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Invasive slugs as under-appreciated obstacles to rare plant restoration: evidence from the Hawaiian Islands

Stephanie M. Joe · Curtis C. Daehler

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Abstract Introduced slugs have invaded many parts of the world where they were recognized as important pests of gardens and agriculture, but we know little about the effects of introduced slugs on rare plants in natural areas. The Hawaiian Islands have no native slugs, but over a dozen introduced slug species are now established. We reviewed Rare Plant Recovery Plans produced by the U.S. Fish and Wildlife Service for Hawaii and found that introduced slugs were specifically mentioned as threats or potential threats to 59 rare plant species (22% of all endangered and threatened plants), based mainly on anecdotal observations by field biologists. We then initiated an experimental field study to assess the impact of slug herbivory on the growth and survival of two endangered plant species (*Cyanea superba*, and *Schidea obovata*), one non-endangered native species (*Nestegis sandwicensis*) and two co-occurring invasive plant species (*Psidium cattleianum* and *Clidemia hirta*). In mesic forest on the Island of Oahu, we tracked the fate of outplanted seedlings in replicated 1 m^2 plots, with and without slug control. Slugs decreased seedling survival of the endangered species by 51%, on average. Slugs did not significantly affect survival of the non-endangered or invasive plant species. Introduced slugs seem to be under-appreciated as a direct cause of plant endangerment. Invasive slugs may also facilitate the success of some invasive plant species by reducing competition with more palatable, native plant competitors. Slug control measures are relatively inexpensive and could facilitate rare plant establishment and population recovery.

S. M. Joe (✉) · C. C. Daehler
Department of Botany, University of Hawaii,
3190 Maile Way, Honolulu, HI 96822, USA
e-mail: sjoe@hawaii.edu

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Introduction

The deliberate and accidental introduction of species around the world has altered native ecological communities and contributed to declines of many native plant species. For instance, Pimentel et al. (2005) report that approximately 42% of endangered and threatened species in the United States are at risk due to direct and indirect effects of introduced pests. In other regions of the world, introduced species may threaten up to 80% of rare native species (Armstrong 1995).

The endangerment and loss of species is particularly acute on oceanic islands that have unusually high rates of endemism (Kaneshiro 1988). Since the arrival of Europeans in the Hawaiian Islands some 250 years ago, 72 described plant species (representing 7% of the flora) are thought to have been driven to extinction (Daehler, unpublished data). In the Hawaiian Islands, where the majority of remaining natural areas is now protected from development, invasive species are the primary threat to the persistence of native flora and fauna (Loope 1992). For native Hawaiian plants, herbivory by invasive animals and competition from invasive plants and are two of the most important factors responsible for declining populations (Bruegmann et al. 2002).

Slugs (Mollusca: Gastropoda) are generalist herbivores (Rathke 1985) that feed principally on plant seedlings and low-statured herbs (Hanley et al. 1995). In European grasslands, slugs and snails affect seedling survival rates (Hulme 1994; Buschmann et al. 2005), shift relative abundances of palatable versus resistant species (Hanley et al. 1996; Wilby and Brown 2001), and may influence both the rate and direction of plant succession (Cates and Orians 1975; Briner and Frank 1998). In forest habitats, application of molluscicide increases seedling recruitment of perennial herbs (Christel et al. 2002). Slugs can also affect woody species. For example, Nystrand and Granström (1997) find that seedling predation by slugs causes a three-fold reduction in Scots Pine seedling recruitment. Even among adult plants, slugs can greatly reduce plant fitness by consuming large amounts of photosynthetic tissue and damaging plant reproductive organs (Rai and Tripathi 1985; Breadmore and Kirk 1998; Scherber et al. 2003).

According to the plant-defense hypothesis (Feeny 1992), plants evolve anti-herbivore defenses in response to herbivore pressure. Consequently, plants native to environments where herbivory is intense should be better defended than plants that evolved in relative isolation from herbivores (Bowen and VanVuren 1997). When non-native herbivores are introduced into a plant community, species composition can change rapidly due to weak herbivore defenses and/or high invader densities, and some plant species can be pushed towards extinction (Schreiner 1997; Coomes et al. 2003). This is a critical issue in many island ecosystems, including the Hawaiian Islands (Stone 1985), where several important guilds of herbivores were historically lacking, and endemism in the flora and fauna is high because of the islands' extreme isolation.

Hawaii lacks native slugs, but has a rich native snail fauna (Gagné and Christenson 1985; Cowie 1995). Yet, there is no evidence that these native snails consume live plant tissue. Tree snails of the genus *Achatinella* (Achatinellidae), for example, are believed to feed exclusively on epiphytic algae and fungi (Hadfield and Mountain 1980; Severns 1981). Other native snails are thought to feed on plant litter (R.H. Cowie, personal communication). Although the diets of most groups of native snails have yet to be quantitatively studied, the conspicuous absence of even anecdotal reports of native snails consuming live plant tissue in Hawaii suggests that Hawaiian plants have historically experienced very little native mollusk herbivory.

At least 12 introduced slug species are now established in Hawaii (Cowie 1997, 1999), and non-native slugs and herbivorous snails have also invaded many other Pacific Islands, often through accidental introductions associated with horticultural trade (Beck et al. 1980; Barker 1999; Cowie 2005). Introduced snails and slugs are widely recognized as pest of gardens and agriculture (Cowie 2005), but no formal studies have been conducted to investigate the impacts of slugs on native flora of Pacific Islands. In freshwater aquatic environments, intense browsing by the invasive apple snail (*Pomacea canaliculata*) can completely transform tropical wetland ecosystems (Carlsson et al. 2004) so it seems feasible that herbivorous snail or slug invaders are also having major impacts in terrestrial ecosystems on tropical islands.

The objective of our study was to assess whether non-native slugs on Pacific Islands (and the Hawaiian Islands in particular) are altering plant community composition in natural areas and endangering populations of rare native plant species. To estimate the number of rare native species vulnerable to slug herbivory, we first reviewed Rare Plant Recovery Plans published by the U.S. Fish and Wildlife Service (USFWS) and tallied the number of plant species for which non-native slugs were mentioned as known, imminent or potential threats. We then used a replicated field experiment to investigate the effects of slug herbivory on native and invasive seedling growth and survival for two endangered endemic species, one non-endangered endemic species and two invasive plants in a mesic forest on the island of Oahu, Hawaii. We hypothesized that non-native slugs would have the largest impacts on the endangered species, moderate impacts on the non-endangered endemic species, and little impact on the two common invasive species.

Materials and methods

Review of Rare Plant Recovery Plans

We reviewed some 1500 pages of Rare Plant Recovery Plans published by the U.S. Fish and Wildlife Service (USFWS) covering the 273 endangered and threatened species in Hawaii in order to determine how often slugs were mentioned as a threat or potential obstacle in the recovery of rare plant populations. We then tallied the total number of plant species affected and recorded the family of each species so that we could assess the range of plants affected. We also recorded the context in which slugs were mentioned as a threat to each rare plant species so as to illustrate the quality and quantity of available information.

Field study

We carried out a field study to assess the effects of slugs on seedling growth and survival at the Kahanahaiki Management Unit (KMU) on the Island of Oahu. KMU is a 36.5 ha parcel of montane, mesic forest (Gagné and Cuddihy 1999) owned and managed by the U.S. Army for the preservation of native species. Situated at 700 m elevation on the northeast rim of Makua Valley, in the Waianae Mountains, the KMU provides habitat for 12 endangered plant and two endangered animal species. Control of feral, alien ungulates began in 1996 with the construction of a fence and eradication of pigs and goats within this area, an outcome that was largely achieved within two years. Rodents are controlled using snap traps and rodenticide deployed seasonally throughout the enclosure (Akau et al. 2006). Four slug species are present in the KMU: *Deroceras laeve* Müller (Agriolimacidae), *Limacus flavus* Linnaeus (Limacidae), *Limax maximus* Linnaeus (Limacidae) and *Meghimatium striatum* van Hasselt (Philomycidae).

Study species

For our field experiment, we selected two endangered species, *Cyanea superba* (Cham.) A. Gray (Campanulaceae) and *Schiedea obovata* (Sherff) W. L. Wagner & Weller (Caryophyllaceae), based on availability of seedlings for experimental outplanting and their historic occurrence within the KMU. In the Rare Plant Recovery Plans, no specific information was available regarding slug damage to *S. obovata*, while slugs were listed as a ''current threat'' to *C. superba*, with no further information available (Table 1). A non-endangered endemic species (*Nestegis sandwicensis* (A. Gray) O. Deg., I. Deg. & L. A. S. Johnson; Oleaceae) was selected for comparison, again based on seedling availability and appropriateness of habitat, and the two most abundant invasive species, *Psidium cattleianum* Sabine (strawberry guava; Myrtaceae) and *Clidemia hirta* (L.) D. Don (Koster's curse; Melastomataceae), were included in the experiment to provide an additional contrast with the endangered species. *Cyanea superba* is a palm-like tree reaching heights of 4–6 m when mature. Although two subspecies of *C. superba* are recognized, we do not distinguish them here because one of them, *C. superba regina*, is probably extinct (Wagner et al. 1999). The extant subspecies, *C. superba superba*, is referred to here as *C. superba*. Presently, it is known from only one small population in the KMU, which in 1998, numbered only five plants (USFWS 1998). *Schiedea obovata* is a branching shrub growing to 3–10 dm height. Historically, *S. obovata* was found throughout the Waianae mountain range scattered on ridges and slopes in diverse mesic forest (Wagner et al. 1999) but by 1998 it had dwindled to four populations with a total of 12 individuals (USFWS 1998). *Nestegis sandwicensis* is an endemic tree 8–25 m tall found in dry to mesic forest on all of the main Hawaiian islands (except Niihau) (Wagner et al. 1999), and it is locally common at the KMU. Both *P. cattleianum* and *C. hirta* are highly invasive weeds native to Central and South America. In Hawaii, they form dense, monotypic stands in mesic to wet areas ranging from 10–1500 m elevation. *P. cattleianum* is a small tree 2–6 m tall while *C. hirta* is a perennial shrub 0.5–3 m tall.

Slug monitoring

We assessed slug species composition and abundance using a total of 30 refugia traps consisting of 1 m^2 pieces of unwaxed cardboard (Hawkins et al. 1998) placed on the ground within 1 m of each study plot.

Table 1 Examples of available information on threats of non-native slugs to rare plants, as extracted from U.S. Fish and Wildlife Service (USFWS) Rare Plant Recovery Plans. The complete table listing available information for all 59 species is available at http://www.botany.hawaii.edu/faculty/daehler/Joe_and_Daehler_Table1_complete.pdf

Family	Species	Description of slug threat	Citation
Campanulaceae	*Cyanea superba* (Cham.) A. Gray	[Slugs appear in a table of current threats to this species; no further information available]	USFWS 1998, p. 29
Gesneriaceae	*Cyrtandra kaulantha* St. John & Storey	“Threats to the species include pigs and slugs that eat this plant.”	USFWS 2005, p. 24880
Malvaceae	*Abutilon sandwicense* (O. Deg.) Christoph.	“Rats and slugs have been cited as probable threats to the Waianae Recovery Plan taxa because they eat the fruits and seeds, and chew on the stems, foliage, and seedlings.”	USFWS 1995, pp. 12–13
Rosaceae	*Acaena exigua* A. Gray	“[C]onsumption of vegetative or floral parts of this species by alien slugs and/or rats could have been a factor in the decline of the species and could continue to be a critical limiting factor.”	USFWS 1997, p. 10
Ranunculaceae	*Ranunculus hawaiensis* Gray	“Threats to the species include competition from nonnative plants, and damage from slugs.”	USFWS 2005, p. 24884
Violaceae	*Viola lanaiensis* Becker	“Slug damage and live slugs have been observed on *V. lanaiensis*.”	USFWS 1994, p. 61

The traps degraded quickly, so we replaced them once a month following a count of slugs on top of or underneath the cardboard square. This sampling method is biased towards detecting larger individuals (McCoy 1999), as are other sampling methods such as timed searches. Our objective of slug sampling was to document the presence of slug species near the plots and to obtain relative estimates of their abundance over time and space, so we consider the refugia sampling method as adequate for this purpose.

Seedling preparation

Schiedea obovata and *C. superba* were grown from seed stored by the Lyon Arboretum Mircropropagation Laboratory (University of Hawaii at Manoa, Honolulu, HI). We reared plants in a greenhouse for six months and then moved them to KMU where they remained in pots on elevated flats for another 30 days. *N. sandwicensis*, *C. hirta*, and *P. cattleianum* were collected from natural field seedlings and transplanted into pots. All plants remained in pots onsite for 30 days to standardize conditions for both wild and greenhouse reared species. At the start of the experiment, seedling heights differed between species, but within-species variance was relatively small. Average starting heights and standard deviations were as follows: *S. ovata* 43 ± 10 mm, *C. superba*, 28 ± 10 mm, *N. sandwicensis* 41 ± 14 mm, *C. hirta* 18 ± 5 mm, and *P. cattleianum* 21 ± 11 mm.

Experimental design

In February 2004, we established 30 plots of 1 m^2 along a contour close to the bottom of Kahanahaiki gulch. The plots fell within an area of roughly 0.6 ha. Fully randomized placement within this area was impossible due a steep slope and presence of dense stands of *P. cattleianum*. Instead, we established plots at sites where the slope was less than 35 degrees and trees did not interfere with placement. Plots were spaced at least 5 m apart. We randomly assigned half of the plots to receive physical and chemical barriers to slugs, while the remaining plots were exposed to natural levels of slug herbivory. In this paper, we refer to the former as the “slug-excluded” treatment and the latter as the “slug-exposed” treatment (control). The slug-excluded treatment would have also excluded snails, but herbivorous snails are not known from the area (see also *Slug monitoring at the field site* below).

We enclosed all slug-excluded plots with a copper mesh fence, 15 cm high, buried to a depth of 5 cm and topped with a 5 cm strip of zinc tape. While copper barriers repel slugs better than barriers constructed of other materials (Hata et al. 1997), the effect is enhanced when copper is combined with zinc (S. Joe unpublished data). The slug-exposed treatment had a galvanized steel mesh fence of similar dimensions, but we cut 5 cm x 5 cm holes into the bottom at 10 cm intervals to allow entry by slugs. We purchased the copper and galvanized steel hardware cloth from TWP Wire Mesh Inc (Berkeley, CA). The material had a wire diameter of 0.7 mm and a mesh density of 3 squares per cm. We purchased zinc tape from BAC Corrosion Control Ltd. (Telford, UK).

We placed a waterproof bait station containing the molluscicide Corry's Slug and Snail Death (Corry & Co. Limited, North Bend, Washington, USA) at the center of each slug-excluded plot to eliminate any slugs that managed to breach the barrier, and to kill any resident slugs. Bait was replenished every 20 days. We placed empty bait stations at the centers of slug-exposed plots.

Prior to outplanting, we cleared all plots of pre-existing vegetation. In half of each plot, we transplanted seedlings ordered randomly in three columns of seven plants (*S. obovata*, $n = 3$; *N. sandwicensis*, $n = 3$; *C. superba*, $n = 5$; *C. hirta*, $n = 5$; *P. cattleianum*, $n = 5$). Columns were spaced 8.3 cm apart and plants within each column were 7 cm apart. We left the other half of the plot fallow to monitor natural seedling recruitment. We planted the seedlings on 23 February 2004, and monitored them through 1 September 2004, for a total of 190 days. We recorded growth (height, number of leaves), herbivore damage to leaves (average percent leaf area missing per leaf, determined by visual inspection of each leaf), and survival of transplanted seedlings every 10 days. We assessed natural seedling regeneration in the fallow half of the plot at the end of the study, but natural seedlings germinating among the transplanted seedlings were pulled throughout the experiment. At 10-day intervals, we added 1.9 l of water to each plot to minimize transplant losses due to drought, and to encourage germination from the seed bank in the fallow side of the plot.

Statistical analysis

We performed all statistical analyses with Minitab® Release 14 (Ryan et al. 2005). We averaged seedling measurements for each species in a plot. Thus, for most statistical comparisons, the sample size was 15 plots per treatment. For analysis of growth and herbivory, the sample size for each species ranged from 12–15 per treatment because a few plots had no surviving representatives of some species at the end of the experiment. Two-way analysis of variance (ANOVA) was used to assess the effects of plant species, treatment (slug-exposed versus slug-excluded) and their interaction on the responses variables. Relative growth rate, in terms of height, was measured as the natural log of the final plant height minus the initial plant height (Harper 1977). For all growth parameters, variance between groups was similar and residuals were normally distributed. When ANOVA detected a significant plant species effect, post-hoc contrasts were employed to identifiy differences between individual plant species using Tukey's test for multiple comparisons.

Results

Rare Plant Recovery Plans

Slugs were reported as a threat or potential threat to 22% (59 out of 273) of Hawaiian plant species listed as threatened or endangered. A few examples are given to illustrate the nature of the available information (Table 1). No specific information was available for *Schidea obovata*, one of the endangered species used in our study, while for our other endangered plant, *Cyanea superba*, slugs were simply identified as a ''current threat'' to this species with no further information (Table 1). The species listed as being threatened by slugs were generally woody or semi-woody plants, and they represented nine different plant families. In all cases, the available information was anecdotal, including reports of slugs climbing on plants or damage that appeared to be caused by slugs.

Slug monitoring at the field site

Slugs were present in the immediate area of the field experiment for the duration of the study (Fig. 1). There was no significant difference in the number of slugs counted adjacent to slug-exposed versus slug-excluded plots (paired *t*-test, $t = -1.19$, $P = 0.3$). Changes in total slug numbers tracked monthly rainfall (USGS 2004) (Pearson correlation coefficient, $r = 0.82$, Fig. 1); however, this correlation was not statistically significant ($P = 0.09$), probably because only five monthly data points were available (Fig. 1). No herbivorous snails were encountered in the refuge traps.

Plant growth and herbivore damage

Plant growth in terms of height (Fig. 2) and number of leaves per plant (Fig. 3) varied among species

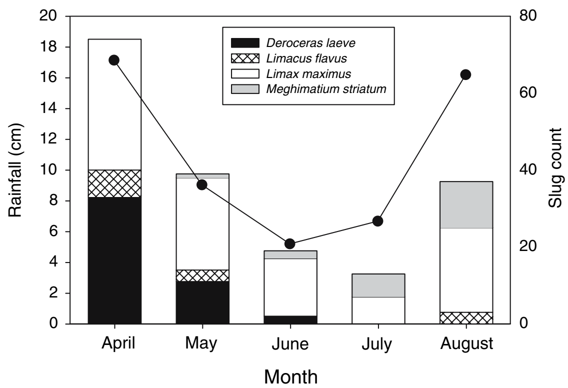

Fig. 1 Counts of slugs at cardboard traps April–August 2004 (bars) showing seasonal changes in the abundance of different species and monthly rainfall (solid circles). Results are pooled for traps near slug-excluded and slug-exposed treatments as there were no significant differences between treatments

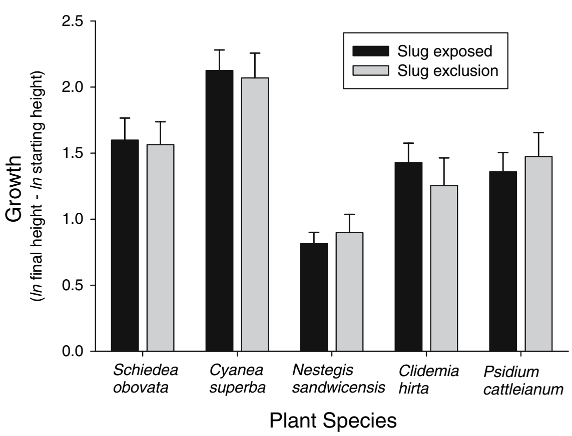

Fig. 2 Height growth after 190 days in the slug-exposed and slug-excluded treatment. There were no significant differences between treatments. Bars indicate one SEM

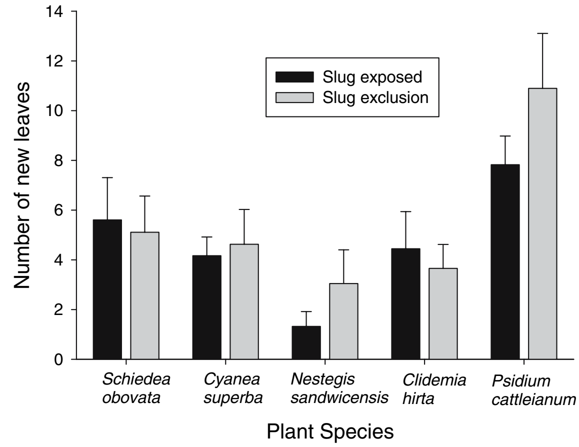

Fig. 3 Net change in number of leaves per plant after 190 days in the slug-exposed vs. slug-excluded treatment. There were no significant difference between treatments. Bars indicate one SEM

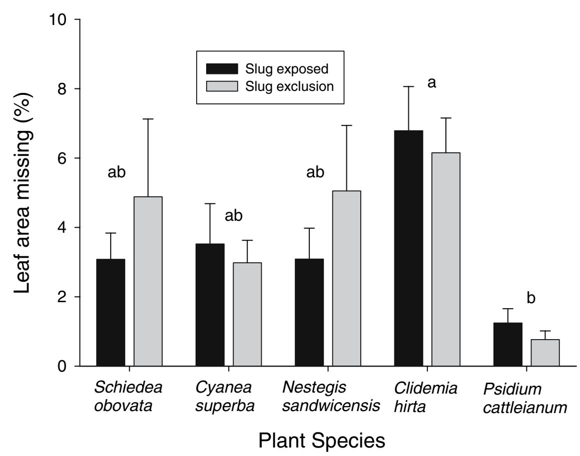

Fig. 4 Average leaf area missing per leaf per plant in the slug-exposed and slug-excluded treatment after 190 days. There were no significant differences between treatments. Differing lowercase letters indicate significant differences between species (Tukey HSD, $P < 0.05$). Bars indicate one SEM

($P < 0.001$, $F_{4,133} = 20.3$, and $F_{4,133} = 11.0$, respectively). But for both responses, the slug treatment and the slug treatment-by-plant species interaction were not significant (all $P > 0.4$).

There were no significant differences in final leaf damage between the slug treatments ($F_{1,133} = 0.34$, $P = 0.6$) (Fig. 4), but there were significant differences in damage among species independent of slug treatment ($F_{4,133} = 6.2$, $P < 0.001$). Post-hoc contrasts indicated that the species with the most leaf damage

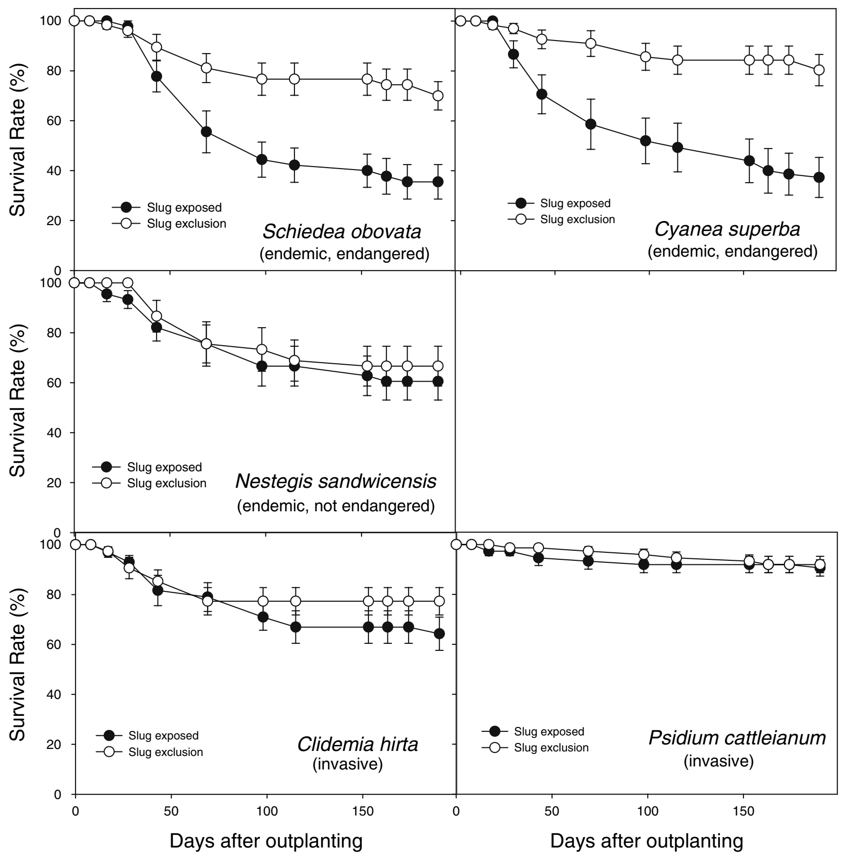

Fig. 5 Seedling survival over time in slug-exposed and slug-excluded plots by species over 190 days. Bars are ± one SEM, representing variation among replicate plots. *Schidea obovata* and *Cyanea superba* had significantly higher final survival in the slug-excluded treatment ($P < 0.05$)

(*C. hirta*, 7%) had a significantly more leaf area loss than the species with the least leaf damage (*P. cattleianum*, 1%, $P < 0.001$).

Seedling Survival

For final survival after 190 days, there was a significant interaction between plant species and slug treatment ($F_{1,4} = 4.2$, $P < 0.01$), indicating that the effect of slugs varied by plant species. We found significant differences in survival between the slug-excluded and slug exposed treatments for two of the five species (Fig. 5). When exposed to slugs, both endangered species (*C. superba* and *S. obovata*) experienced significantly higher final mortality (Tukey's HSD, $P < 0.01$). Final survival rates for *C. superba* and *S. obovata* were 49% and 53% lower, respectively, in the slug-exposed treatments. In examining the pattern of morality over time (Fig. 5), the mortality rate (as indicated by the slope of the survival rates plotted in Fig. 5), tended to be highest for the two endangered species early in the experiment in the slug-exposed treatment, suggesting that smaller plants are most susceptible to slug damage.

Comparisons across species

While differences between the two tree species, *N. sandwicensis* and *P. cattleianum*, were non-significant in the slug-excluded treatment (Tukey's HSD, $P > 0$ .05), in the slug-exposed treatment the native *N. sandwicensis* had significantly lower survival than the alien *P. cattleianum* (Tukey's HSD, $P < 0.05$). In the slug-exposed treatment, the small endangered tree, *C. superba* differed significantly from *P. cattleianum* (Tukey's HSD, $P < 0.001$), and again, this difference in survival was eliminated when slugs were excluded (Tukey's HSD, $P = 0.95$). A similar trend was observed in comparing native and invasive shrubs. *Schiedea obovata*, when exposed to slugs, had significantly higher mortality than invasive *C. hirta* (Tukey's HSD, $P = 0.05$), but *C. obovata*'s survival rate did not differ from *C. hirta* under slug-excluded conditions.

Natural seedling recruitment

Only 68 seedlings emerged naturally from all the plots during the 190-day study, and *C. hirta* represented 84% of the seedlings. There was no statistical difference between slug-exposed and slug-excluded plots in *C. hirta* emergence. Statistical analysis for other species was not possible due to the small number of observed seedlings.

Discussion

Invasive slugs as threats to rare plant restoration

Although recent research attracts attention to the widespread replacement of endemic terrestrial mollusk faunas on Pacific Islands with a relatively small number of introduced snails and slugs (Cowie 2002), little research has addressed the impacts of these changes on natural plant communities or endemic plant species. The results of our field experiment supported our hypothesis that the endangered, endemic plant species are more vulnerable to slug damage than the invasive species. Pimentel et al. (2005) report that approximately 42% of endangered and threatened species are directly or indirectly threatened by invasive species of all types. The fact that Rare Plant Recovery plans identified slugs specifically as direct threats to 22% of endangered and threatened plant species in Hawaii, but documentation is largely lacking, suggests that slugs are an important but understudied threat.

Slug and snail control measures have generally not been used in the management of rare plants in Hawaii, nor have published studies documented their use to facilitate rare plant restoration on other islands around the world, where endemic plants might be expected to be highly susceptible to introduced herbivores (Bowen and VanVuren 1997). In our field study, both of the critically endangered species (*C. superba* and *S. obovata*) had 50% higher mortality when exposed to slugs. This finding is of particular concern because the outplanted seedlings in our experiment were fairly large (averaging 28–42 mm tall). We expect that mortality rates for naturally germinating seedlings could be much higher, as smaller seedlings seem to be more easily killed (see Fig. 5).

Although mortality was clearly higher for the endangered species in the slug-exposed treatments, slug exposure did not obviously increase leaf area lost to herbivory or decrease growth rates among surviving plants. This may indicate that slugs feed on most or all of a seedling before moving on. Slugs may return to the same plant on sequential nights, killing the plant in a short time (plants were only checked every 10 days). The Rare Plant Recovery Plans often mentioned slug damage to stems, and this may have been an important component of damage that contributed to rapid mortality. If stem chewing were the main form of slug damage, differences in leaf damage or growth rates between treatments might not be detected. Slugs are most commonly recognized for their impacts on herbaceous species (e.g. Buschmann et al 2005), but our findings show that woody species can also be strongly impacted.

Both endangered species were initially grown in a greenhouse then transferred to the field for 30 days prior to outplanting. During this time, the seedlings grew new leaves, so all of the outplanted plants had experienced growth under common field conditions, reducing the likelihood that early greenhouse growth alone made plants unusually attractive to slugs. Nevertheless, we cannot exclude the possibility that initial greenhouse growth may have influenced susceptibility of the endangered plants to herbivory. In practical terms, it is usually not possible to grow endangered plants from seeds in the field due to extremely limited quantities of seeds. Therefore, our findings based on greenhouse-grown seedlings are likely to be relevant for real-world outplanting efforts using endangered plants.

Although slug abundance appeared to track monthly rainfall, it is difficult to know whether endangered plant mortality due to slugs would correlate with increased rainfall. This is because increased rainfall increases availability of fresh tissue in a wide range of plants, so the increase in slugs associated with rainfall does not necessarily translate into increased feeding pressure on endangered plants.

Comparison of native and invasive plants

In comparison to the endangered species, the seedlings of both invasive species (*C. hirta* and *P. cattleianum*) were not significantly impacted by slugs. The non-endangered endemic, *N. sandwicensis*, also had similar seedling survival in slug-excluded and slug-exposed plots. Numerous *N. sandwicensis* seedlings were observed naturally germinating underneath parent plants, further suggesting their relative resistance to slugs. The reasons that the latter three species escape slug predation are unknown, but leaf toughness, which can influence slug feeding (Dirzo 1980), may help protect both *N. sandwicensis* and *P. cattleianum*, while *C. hirta* leaves have stiff, prickly hairs, which can discourage mollusk herbivory (Westerbergh and Nyberg, 1995). Alternatively, *C. hirta* may grow rapidly enough to replace damaged leaves (S. Joe, personal observation). High compensatory growth in response to slug attack is known in other invasive plants (Buschmann et al. 2006).

Because of the small number of species tested, as well as their non-random selection, it is impossible to statistically conclude that native plant species tend to be more vulnerable to slugs than invasive plant species. This study does reveal, however, that slug herbivory may be skewing species abundance in favor of certain non-native and native plants. Slugs change the rank order of seedling survival rates. Specifically, in the slug exclusion treatment, survival of the endangered species, *C. superba*, was not statistically different from either invasive species, and the survival rate of the endangered *S. obovata* matched that of invasive *C. hirta.* In addition to directly affecting survival of preferred species, slug herbivory can weaken the competitive ability of preferred species (e.g., Rai and Tripathi, 1985), thereby affecting plant community structure. The present experimental study did not directly address shifts in competitive ability due to slugs (also known as apparent competition) because seedlings in the field were spaced to minimize competition, and naturally recruiting seedlings near the outplantings were removed.

The low rate of natural seedling regeneration, even with slug exclusion, suggests that additional factors limit native seedling recruitment. These factors may include limited native seed rain (Moles and Drake 1999), low seed viability, lack of persistence in the seed bank (Drake 1998), destruction of seeds by predators, and/or poor soils (for example due to erosion or allelopathy by established plants). It is telling that most of the naturally germinating seedlings were of the highly invasive *C. hirta*, and that its naturally germinated seedlings, like the outplanted ones, were not impacted by slugs.

Conclusions

As commonly noted in the Rare Plant Recovery Plans, many native plants are found as widely separated, mature adults, but natural seedling recruitment has rarely or never been observed. Although a wide range of factors might explain a lack of recruitment, invasive slug herbivory seems to merit more attention from conservation biologists. The implications are especially relevant for rare plant outplantings and population restoration efforts, which can be both expensive and risky due to the paucity of outplanting material. Outplanted seedlings that are unprotected from slug predation may suffer from high mortality.

Slugs now seem to occur in nearly all mesic to wet habitat types in Hawaii and on many other Pacific Islands (Cowie 2005), but a lack of slug distribution and abundance data makes it difficult to gauge the extent of the possible impacts, especially in more remote natural areas. Slug and snail control measures have generally not been used in the management of rare plants. Control of invasive snails and slugs is feasible only on a local scale (Cowie 2002), but local control efforts at outplanting sites or during specific windows of natural seedling germination might be an effective way to improve establishment of rare plants. Local slug control seems to be especially practical when susceptibility to slug mortality decreases with plant size, allowing control efforts to be focused on a specific window of time.

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