

Self-reinforcing impacts of plant invasions change over time

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Returning native species to habitats degraded by biological invasions is a critical conservation goal¹. A leading hypothesis poses that exotic plant dominance is self-reinforced by impacts on ecosystem processes, leading to persistent stable states^{2–6}. Invaders have been documented to modify fire regimes, alter soil nutrients or shift microbial communities in ways that feed back to benefit themselves over competitors^{2,5–7}. However, few studies have followed invasions through time to ask whether ecosystem impacts and feedbacks persist^{8,9}. Here we return to woodland sites in Hawai'i Volcanoes National Park that were invaded by exotic *C₄* grasses in the 1960s, the ecosystem impacts of which were studied intensively in the 1990s^{10–12}. We show that positive feedbacks between exotic grasses and soil nitrogen cycling have broken down, but rather than facilitating native vegetation, the weakening feedbacks facilitate new exotic species. Data from the 1990s showed that exotic grasses increased nitrogen-mineralization rates by two- to fourfold, but were nitrogen-limited^{10,12,13}. Thus, the impacts of the invader created a positive feedback early in the invasion. We now show that annual net soil nitrogen mineralization has since dropped to pre-invasion levels. In addition, a seedling outplanting experiment that varied soil nitrogen and grass competition demonstrates that the changing impacts of grasses do not favour native species re-establishment. Instead, decreased nitrogen availability most benefits another aggressive invader, the nitrogen-fixing tree *Morella faya*. Long-term studies of invasions may reveal that ecosystem impacts and feedbacks shift over time, but that this may not benefit native species recovery.

Invasive species have come to the forefront of the conservation movement because of the considerable impact they have on ecosystem composition and functioning, including their impact on threatened and endangered species¹⁴. In addition to direct competitive effects, invasive species alter disturbance regimes, hydrologic cycles, soil erosion, productivity and nutrient dynamics^{2,15–18}.

Species that alter ecosystem processes are of special concern for conservation because they alter the rules of the game for resident species². Such changes in ecosystem function are often proposed to feedback positively on the initial invaders by establishing conditions that promote or maintain dominance^{2,4–7}. For example, exotic plants that increase soil nitrogen (N) by producing large quantities of nutrient-rich litter may achieve higher growth rates in fertile soils^{7,17}. If high soil N is more favourable to exotic than to native species, exotic plants are reinforcing themselves via their ecosystem effects^{7,19}. Positive feedbacks can lead to alternative stable states, in which exotic-dominated species assemblages are persistent owing to internal reinforcement^{20–22}. Because degraded ecosystems are difficult to restore, the existence of internal feedbacks has become a widely accepted explanation for seeming stability, despite a paucity of evidence.

Although ecosystem impacts of exotic species are commonly studied, there is surprisingly little long-term work in field settings^{8,20}. This is an important missing link in our understanding of invader impacts: if ecosystem impacts change over the course of invasion, this may lead to incorrectly predicting invasion outcomes such as alternative states, and

result in misdirected management strategies²⁰. Ecosystems in alternative stable states typically need large shifts in community composition or environmental conditions to be restored^{20,22}, yet some invader effects might not be expected to be stable in the long term. For example, as resources such as soil N increase, it is probable that other resources will become limiting (for example, light or phosphorus)²³, changing the relative benefit derived from the invader's enhancement of N cycling. Indeed, some observational studies have shown that seemingly stable invasions have become less robust over time, giving way to successional progression^{24,25}. Understanding when and why invasions are self-reinforcing will guide management and inform ecological theory.

In Hawai'i, invasions by exotic *C₄* perennial grasses have considerably altered plant community composition and ecosystem processes in seasonally dry woodlands dominated by the native tree *Metrosideros polymorpha*. In the 50 years since widespread invasion, exotic grass species have increased both fire frequency and size in Hawai'i Volcanoes National Park, leading to local declines in native species and loss of net primary productivity^{16,26}. Dominance of the exotic grass *Melinis minutiflora* in the initial decade after fire (1988–1998) was associated with increased (2–4-fold) annual N-mineralization rates compared to unburned native woodland¹⁶, whereas N-fertilization studies showed strong N responsiveness of the grasses¹³. Accelerated N cycling, in combination with N limitation of grasses, appeared to contribute to a positive feedback facilitating exotic grass dominance.

Here, we return to Hawai'i Volcanoes National Park to repeat measures of nutrient cycling and plant community change. Our data show that, in the last 17 years, N-mineralization rates in sites dominated by the exotic grass *Melinis minutiflora* have declined by half, thereby returning to pre-invasion levels, while rates in native woodland sites have remained constant (Fig. 1a). This reversal of invader impacts is possibly due to a previous mismatch between N availability and N uptake, leading to high potential for soil N loss¹⁶. Biomass and net primary productivity in grassland were greatly reduced after invasion and fire, such that plants in invaded sites did not take up the quantity of N being mineralized early in *Melinis* invasion. By contrast, native woodland showed similar annual rates of plant N uptake versus net N mineralization¹⁶. There was also a mismatch between the annual timing of N mineralization and phenology of *Melinis*. A high amount of N mineralization was found to take place in winter when exotic grasses are less active but rainfall is relatively high, potentially leading to N loss through leaching or denitrification^{10,16}.

It is possible that differences in N mineralization in years 1994–95 versus years 2011–12 were due to differences in rainfall. However, rainfall during the two sampling periods was similar (Extended Data Fig. 1) and rainfall did not correlate with differences between grassland and woodland sites (Extended Data Fig. 2). Finally, recent laboratory N-mineralization incubations with constant soil moisture showed similar patterns to the 2011–12 field data (Extended Data Fig. 3). Taken together, this suggests that changes in the relative difference in N mineralization between *Melinis*-invaded and intact woodland were not simply due to differences in rainfall.

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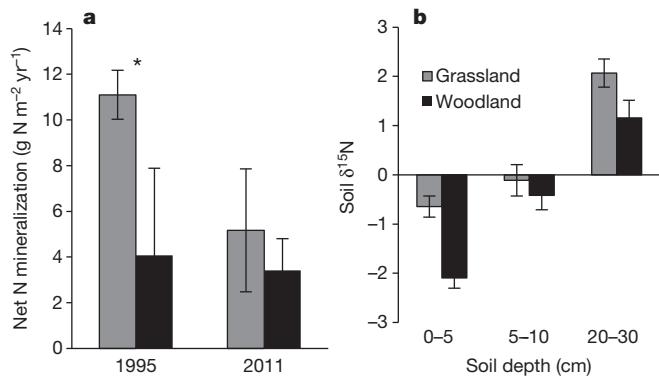


Figure 1 | Ecosystem impacts of *Melinis* invasion over time, and through the soil profile. **a**, Net N-mineralization rates in 1995 and 2011 in exotic grassland versus native *Metrosideros* woodland sites. 1995 data showed differences¹⁰ ($P < 0.05$), whereas data from present conditions do not (one-way analysis of variance (ANOVA), habitat as fixed effect and site as random effect, $n = 15$; $P = 0.65$). **b**, Soil $\delta^{15}\text{N}$ from grassland and woodland sites at varying depths taken during 2011. Grassland soils are consistently less negative, suggesting greater N losses (two-way ANOVA, habitat and soil depth as fixed effects and site as random effect, $n = 5$; habitat, $P < 0.01$; soil depth, $P < 0.01$). Bars represent means ± 1 s.e.

Consistent with the hypothesis that N-cycling rates have declined in the invaded ecosystem, *Melinis* foliar N has decreased by 30%. In 1995, foliar %N was 0.43 ± 0.02 , whereas present values average 0.32 ± 0.01 . In addition, *Melinis* soil $\delta^{15}\text{N}$ values currently have a greater proportion of the heavier isotope than woodland soils (Fig. 1b). This suggests that exotic systems experience greater N losses than woodlands because N lost to pathways such as denitrification is depleted in the heavier isotope²⁷. That invasion has lowered ecosystem N supply rates suggests that N limitation of *Melinis* may be exacerbated¹³, causing initial positive feedbacks to weaken. Indeed, recent vegetation data show that, concurrent with shifting N mineralization, *Melinis* live cover has decreased²⁶, and live biomass has decreased from values of 600 g m^{-2} (refs 13, 16) to an average of 413 g m^{-2} during 2011 (Fig. 2). Although positive feedbacks are an important contributor to alternative stable states, many other life history (for example, seed set, growth rate) and stochastic variables have a role in overall community dynamics^{9,21,22}. However, this is, to our knowledge, the first study in which a positive feedback that coincides with dominance has been shown to shift to a negative feedback, and decreasing dominance, over time.

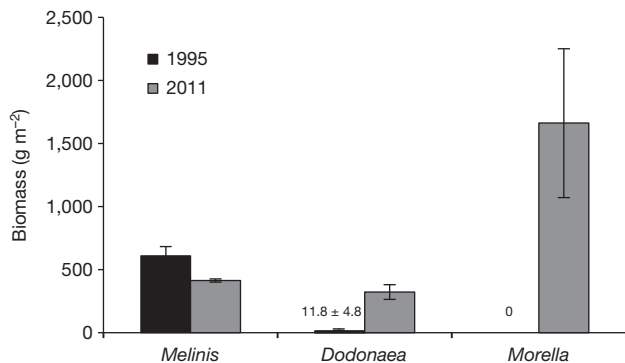


Figure 2 | Changes in dominant species biomass in exotic grassland habitat over time. The exotic grass *Melinis* has decreased in biomass over time, whereas *Dodonaea* and *Morella* have increased since the 1990s. Note that *Morella* biomass has increased more dramatically than *Dodonaea*, potentially owing to its greater response to the changing ecosystem impacts of *Melinis*. Bars are means ± 1 s.e.; all species 2011 biomass, $n = 11$; 1995 *Melinis* biomass^{11,13}, $n = 5$; 1995 *Dodonaea* biomass³⁰, $n = 3$. *Morella* was not found on grassland transects in 1995.

If changes in self-reinforcing invader impacts are leading to a loss of *Melinis* dominance, we wanted to know which species would benefit from gaps or declines in *Melinis* cover. We used a large outplanting experiment to test how a suite of regionally available native and exotic woody species responded to shifting ecosystem impacts of *Melinis*. Specifically, we added N (simulating higher soil N in early *Melinis* invasion) and/or clipped aboveground *Melinis* (simulating gaps in cover later in invasion) in a factorial field experiment that included seven species, replicated over seven sites in invaded grasslands. We refer to clipped *Melinis* as 'reduced competition' because intact root systems continued to produce shoots and take up resources. Those outplanted species that receive a greater relative benefit from reduced *Melinis* competition than from added N are favoured later in *Melinis* invasion, and therefore are predicted to be more likely to fill open space in degraded *Melinis* grasslands.

Five out of the seven outplanted species responded similarly to treatments, with growth rates and survivorship increasing from both reduced *Melinis* competition and N additions (Fig. 3). Because there were no differences between treatment effects for these native and exotic species we suggest that the changing ecosystem impacts of *Melinis* have not altered their ability to colonize *Melinis* grasslands. Exceptions to this pattern included the N-fixing trees: native *Acacia* *koa* and exotic *Morella* *faya*. These species benefited more from reduced *Melinis* competition than from N addition, suggesting that a change in ecosystem impact would release them from *Melinis* competition to the greatest degree out of the species tested (Fig. 3). It should be noted that other species

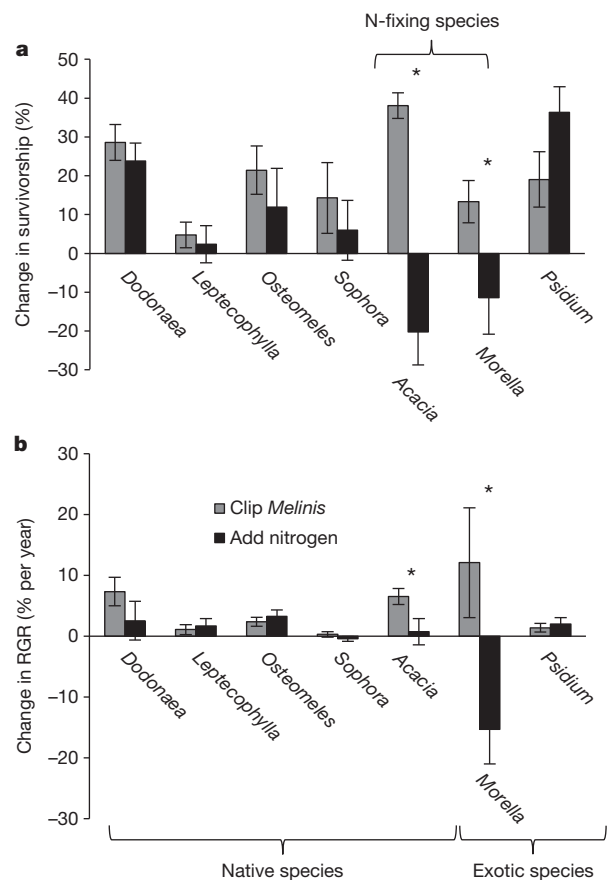


Figure 3 | Assessing the changing impacts of *Melinis* invasion on native and exotic seedlings. **a**, **b**, We compared the effects of adding N fertilizer (similar to gaining benefit from increased soil N in early *Melinis* invasion) to clipping *Melinis* (similar to gaining benefit from reduced competition later in *Melinis* invasion) on seedling survival rate (**a**) and RGR in outplantings (**b**). Asterisks show significant differences between clipping and fertilization effects at the $P < 0.05$ level ($n = 7$), and suggest that changing ecosystem impacts of *Melinis* over time will alter growth rates and survivorship of these species. Bars represent means ± 1 s.e. See Methods for statistics.

benefitted from reduced *Melinis*, including the native shrub *Dodonaea*, which also has greater biomass on the landscape than in 1995. However, its increase in biomass is much less than *Morella* over time (Fig. 2), which may be because the benefit received from shifting ecosystem impacts of *Melinis* is not as great for *Dodonaea*.

Taken together, our results suggest that changing *Melinis* impacts are leading to negative feedbacks with N-fixing species in the long term. During early invasion (Fig. 4a), *Melinis* increased soil N availability¹⁰, which, given that it was N limited¹³, would be a positive feedback. However, during late invasion (Fig. 4b), *Melinis* is associated with ecosystem N depletion (Fig. 1a), which we have shown benefits N fixers (Fig. 3). At the same time, N fixers have large localized positive effects on soil N pools¹⁸, which benefits grasses more than N fixers, as N-fixing trees respond negatively to N additions (Fig. 3). Therefore, each functional group is ultimately altering soils in ways that benefit the other more than itself. Such negative feedbacks are stabilizing and foster co-existence^{7,19}, which, all else being equal, allow each functional group to colonize areas dominated by the other.

In fact, the N-fixing tree *Morella* is moving rapidly into exotic grass sites. Although there were none established on permanent transects in the 1990s, this species currently makes up >60% of standing biomass in exotic grasslands (Fig. 2). By contrast, no *Acacia* trees have recruited into study sites, a difference potentially due to dispersal limitation. Whereas *Morella* is bird dispersed and invades widely across Hawai'i, *Acacia* is a heavy seeded, slow disperser²⁸ that is locally of limited distribution. A trait-based management option would be to facilitate species with the same trait—N fixation—that is allowing *Morella* to increase in abundance in this later *Melinis* invasion stage²⁹. Aggressively outplanting *Acacia* would overcome dispersal limitation, allowing it to pre-empt resources before *Morella* arrival, although whether or not this novel ecosystem is desirable should be explored with managers. Although *Sophora* is also a native N-fixing tree, its low relative growth rates (RGRs; Extended Data Fig. 4) makes it an imperfect restoration species, especially if a goal is to outcompete the non-native *Morella*.

Understanding how plant invasions alter ecosystems in the long term, and what this means for community trajectories, is critical for informing restoration practices^{3,8,15}. We offer what is to our knowledge the first long-term study of invader feedbacks, and show that they weaken over time. Although this facilitates community succession away from the initial invader, our data suggest that without further management, native species may not gain the advantage of altered invader impacts. Taking a mechanistic perspective to feedbacks and stable states in more case studies will help ecologists to gain a general understanding of when feedbacks can be predicted to be persistent in the long term. For example,

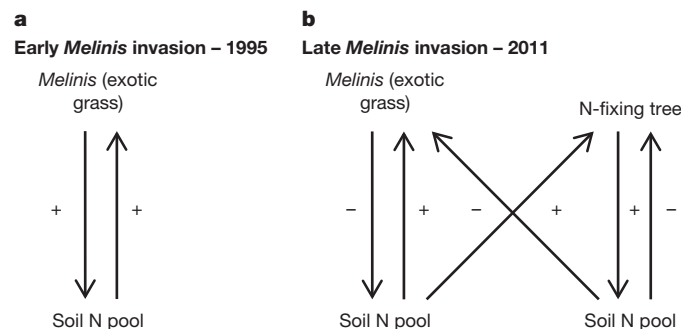


Figure 4 | Feedbacks between *Melinis* and soils change over time, ultimately leading to negative feedbacks with N-fixing species. **a**, Early in invasion, *Melinis* increases soil N cycling¹⁰, increasing its own productivity¹³. **b**, Over time ecosystem N losses deplete soil N (Fig. 1), reducing *Melinis* cover (Fig. 2). Open space is beneficial for N-fixing trees (Fig. 3), which, over time, increase localized soil N pools. In these locations, *Melinis* production is increased¹³. Thus, the effect of each species on localized soil N benefits the other species more than itself, which, all else being equal, promotes co-existence. *Melinis* follows model in ref. 19.

feedbacks that are created by the effects of a single species on soil nutrient cycling might break down as other nutrients become more limiting. Conversely, feedbacks with fire may be more persistent, as they are consistently reset, and thus in a state of constant disequilibrium. Long-term studies of invader feedbacks are needed to test these important ecological ideas.

METHODS SUMMARY

Native unburned *Metrosideros* woodland and burned exotic grassland habitats, corresponding to those used for collecting previous data, were located in Hawai'i Volcanoes National Park^{11–14,17,26}. We sampled soil and foliage from three replicate locations within five sites in each habitat type between 2010 and 2012 to compare to 1990s data. We used intact soil cores to measure net N mineralization using protocols from 1995 (ref. 17). These were repeated bimonthly over 1 year in both habitats. *Melinis* foliage for %N was taken from fully expanded green leaf material. Soils were cored to 5, 10 and 30 cm to explore changes in $\delta^{15}\text{N}$, informing ecosystem N loss. Woody biomass densities were measured in 11 randomly chosen 10×10 m plots in the exotic grassland habitat. All woody plants were measured for height and basal diameter and allometric equations obtained by harvesting 6–20 measured shrubs per species. Data for 1990s *Dodonaea* biomass were obtained from ref. 30. *Melinis* biomass was estimated in the 1990s by harvesting one 4 m^2 plot of grass for each of the five sites in summer and winter and averaging values across seasons. Biomass for 2010–11 was obtained by harvesting three 0.25 m^2 quadrats for each of the five sites with 100% live *Melinis* cover on seven dates between October 2010 and December 2011. We then multiplied the average live biomass values at 100% cover times the actual live per cent cover of *Melinis* censused in 20 m^2 subplots within each 10×10 m woody plant density plot. Finally, we established an outplanting experiment in exotic grasslands exploring the differential effects of *Melinis* invasion over time, using a fully factorial design of added N and reduced *Melinis* competition, in December 2011. We used seven species (native and exotic) found locally, planted in monoculture. Seedlings were measured for relative growth rates and survivorship after 8 months. See Methods for detailed protocols.

Online Content Any additional Methods, Extended Data display items and Source Data are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Author Contributions S.G.Y. and C.M.D. conceived and designed the study, managed the project, performed laboratory and field work and edited the manuscript. S.G.Y. analysed the data, developed the figures and drafted the initial manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to S.G.Y. (syelenik@usgs.gov).

METHODS

Sites. Native unburned *Metrosideros* woodland and burned exotic grassland habitats, which corresponded to those used for collecting previous data^{10–12,16,26}, were located in Hawai'i Volcanoes National Park. We took soil and foliar samples from three replicate locations within five sites in each habitat (exotic grassland versus native *Metrosideros* woodland) type. These five sites per habitat are adjacent to the five transect locations studied in all of the previous published work^{10–12,16,26}.

Soil N cycling. We used intact core soil N-mineralization protocols from 1995 to quantify net N mineralization under field conditions¹⁶, which were replicated seven times over 14 months starting in October 2010. Although intact cores were located at random points within sites, in the grassland habitat we avoided pig-disturbed, bare areas, or entirely dead patches of *Melinis* as well as *M. faya* individuals. Random points were selected along a central transect through the centre of each site. Then at each of the three random points, we flipped a coin as to whether to core on the left or right side of the transect tape and a second random number was generated between 0 and 5 m to place the core location at a random distance from the transect. We also conducted laboratory assays of potential net N mineralization to assess rates without the confounding effects of different microclimates. For these we took two randomly placed (as described previously) 10-cm-deep cores at each site, sieved to 2 mm, and held the soil at constant moisture (70% water-holding capacity) and temperature (23 °C). We extracted the t_0 soils 24 h post wet up and the t_1 soils 30 days later.

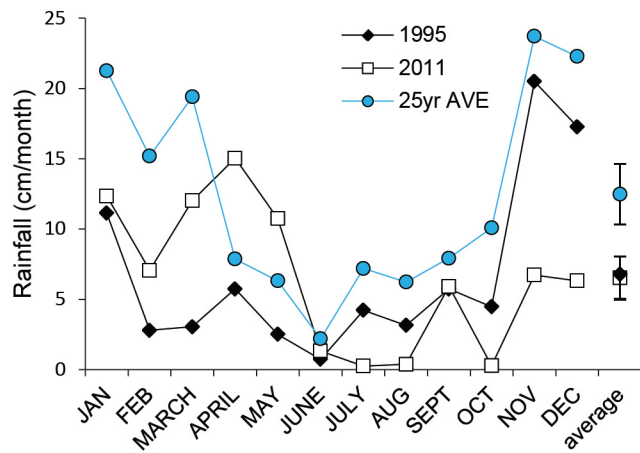
Soil for ^{15}N analysis was taken using a 3.8-cm diameter core to 5-, 10- and 30-cm depth in both January and July 2012 at random locations within sites as described above. All soil was air dried and ground with a mortar and pestle. Data were identical between time points, and so only July is presented. *Melinis* foliage for %N was taken from fully expanded green leaf material in November 2010 and July 2011, dried and ground with a ball mill. To be consistent with 1990s timing we present July data here but values were similar. Foliar C:N and ^{15}N samples were analysed the University of Hawai'i, Hilo Analytical Laboratory using a Costech ECS CHNSO Analyzer (Costech Analytical Technologies), and inorganic N in soil extracts were analysed at UC Santa Barbara with a Lachat flow-injection auto analyser (Lachat Instruments). For all soils data, outliers ($\geq \text{mean} \pm 2 \text{ s.d.}$) were discarded from the analyses. Data were tested for normality to assure that assumptions of parametric tests were met. See figure legends for statistics.

Plant biomass. Woody biomass densities were measured in 11 randomly chosen locations near the end points of the original transects studied in the 1990s^{12,26}. The sampled subplots were $10 \times 10 \text{ m}$. All woody plants were measured for height and basal diameter and allometric equations obtained by harvesting 6–20 measured shrubs per species. Data for 1990s *Dodonaea* biomass were obtained from ref. 30. *Melinis* biomass was estimated in the 1990s by harvesting one 4 m^2 plot of grass for each of the five sites in summer and winter, separating it into live versus dead plant material, and drying subsamples to correct for field moist weights. Values were

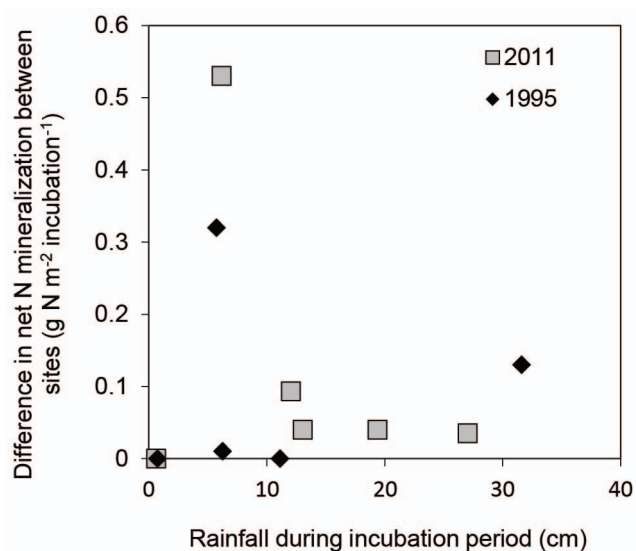
averaged across seasons. Biomass for 2010–11 was obtained by harvesting three 0.25 m^2 quadrats for each of the five sites with 100% live *Melinis* cover on seven dates between October 2010 and December 2011. Quadrat locations were random except to avoid *M. faya*. Biomass was separated into live versus dead and dried. We then multiplied the average live biomass values at 100% cover times the actual live per cent cover of *Melinis* censused in 20 random 1 m^2 subplots within each $10 \times 10 \text{ m}$ woody plant density plot. This method probably overestimates *Melinis* biomass because of the larger edge to interior ratio for the small harvest plots compared to those harvested in the 1990s, but the values were still lower. Thus, our results of declining *Melinis* biomass and cover over time may be conservative.

Outplanting experiment. We established an outplanting experiment in which we explored the differential effects of *Melinis* invasion over time: higher soil N, representative of early invasion, and lower *Melinis* competition, representative of later *Melinis* invasion. We used seven replicate sites across the invaded grassland habitat to establish the outplant experiment using a fully factorial design with N fertilization (10 g N m^{-2} as urea, half added September 2011, and half added January 2012) and competition removal (clipping *Melinis* at soil surface) treatments. These seven replicate sites were chosen to be at least 100 m apart, away from *M. faya*, with soil at least 30 cm deep, and not a part of the soil N-mineralization core sampling areas. Seedling species, which were the most common in the local species pool (Extended Data Fig. 4), were grown from local seed for 5 months before outplanting in December 2011 at a density of six individuals per 0.25 m^2 monoculture plot. We planted multiple individuals (six) per species per site to account for mortality, which can be high in this dry ecosystem, and to track survivorship. We separated seedlings into three size classes and included equal numbers from each size class in each replicate to control for initial seedling size effects. Seedlings were small and planted far enough apart, and remained small enough, that we do not feel that they experienced intraspecific competition.

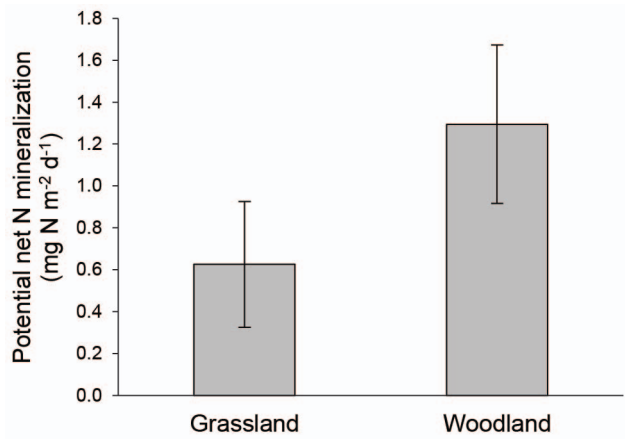
We measured seedlings for initial height and width, re-measured at 8 months, and calculated RGRs by modelling them as inverted cones. We used the average RGR of the initial six seedlings per monoculture plot to compare treatment effects (Extended Data Fig. 4). To calculate change in RGR (Fig. 3), we subtracted the average RGR in control plots (for example, no N fertilizer added in clipped and non-clipped plots) from RGR in treatment plots (for example, N added in clipped and non-clipped plots). We used one-way ANOVAs ($n = 7$) to test for treatment differences (adding N versus clipping *Melinis*). Although all data were normally distributed, we did find unequal variances for some species. However, non-parametric Kruskal–Wallis tests, which do not assume equal variances, showed similar results (that is, the same species showed significant differences between treatments). Survivorship data were percentages based on the number surviving of the initial six seedlings. We therefore used logistic regression to compare treatments for each species ($n = 7$). For outplanting data, outliers ($\text{mean} \pm 2 \text{ s.d.}$) were discarded from the analyses, which resulted in removing one data point from the growth rate data.



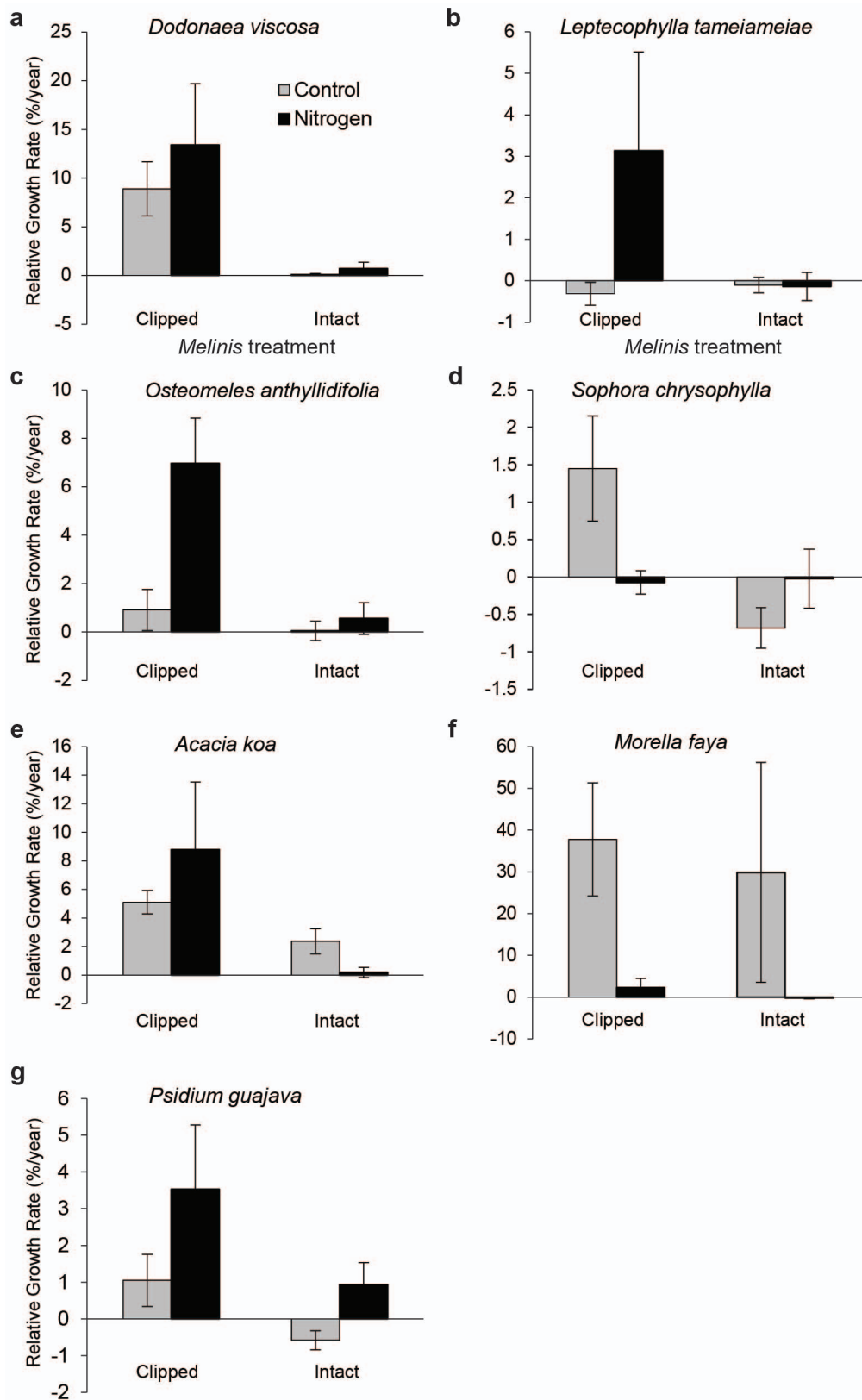
Extended Data Figure 1 | Monthly rainfall over the study periods, and the 25-year average monthly rainfall. Monthly rainfall over the course of 1 year during the 1995 and 2011 year-long sampling periods for net N mineralization (Fig. 1a). The last point in the series shows the average monthly rainfall for that year (points are means \pm 1 s.e.). Also shown in blue is the same data for the 25-year rainfall average. Note that 1995 and 2011 have similar rainfall on average over the year, approximately 45% lower than the 25-year rainfall average.



Extended Data Figure 2 | Relationship between net N mineralization and rainfall over the study periods. Differences in net N mineralization between exotic grassland and native *Metrosideros* woodland sites in relation to monthly rainfall for the 1994–95 and 2011–12 study periods. The lack of relationship ($r^2 = 0.01$, $P = 0.74$, $n = 11$) between site differences and monthly rainfall suggests that rainfall did not drive patterns in net N mineralization, or the relationship between invaded and intact woodland sites (Fig. 1a).



Extended Data Figure 3 | Potential net N mineralization from laboratory assays. Net N-mineralization incubations from the laboratory, where soils were held at 70% water-holding capacity and 23 °C. That there was no difference between exotic grassland and native woodland habitats (one-way ANOVA, habitat as fixed effect: $P = 0.19$, $n = 10$) matches results from intact field cores (Fig. 1a), suggesting that differences in climate between sites, which may have varied in the field, did not alter general results for net N mineralization. Bars represent means \pm 1 s.e. We also ran the analysis with a Kruskal–Wallis test to account for unequal variances, although results were similar ($P = 0.43$, $n = 10$).



Extended Data Figure 4 | RGRs for seedlings in the outplanting experiment. RGRs were calculated after 8 months for the native seedlings (a–e) and the exotic seedlings (f, g). **a.** *Dodonaea viscosa* ('ā'ali'i). **b.** *Leptecophylla*

tameiameia (pūkiawe). **c.** *Osteomeles anthyllidifolia* ('ūlei). **d.** *Sophora chrysophylla* (māmane). **e.** *Acacia koa* (koa). **f.** *Morella faya* (faya). **g.** *Psidium guajava* (guava). Bars represent means \pm 1 s.e.