

# Disturbance and the (surprising?) role of ecosystem engineering in explaining spatial patterns of non-native plant establishment

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## Abstract

The Intermediate Disturbance Hypothesis is widely considered to be wrong but is rarely tested against alternative hypotheses. It predicts that soil disturbances and herbivory have identical impacts on species richness via identical mechanisms (reduction in biomass and in competition). An alternative hypothesis is that the specific traits of disturbance agents (small mammals) and plants differentially affects richness or abundance of different plant groups. We tested these hypotheses on a degu (*Octodon degus*) colony in central Chile. We ask whether native and non-native forbs respond differently to degu bioturbation on runways vs. herbivory on grazing lawns. We ask whether this can explain the increase in non-native plants on degu colonies. We found that biopedturbation did not explain the locations of non-native plants. We did not find direct evidence of grazing increasing non-native herbs either, but a grazing effect appears to be mediated by grass, which is the dominant cover. Further, we provide supplementary evidence to support our interpretation that a key mechanism of non-native spread is the formation of dry soil conditions on grazing lawns. Thus ecosystem engineering (alteration of soil qualities) may be an outcome of disturbances, which each interact with specific plant traits, to create the observed pattern of non-native spread in the colony. Based on these results we propose to extend Jentsch & White's (2019) concept of combined pulse/ disturbance events to the long-term process duality of ecosystem engineering/ disturbance.

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Abstract

The Intermediate Disturbance Hypothesis is widely considered to be wrong but is rarely tested against alternative hypotheses. It predicts that soil disturbances and herbivory have identical impacts on species

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Keywords: *Octodon degus* , non-native plants, bioturbation, herbivory, ecosystem engineering, disturbance

Words total: 5643

## Introduction

Disturbances and perturbations are key factors determining change in vegetation composition over time (Pickett & Cadenasso 2005). Herbivory and granivory may be considered to be endogenous “perturbations” rather than exogenous non-trophic disturbances *per se* (Proulx & Mazumender 1998). Others consider perturbations, along with disturbances e.g. to the soil, as all being forms of intermediate disturbance (Mackie & Curry 2001). According to the Intermediate Disturbance Hypothesis (IDH), the expected outcomes of herbivory are the same as, for example, those of soil disturbances (e.g. biopedturbation) (Proulx & Mazumender 1998). The IDH proposes that all forms of disturbance/ perturbation equivalently allow some species to escape competition through the destruction of other species’ biomass: in theory, two different kinds of disturbance regimes could be plotted as IDH humps, scaled, and an equivalence of rate of disturbance per species richness increment could be calculated. The IDH is widely believed to be wrong or at least non-predictive, although no alternative theory has been developed to explain how disturbance affects species composition or richness.

However, an interesting new conceptualization of disturbance is offered by Jentsch & White (2019). They proposed that all disturbances are simultaneously pulses, as every pulse/ disturbance is a multi-factorial event that increases some variables, decreases other variables, and perhaps does not affect another set of variables. This implies that different pulse/ disturbance events produce unique combinations of multifactorial effects.

In line with Jentsch & White’s (2019) multifactorial pulse/ disturbance event concept, some data demonstrates that the identities of the disturbing and disturbed species can affect disturbance outcomes, which should be expected if each kind of pulse/ disturbance produces a different set of increases and decreases in a unique set of variables. The literature on non-native herb establishment or invasion provides some examples of non-identical effects of disturbance or perturbation. For example, species identity—native or non-native—of both the disturbing/ perturbing (animal) and establishing (plant) species, has been shown to lead to different trajectories of plant community composition (e.g. invasion of non-native plants) (Parker et al. 2006). Soil disturbance by a native small mammal, but not herbivory by invasive herbivores, leads to expansion of a non-native herbaceous plant in central Chile (Torres-Díaz et al. 2012). A plausible explanation for how the identities of interacting species drive plant community change is that disturbance/ perturbation effects are highly sensitive to not only the type of disturbance/ perturbation (e.g. herbivory vs. mounds vs. runways), but also to the timing, spatial distribution, scale, etc. in which a given disturbance is carried out by different species (Maschinski & Witham 1989). Plant species tolerate and respond to these disturbances differently, with different competitive advantages (Grace 1991). For example, non-native plants are often ruderals adapted to intensive grazing, making them potentially superior competitors to native plants under herbivory

and large mammal trampling (Schiffman 1994, Kean & Crawley 2002, Fraser & Madson 2008, Seabloom et al. 2009).

Non-trophic disturbances of small mammals such as burrow digging have attracted attention since the origins of ecology (Whitford & Kay 1999; Kelt 2011). In addition, long-term studies have examined trophic impacts of small mammals on plant community change, for example in kangaroo rats (Brown et al. 2001). Small mammal disturbances/ perturbations frequently lead to increases in plant richness and diversity (Root-Bernstein & Ebensperger 2012). Native small mammal disturbances can also present a threat to native herbaceous plant communities by favouring grazing-adapted non-native plants (Torres-Díaz et al. 2012).

In this study we ask whether native and non-native herbaceous plants respond differently to degu runway-related bioperturbation (running up and down the runways) and to degu herbivory. The degu *Octodon degus* is a group-living, colonial burrow-dwelling rodent in central Chile (Ebensperger et al. 2019), that creates runways between burrow entrances and grazes aboveground (Figure 1; Madrigal et al. 2011). Their grazing lawns on colonies increase herbaceous plant richness along with other elements of biodiversity (Root-Bernstein et al. 2013; Root-Bernstein et al. 2014). Degu colonies exhibit central areas with high runway density and multiple-entrance burrows < 10 m apart, as well as extensive, less-dense peripheries constructed by dispersing juveniles and occupied during high degu-population years (Ebensperger et al. 2011, Quirici et al. 2011, Ebensperger et al. 2009). Bioperturbation is concentrated on runways especially before grazing lawn creation, but grazing occurs both on and off runways (Root-Bernstein et al. in submission). Surrounding grassland is expected to be mainly annual herbs, and at least half non-native (Deil et al. 2007).

We predict that the non-native herbs that are ruderal should be more common where bioturbation on runways is the highest. We also predict that non-native herbs adapted to herbivory, should be more common at sites with higher grazing pressure (Holmgren et al. 2000). We also expect the relative importance of herbivory and bioturbation on runways to vary with accumulated disturbance pressure at different locations of the colony, being highest in the older colony center. Finally, we predict that the impacts of perturbation and disturbance on the dominant native taxon, grasses, may mediate increases in non-native herbs (Holmgren et al. 2000, del Pozo et al. 2006).

## Materials and Methods

*Study site* . The study took place in September and October 2011 at the Estación Experimental Rinconada de Maipú (33°23' S, 70deg31' W, altitude 495 m), a field station of Universidad de Chile, Santiago, Chile. The field station consists of espinal (*Acacia cavensavanna*) subject to occasional fires (1-2 events per decade) and grazing by cattle and sheep (< 1 sheep per hectare over almost 900 ha, C. Araneda pers. comm. 2014), open grasslands dominated primarily by native perennial grasses, and denser matorral (evergreen shrubland), dominated by sclerophyllous shrubs and perennial herbs. The study site includes extensive degu colonies with lawns of herbaceous species, found essentially in the valleys of a small mountain range (less than 1000 m in elevation) forming one side of the field station.

*Plot selection* . We set up 13 “peripheral plots” and 10 “central plots” on the degu colony (Figure 2). Central plots were defined as 10 m x 10 m squares containing > 20 degu runways. Central plots were separated by at least one burrow system. Peripheral plots were defined as 10 m x 10 m squares with < 5 degu runways. The colony center-periphery distance at our field site is a radius of a minimum of approximately 300 m. Additional selection criteria for plots included evidence of fresh soil from recent excavation at burrows in or adjacent to the plot, and little or no evidence of rabbit droppings or cururo mounds. We considered the presence of fresh soil from excavations or the presence of fresh droppings to determine that a burrow was occupied (Ebensperger et al. 2011). There were no rabbit burrows within the degu colony. None of the plots included cururo (*Spalacopus cyanus*) mounds. Plots were oriented so that they were bisected by one or more degu runways forming a transect across the plot.

*Disturbance accumulation proxies*. Our methods are based on a form of space for time substitution (Pickett 1989). Following the advice of Pickett for appropriate design of space for time substitutions, we selected several space-for-time proxies, drawing on our knowledge of the local vegetation community change process

on degu colonies (Root-Bernstein et al. 2014). We also draw on long-term studies of prairie dog (*Cynomys ludovicianus*) colonies, since this species has a similar life history, ecological niche, and use of habitat, compared to degus. Prairie dog colonies expand outwards, so that central areas are older than peripheral areas (Whicker & Detling 1988). Since we have observed similar patterns for degus (see Introduction), our first proxy for disturbance and perturbation accumulation is the location, peripheral or central, of the plots examined. Over time, cover of tall grass in prairie dog colonies declines and is replaced by low herb cover, starting in the colony center and moving outwards to the periphery (Garrett et al. 1982, Archer et al. 1987). In central Chile, grasses are also dominant taxa that decline under herbivory (Holmgren et al. 2000, del Pozo et al. 2006). We therefore expect grass cover to be negatively correlated with age of colony sections, as well as potentially mediating the increase in other herb species through reduction in competition. A third proxy is derived from field observations at our research site: moss is common on runways and may be an early colonizer of runways. We thus used moss cover on runways as a third proxy for accumulated disturbance over time.

*Herbaceous plant data* . Along each runway-transect, we collected quadrat data at two distances from the runway-transect: over the runway (“on-runway”) (runways are about 8 cm wide) and 25 cm from the runway edge (“off-runway”). Each quadrat was a square cardboard frame of 10 cm<sup>2</sup> which we laid on the ground over the sample and photographed with digital cameras in autofocus mode at a distance of approximately 1 m from the ground. Five quadrats of on-runway samples were recorded every 2 m along the runway-transect at odd-numbered meter marks. Five quadrats of off-runway samples were recorded at even-numbered meter marks. Quadrats alternated to the left and right of the transect.

*Plant identification* . Plant species rarely completely overlapped each other due to an absolute low abundance in all plots and it was possible to identify each species from the photographs of the quadrats by the shape of cotyledons, leaves, and flowers. Names and distributions are according to Hoffmann (1978), except for mosses and grasses. We classified mosses as endemic following Larrain (2009), which indicated that the majority of mosses found in Chile are native to Chile. We were not able to identify grasses to species, but grasses were assumed to be mainly native or endemic species (Finot et al. 2011). Whenever herbs could not be identified by species, they were classed according to morphospecies according to cotyledon, colors and leaf shapes.

Plants were identified and counted using SamplePoint (in R), which records the classification into user-defined categories for pixels at crosshairs arranged in a regular grid over the digital photograph. We set our grid to 25 crosshairs per photo. Dead plants were not counted. When plants overlapped, we counted the top (visible) species only. Overlap occurred only rarely (estimated < 10% of all crosshairs). Cover was calculated as count number.

*Measures of herbivory* . We assessed herbivory by measuring the amount of rolled oats eaten from dishes. Oats are a favorite food of degus and are used to trap them (e.g. Ebensperger et al. 2011, Quirici et al. 2011). During the study season (spring), degus graze diurnally, alone or in loosely associated foraging groups (Lagos et al. 2009). We placed small metal dishes 11 cm in diameter in each plot, near the degu runway-transect. Dishes were filled with 25 g of rolled oats on the mornings of 3/10/11, 16/10/11 and 23/10/11. Dishes were checked and weighed with an electronic weight (Acculab GS-200) 24 hours later. The amount of oats eaten was calculated as the difference between the weight of oats with which the dish was filled the previous day, and the current weight. In some cases the dishes of oats gained up to 2 g of water from dew. The amount eaten is thus precise to within [?] 2 g. We did not observe ant activity at the oat dishes. Spillages were noted and not treated as eaten. Just prior to data collection, another experiment started in the same research site, which involved baiting Sherman traps with oats, and some of these traps were close to one of our central plots. Thus we did not collect foraging data from this plot.

*Measuring bioturbation on runways* . We measured bioturbation on runways as the amount of degu traffic along the runway-transect in each plot. We recorded degu traffic using tracking cards (Meserve 1981). We cut strips of rag paper approximately 32 cm x 7 cm (to fit within a degu runway). A central square on the paper strip about 7 cm<sup>2</sup> was colored in with a black hard pastel. Two such tracking cards were placed

end-to-end along the runway-transect in each plot, and fixed in place with nails. Tracking cards were put in place on 17/10/11 and collected 27/10/11. Collected tracking cards were sprayed with a fixative for pastels to prevent smudging. Tracking cards were photographed and the images were analyzed in Adobe Photoshop (r), using the “count” function. We counted discrete toe and palm marks (“foot marks”). We summed the total number of foot marks for the two tracking cards for each site to yield a measure of bioturbation along runways. We observed only one footprint from another species, not identified. We did not collect bioturbation data for the site omitted from the foraging data collection.

*Statistical note* . Because space-for-time substitutions involve interpretive assumptions that are not present in long-term manipulative experiments, we chose to use the most conservative (least powerful) statistical approaches available to decrease the likelihood of detecting ecologically weak effects (Amrhein et al. 2019).

## Results

*Plant community description* . We observed 10 native or endemic forb species or morphospecies, two taxonomic groups dominated by native species (mosses and grasses) and 3 non-native species along all of our transects. There was no significant difference in cover per taxa between native and non-native forbs (Kruskal-Wallis test,  $H = 0.092$ ,  $df = 1$ ,  $p = 0.756$ ).

*Native and non-native herb distributions* . Natives and non-natives were distributed differently across the plot locations, with non-native cover higher in central plots, and native cover higher in peripheral plots, which was significantly different from the expected cover distribution ( $\chi^2$  test,  $\chi^2 = 177.73$ ,  $df = 3$ ,  $p = 2.2 \times 10^{-16}$ ). At a finer scale, natives and non-natives were also distributed differently on or away from runways: native cover was higher off of runways than on, and higher than non-natives; non-natives were also higher off runways ( $\chi^2$  test,  $\chi^2 = 232.84$ ,  $df = 3$ ,  $p = 2.2 \times 10^{-16}$ ). We found an interaction between colony location (center/ periphery) and runway location (on/ off) on the total cover of non-native species: the cover of non-natives is higher in colony center than peripheries, and higher on runways than off runways, a distribution significantly different from expected (Figure 3;  $\chi^2$  test,  $\chi^2 = 61.5$ ,  $df = 3$ ,  $p = 2.8 \times 10^{-13}$ ).

*Space for time proxies* . Mean grass cover on off-runway quadrats, the proxy for colony age, was not lower in central plots, differing from our expectation (Student t-test,  $t = 0.193$ ,  $df = 15.98$ ,  $p = 0.84$ ). As the grass proxy, mean grass cover on off-runway quadrats, decreased, the ratio of non-native to native herb abundance increased ( $r = -0.684$ ,  $df = 19$ ,  $p = 0.0006$ ). Focusing on moss as a proxy of colony age, we find that the mean percent cover of moss different significantly across on-off and center-periphery, and was highest on peripheral runways ( $\chi^2$  test,  $\chi^2=38.03$ ,  $df = 3$ ,  $p = 2.785 \times 10^{-08}$ ).

*Grass distribution as a mediator of competition with other herbs* . The ratio of grass cover on vs. off runways per plot was not correlated to the general distribution of other herbs on and off runways per plot, with grass tending to have relatively greater cover on runways, unlike other herbs which tended to have relatively greater cover off runways (Figure 4;  $r = 0.073$ ,  $df = 19$ ,  $p$ -value = 0.75).

*Herbivory and bioturbation on runways*. The average amount of oats eaten per day did not differ between peripheral and central plots (Student t-test,  $t = 1.31$ ,  $df = 21$ ,  $p = 0.203$ ). The number of foot marks registered on runways also did not differ between peripheral and central plots (Student t-test,  $t = 0.54$ ,  $df = 21$ ,  $p = 0.592$ ). Foot marks and total amount of oats (on and off runways) eaten in each plot were highly correlated ( $r = 0.99$ ,  $df = 19$ ,  $p < 0.0001$ ). Foot marks increased as the percent cover of grass on *off-runway* quadrats increased ( $r = 0.508$ ,  $df = 21$ ,  $p = 0.0134$ ). However, there was only a weak, non-significant relation between percent grass cover *on runways* and foot marks ( $r = 0.262$ ,  $df = 19$ ,  $p = 0.251$ ). Biopedturbation was not correlated with the ratio of non-native to native herbs ( $r = -0.189$ ,  $df = 18$ ,  $p = 0.43$ ).

## Discussion

We found that richness of native non-woody herbaceous taxa ( $N = 11$ ) was almost four times that of non-native species ( $N = 3$ ) on degu colonies. The number of native or endemic species may have been underestimated as we were not able to identify mosses or grasses to species level. As expected, the cover of non-native plants was higher in the center of the colony, compared to the periphery. At a smaller scale,

the runways also influenced the distribution of native and non-native plants. Non-native plants had higher cover on runways in central plots than in peripheral plots.

We find at least partial support for our interpretation of peripheral colony sites as having been formed more recently, and/or occupied more sporadically over time, compared to colony centers. The grass proxy for accumulated disturbance did not lend support to the center/ periphery split, with patches of grass found in both peripheral and central plots. Moss, as expected, had different distributions across central and peripheral plots. Although we expected moss to increase in extent over time on runways, we interpret the result to mean that moss is an early colonizer of runways created through biopedturbation (as expected), but reduces in extent as the microhabitat becomes more dry (see below).

The distribution of high and low biopedturbation and herbivory were not explained by colony position, but were explained by grass cover off runways. As grass cover in the off-runway quadrats increased, foot traffic on runways and amount of herbivory on oats increased. Grass avoidance may thus mediate degu biopedturbation on runways. Grass was also expected to mediate plant composition change through herbivory on grass reducing its competition with other herbs. Indeed, as grass cover decreased off runways, the relative cover of non-native species increased. Although degus eat both grasses and forbs, including the non-native forbs we observed in this study (Quirici et al. 2010), the persistence of grass along runway edges suggests that it is not opportunistically eaten (unlike the oats). In addition to eating grasses, degus also gather them to line their nests, which requires long grass (pers. obs. MR-B): both of these might account for reduction in grass off runways.

Our interpretation of the temporal process resulting in the observed spatial pattern of non-native herb distribution is that grass reduction off runways over time leads to increased non-native populations and the eventual colonization of the runway edge by non-natives. However, it is not clear that eventual grass reduction on runways is what allows non-natives to colonize runway edges in the center of the colony, since the grass did not reliably disappear in the colony center and was uncorrelated with other herb distributions relative to runway structure. Thus, non-native expansion to runway edges may not be mediated by competition with grass, but by some other mechanism.

Ecosystem engineering effects on the soil may help explain how the increase in non-natives first seen off runways spreads to runway edges. Runways are exposed to the sun. Grazing lawns, with vegetation only ~2-4 cm high, can be expected to lead to lowered evapotranspiration and less water being drawn into the soil by plant roots. These effects may lead to drier soils: the loss of or lack of moss in central runways may also point to drier soils in colony centers. Although we did not measure soil moisture in this study, as we did not anticipate its importance, other researchers have measured soil characteristics at the same research site. Bauer et al. (2013) show that soil penetrability, directly related to soil moisture (Ebensperger & Bocinovic 2000), is highest at sites with shade cover and lowest at sites with the most bare earth (see also Ovalle & Avedaño 1984). This bare earth would mainly correspond to areas of degu biopedturbation. Ebensperger & Bocinovic (2000) also show that in colony centers, soil moisture declines dramatically during the low-precipitation months (summer and autumn). At the same time, where the grass is less productive due to being kept short through herbivory lawns, this may lead directly to a reduced competitive advantage of grass. In fact, the two most abundant of the three non-native species observed at our field site, *Camissonia sp.*, and *Erodium cicutarium*, are considered to be desert-adapted species and poor competitors with grass (Ehlerginger et al. 1979; Stamp 1984; Holmgren et al. 2000; Schutzenhofer & Valone 2006), while only *E. moschatum*, which was much less abundant, is considered ruderal (IUCN Invasive Species Database, <http://www.iucngisd.org/gisd/species.php?sc=518>). If an important impact of degus is via soil aridity in grazing lawns, this might also account for Madrigal et al. (2011)'s finding that degu presence resulted in a numerical dominance of non-native species. Their research site is more arid than ours, and a further increase in soil aridity may more strongly favour non-native desert-adapted herbs.

In summary, contrary to the implication of the IDH, non-trophic disturbance (biopedturbation) and perturbation (herbivory), appear to have different impacts that interact with one another and with specific plant traits to create ecosystem engineering that favours non-native herbs on degu colonies (see Figure 5). We

found the least evidence for impacts of disturbance via biopedturbation. Biopedturbation clearly creates the runways, which appears to initially favour mosses. However, ongoing current biopedturbation disturbance effects could not clearly be separated from grazing effects as they were highly correlated. Further, only the least-abundant non-native herb found is ruderal. Perturbation in the form of grazing effects could be interpreted from the reduction in grass, relative to other herbs, off runways, associated with increasing non-native plants. We did not anticipate that ecosystem engineering affecting soil properties (soil aridity) might explain the expansion of non-native species, since the majority of literature on non-native herbs in central Chile focuses on their adaptations to herbivory rather than aridity, and disturbance/ perturbation literatures focus on the mechanisms of competition and biomass loss, without linking to ecosystem engineering. However, pre-existing measurements of soil hardness and moisture at the same degu colony, and the desert adaptations of the most abundant non-native species, provide evidence for the hypothesis that ecosystem engineering of the soil conditions contributes to the spread of non-native herbaceous species on degu colonies.

In general terms, these results further expand the notion of pulse/ disturbance developed by Jentsch & White (2019). Not only are pulse/ disturbance events multi-factorial, they have multi-temporal impacts that develop over time in ways that do not simply reduce competition or increase biomass loss (they may not do this at all), but also may accumulate or interact to form what we call ecosystem engineering. Wilby et al. (2001) come to a similar conclusion in a study of desert porcupines. However, the vast majority of other studies either do not mention both concepts together, or contrast the supposedly independent and indeed *opposite* processes of disturbance and ecosystem engineering (e.g. Soissons et al. 2019). This conception of ecosystem engineering as opposite to disturbance can partly be understood from the perspective where pulses are also opposite to, rather than dimensions of, disturbance. The lack of integration of ecosystem engineering ecology with disturbance ecology also simply reflects the different, and non-integrated literatures from plant ecology, animal ecology, and plant-animal interaction ecology (see Root-Bernstein 2013). Further developing the conceptual link between pulse/ disturbances and ecosystem engineering offers an interesting direction for development of theoretical alternatives to the IDH.

#### Data Accessibility Statement

Data will be uploaded to Dryad upon manuscript acceptance.

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Figure 1. Left, a degu runway recently formed by pushing the grass down or aside. Right, more established

degu runway in a degu grazing lawn. Both photos are taken during 2013 in early spring. Photos © MR-B.

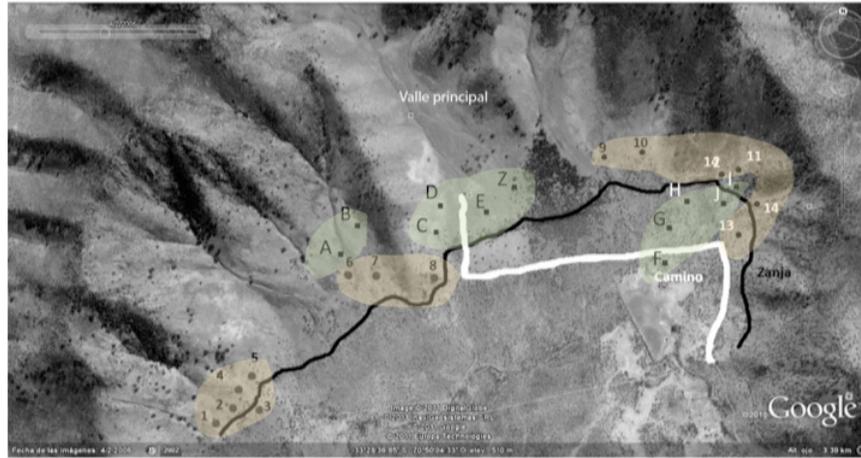


Figure 2. The field site with the central and peripheral plots marked. The letters highlighted in green are the ten central plots, and the numbers highlighted in yellow are the thirteen peripheral plots. The white line represents an access road and the black line represents a dry ditch.

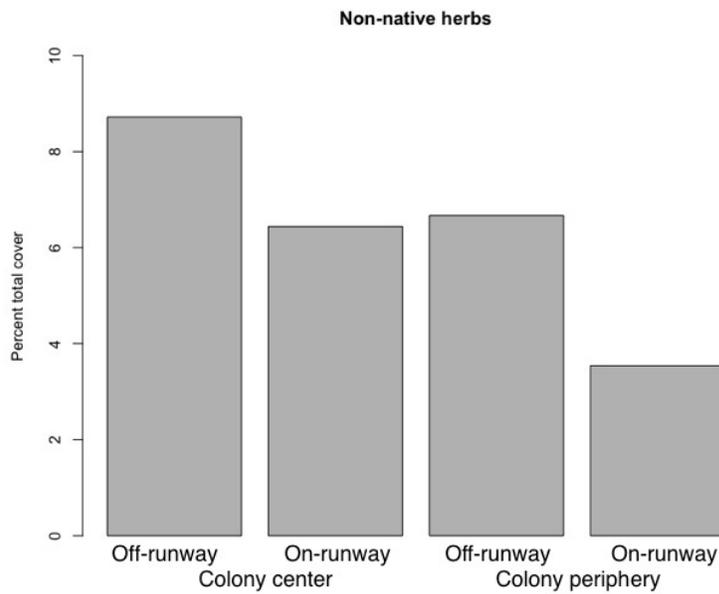


Figure 3. The distribution of non-native herbs across colony areas and on and off runways, expressed as a percent of the total cover available in each category.

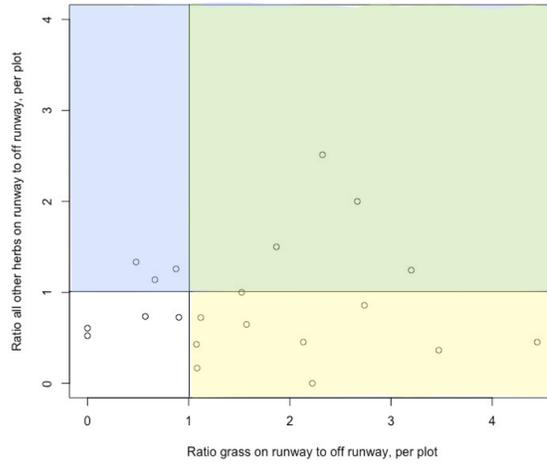


Figure 4. Each point represents a plot, and its ratio of grass on the runway to off the runway, plotted against its ratio of all other herbs (forbs) on the runway to off the runway. The shaded areas indicate where there are more grasses or more other herbs (forbs) off runways than on runways, the unshaded area has fewer grasses AND forbs off runways than on runways. Where the blue and yellow shading overlap and make green, there is more grass on the runways than off, AND more of all other herbs (forbs) on the runways than off: thus there are more herbs of all kinds on the runways than off. Note that the majority of the plots are in the yellow section, in which grass is relatively more abundant on runways and other herbs are relatively less abundant on runways.

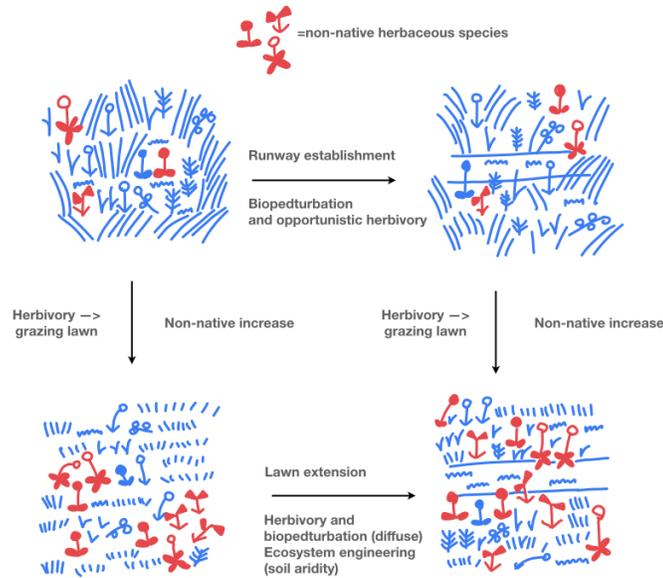


Figure 5. Diagram of the mechanisms of disturbance and their accumulation over time into an ecosystem engineering effect, which favours non-native dry-adapted species.