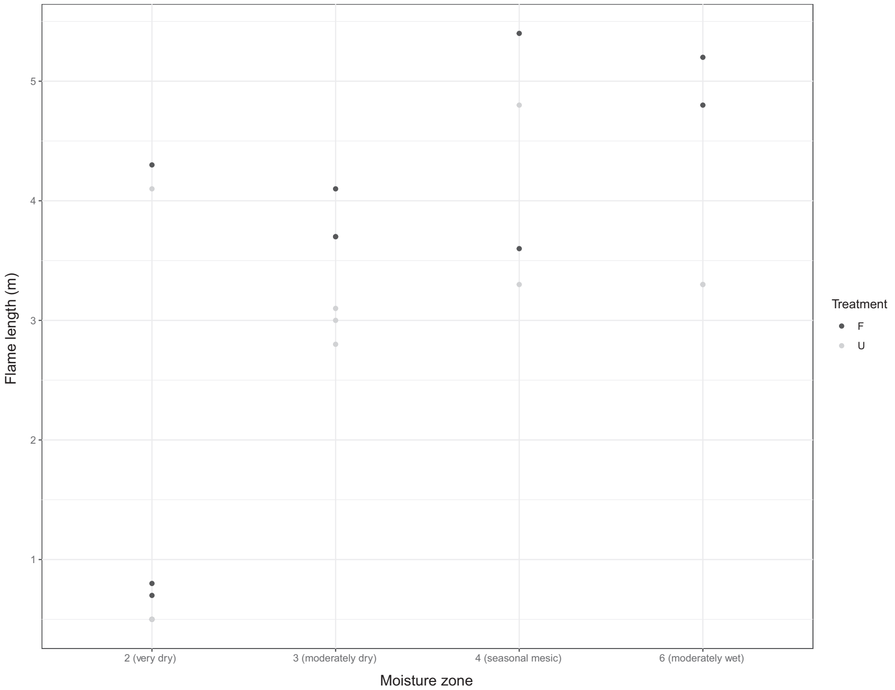

**FIGURE 4** Modelled flame length by fencing treatment [fenced ungulate removed (F) and unfenced ungulates present (U)] and moisture zone at all paired plots (with the exception of restoration sites). Modelled results are based on site-level averages

in wetter sites eliminates an essential alternative consumer of fine fuels, creating an increased risk of wildfire (Bond & Keeley, 2005).

Ungulate removal resulted in an average 47% increase in dead fine fuel loading, the more flammable portion of the total fuel loading that is a primary driver of grassland fire activity (Cheney & Sullivan, 2008). Because a sufficient amount of dead fuel is required to carry wildfire, sites that experience a subsequent build-up of dead fine fuels after ungulate removal will be at a greater risk for fire. The increase in dead fine fuel loads seen in this study aligns with past observations on the removal of ungulates from grasslands (Leonard et al., 2010). Ungulates likely prevent the accumulation of dead fine fuels through grazing and trampling (Morgan & Lunt, 1999; Whalley, 2005). Similarly, Evans et al. (2015) observed that grazing by domestic cattle in non-native grasslands in Hawaii resulted in a reduction in dead fine fuels relative to live fine fuels.

Both wildfire and ungulate consumption of fuels are selective: wildfire consumption of fuels depends on factors such as climate, weather, plant phenology, fuel continuity and ignition sources, while ungulate consumption depends on factors such as forage palatability, seasonality and ungulate species dynamics (Olff & Ritchie, 1998; Parker et al., 2006). Further complicating matters, feedback loops exist between wildfire, fuels and ungulates (Fuhlendorf et al., 2009). For example, wildfire can increase the availability of palatable forage, while ungulate consumption can push back forest edges and create openings for more fire-prone species to thrive (D'Antonio & Vitousek, 1992; Hoffmann et al., 2012). Alternatively, overgrazing can reduce fire and increase woody plant establishment and shrub encroachment into fire-prone, grassy ecosystems (Eldridge et al., 2011; Roques et al., 2001). We observed evidence that non-native ungulate removal resulted in increased shrub biomass at low and medium moisture sites. Meanwhile, at high moisture sites where non-native cattle dominated, shrubs were absent from all plots. A similar dynamic was observed by Blackmore and Vitousek (2000), where cattle reduced woody cover in Hawaiian ecosystems through trampling and suppressing recruitment. However, the exclusion of non-native ungulates is not enough to promote woody cover. Even in fenced exclosures free of non-native ungulates in a landscape that was once native wet forest, no woody establishment was detected. It is likely that established heavy non-native grass cover in these sites was effective at suppressing any woody recruitment, as seen in our control plots (Elgar et al., 2014; Setterfield et al., 2018). Further study is needed to explore the feedbacks between specific vegetation preference, ungulate species and fuels across a climatic gradient.

The combination of non-native ungulate removal and active ecological restoration reduced fine fuel loads and modelled wildfire flame length (i.e. wildfire intensity), with the strength of this effect increasing with time since non-native ungulate removal, confirming our third hypothesis (*H3*). While sampling of restoration sites was limited to three fenced units in the same moisture zone and overall management unit, these results suggest that active ecological restoration can effectively suppress the growth of fuels that occurs with ungulate removal, and offer evidence of the longer term utility of shading to reduce fine fuels with active ecological restoration (Ammondt & Litton, 2012; Cabin et al., 2002; Ellsworth et al., 2015; Medeiros et al., 2014). At 6 years after ungulate removal and active restoration, fuel loads had decreased by 9% and by the 10th year fine fuel loads had decreased by 41% (Figure 3). Active ecological restoration at these sites consisted of planting native trees and shrubs combined with initial non-native grass control with herbicide, offering additional evidence for the effectiveness of native species planting for reducing fuel loading compared to only using herbicide (Ellsworth et al., 2015), as well as the efficacy of relying only on herbicide in the initial establishment stage (Yelenik & Levine, 2010). The observed reduction in fuels with ungulate removal and active ecological restoration is likely dependent on the intensity of restoration and the initial degradation of a site (Weller et al., 2011). Non-native ungulates are known to facilitate non-native plants, such that exclusion on its own once invasive plants are established is frequently not enough to promote native species over fire-prone non-native grass and herbaceous plants (Leopold & Hess, 2017; Parker et al., 2006; Stohlgren et al., 1999). Our results suggest that significant decreases in fuel loading from active ecological restoration following ungulate removal are achievable, albeit over somewhat longer time-scales (i.e. up to 5–10 years).

Ungulates mediate trade-offs between wildfire risk, biodiversity and ecosystem services such as carbon storage and watershed conservation (Lecomte et al., 2019), as well as human recreation and economic activities. Land managers seeking to balance conservation and restoration objectives with wildfire risk should be cognizant of the impacts of non-native ungulate removal on fuels and wildfire behaviour. Dry and mesic moisture zones where wildfire occurrence is more frequent are of particular concern, but in drought years even wet zones are at risk for wildfire (Chu et al., 2002; Frazier, 2016; Trauernicht, 2019). For example, study sites on the wettest end of the rainfall gradient (~3,200 mm/yr) experienced multiple prolonged periods of severe to extreme drought and multiple periods of moderate drought between 2000 and 2019 (Svoboda et al., 2002). Furthermore, non-native grasslands in Hawaii have demonstrated high-intensity wildfire behaviour in what would be considered benign weather conditions, such as high relative humidity and low wind (Trauernicht et al., 2015). Despite these risks, non-native ungulate removal is a prerequisite for protecting remaining native ecosystems from degradation and promoting ecological restoration. Given limited resources, managers in mesic and wet forests might focus first non-native ungulates in non-native grass-dominated areas that contribute disproportionately to wildfire spread and are adjacent to fenced, higher value conservation areas (Wada et al., 2017), while managers in dry to mesic areas might focus on removing non-native ungulates. Where possible, land managers in all situations should invest in long-term fuel management strategies such as active ecological restoration to reduce fuel loads and the occurrence and intensity of wildfires.

Shifting climate envelopes may also impact the susceptibility of sites to wildfire. Recent projections of climate change in Hawaii predict that mesic zones will decrease in extent, with a subsequent increase in dry and wet zones (Selmants et al., 2017), which could shift peak wildfire risk to higher elevations with higher fuel loads (Trauernicht, 2019). Global climatic projections by Abatzoglou et al. (2018) of increased fuel aridity by mid-century will also potentially increase burned area, particularly in wet forests. As a result, ungulate removal in wet moisture zones may entail an even greater wildfire risk in the future given the greater impact of their removal on fine fuel loading (Figure 2), thereby promoting a grass-fire cycle where one currently does not exist. Mowing, thinning, green strips, managed grazing and prescribed fire are among a number of potential fuel management strategies available for land managers to reduce fuel loads after non-native ungulate removal (Trauernicht et al., 2015). In the long-term, active ecological restoration will also be necessary to reduce fuel loads, particularly those associated with non-native grasses, to break the positive feedback between non-native plant invasions and wildfires. Importantly, evidence suggests that active ecological restoration after non-native ungulate removal is most cost-effective over large spatial scales (Powell et al., 2017), and in the case of wildland fuel mitigation, is likely to be the most impactful over longer temporal scales.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## AUTHORS' CONTRIBUTIONS

T.R.Z., C.M.L. and C.P.G. conceived the ideas and designed the methodology; T.R.Z. collected the data; T.R.Z. and C.T. analysed the data; and T.R.Z. and C.M.L. led the writing of the manuscript. All the authors contributed critically to revisions and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the GitHub repository https://github.com/lodgepolepines/ungulates (Zhu et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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