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Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park

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Abstract

Association analysis was used to assess relationships among 25 important alien plant species and their association with feral pig rooting in Hawaii Volcanoes National Park, Hawaii, U.S.A. Results of the association analysis were summarized by means of a simplified, rank-based, polar ordination which yielded three subjective species assemblages. One group was characterized by an association with the endpoint species, *Ehrharta stipoides*. A second group consisted of species associated with the other endpoint species, *Andropogon virginicus*. The third group comprised a diverse assemblage of 14 species in the middle of the ordination.

Comparison of ordination scores with each species's association with pig-induced soil disturbance revealed that members of the *Ehrharta* group were strongly positively associated with pig activity, whereas members of the *Andropogon* group were generally negatively associated. The third group showed no association with pig-induced soil disturbance.

These results suggest a strong relationship between feral pig activity and the composition of the alien portion of the plant community. Analysis of the ecologies of both plants and pigs suggests that some species may both encourage pig activity and benefit from it. Likewise, other alien plants appear to neither require nor benefit from pig-induced soil disturbance. While pigs appear to play an important role in the organization of these communities, their removal may have a negligible impact on the success of many of the common weeds in the area.

Nomenclature: Wagner, W. L., Herbst, D. R., & Sohmer, S. H. 1990. Manual of the Flowering Plants of Hawai'i. University of Hawaii Press/Bishop Museum Press, Honolulu.

Introduction

The absence of mammalian herbivory in the evolutionary history of the Hawaiian Islands has left the native flora poorly adapted to the impacts of large alien herbivores. Characteristically brittle construction and the lack of thorns, toxins, and distasteful oils make native Hawaiian plants highly susceptible to damage by feral ungulates (Carlquist 1980). Indeed, the feral pig *Sus scrofa* is considered to be one of the most damaging agents in Hawaiian forests, perhaps even exceeding man (Stone 1985). Through trampling, rooting, and preferential feeding across a broad spectrum of habitats, pigs have impacted almost every native plant community in the Hawaiian Islands (Jacobi 1981; Warshauer & Jacobi 1982; Gagne 1983; Sohmer & Gustafson 1987; Stone & Anderson 1988).

The relationship between pig activity and the *alien* plant community is not as well documented. Soil disturbance, such as that associated with pig activity, is known to facilitate the spread of weeds in many communities (Baker & Stebbins 1965; Baker 1974), and many invaders of Hawaiian communities are thought to be enhanced by pig disturbance (J. K. Baker, unpubl. data as cited by Stone (1985)). Pigs are also known to feed preferentially on the fruits of many alien plants such as *Myrica faya* (firetree), *Passiflora mollisima* (banana poka), and *Psidium cattleianum* (strawberry guava) and thereby facilitate their spread (Smith 1985; Stone & Loope 1987).

The reasons for biological invasions such as these are often more complex than simple disturbance/seedbed or seed/vector relationships, however. Communities may be altered by suites of species that invade for a variety of reasons. Some plants may require disturbance for invasion while other species may not. In the case of coincidental invasion of weed and vector, the story may be circular. Did the plant invade because of disturbance or because of the vector or both? Alternatively, did the vector disturb the site because of the presence of the plant or because of an independent factor favoring both plant and animal? In an attempt to understand the nature of soil disturbance relationships among invading species, we investigated the associations among some important alien plants of Hawaii Volcanoes National Park and their distribution with respect to pig-induced soil disturbance.

Study site

The Thurston-Puhimau pig control area (6.2 km^2) is located on the upper east rift zone of Kilauea Volcano between 1100 and 1300 m elevation in Hawaii Volcanoes National Park (HVNP), Hawaii, U.S.A. (19°20′N, 155°15′W). The entire area is classified by Mueller-Dombois and Fosberg (1974) as Montane Rain Forest Environment, experiencing a humid climate without pronounced dry seasons. Nevertheless, a rainfall gradient transects the area, and rainfall decreases from 2500 mm/yr at 1300 m to 1500 mm/yr at the lower elevations. Average temperature at 1300 m is 14 °C in January and 17 °C in July.

The upper elevations support closed-canopy 'o'hia (*Metrosideros polymorpha* (Myrtaceae)) rainforest with a secondary canopy of tree ferns (*Cibotium glaucum*). Associated native species include the subdominant trees *Cheirodendron trigynum* (Araliaceae), *Coprosma ochracea* (Rubiaceae), and *Ilex anomala* (Aquifoliaceae), the mostly epiphytic *Astelia menziesii* (Liliaceae), and numerous ferns. The lower elevations are also dominated by *Metrosideros*, but the canopy is more open and the understory more dense. Common native understory species include the shrubs *Dodonaea viscosa* (Sapindaceae), *Styphelia tameiameiae* (Epacridaceae), and *Wikstroemia phillyreifolia* (Thymelaeaceae), and the sprawling, mat-forming fern, *Dicranopteris linearis*.

Cover is primarily native, especially in the rainforest, but several alien plants are becoming increasingly important. The nitrogen-fixing tree, *Myrica faya* (firetree), is spreading rapidly through the area and shares dominance with *Metrosideros* at lower elevations. *Andropogon virginicus* (broomsedge) and *Schizachyrium condensatum* (bush beardgrass) can form dense stands in open areas, and *Hedychium gardenerianum* (kahili ginger) is becoming a serious pest of the rainforest understory. During the course of the study, feral pigs ranged throughout the area at estimated densities of 12 pigs/km^2 (C. P. Stone and S. J. Anderson unpublished data).

Methods

In the fall of 1983, 14 5 m wide belt transects of various lengths were established to cover the range of environments found within the study area. The total of 6660 m of transect was subdivided into 10 m lengths, and the resulting 5 × 10 m plots were assessed for pig activity bimonthly from November 1983 to November 1984. Evidence of pig-induced soil disturbance was assigned to three age classes (fresh, intermediate, and old). During sampling, however, it became evident that, due to the effect of weather and observer differences, distinction between fresh and intermediate sign was unreliable. Thus, fresh and intermediate sign were pooled into one class called 'recent'; this class can be reliably aged at < 1 mo. If at any time during the sample period the plot contained recent sign, it was considered to have been disturbed.

At the end of the sample period, transects were examined for the presence of alien plants. A list of 25 species with a frequency ≥ 3% (20 plots) was pared from the total in order to keep the data set manageable. Our data set thus consists of the presence or absence of recent pig activity and 25 important alien plant species on 666 5 × 10 m plots.

Species associations were assessed using 2 × 2 contingency tables, which generated Chi-square (χ^2) statistics for all possible pairs of species (Table 1). The same procedure was used to assess species' associations with pig activity.

Association among alien plants was summarized by means of a simplified, rank-based, polar ordination. The first step was to determine the two most negatively associated species, based on χ^2 scores, as endpoint species in the ordination. The remaining species were then arranged in two rank orders based on their associations with each endpoint species (see Table 2). Finally, the location of each species along the ordination axis was calculated using Beals's (1965) formula, where rank score was substituted for percent dissimilarity.

The relationship between pig disturbance and the resulting ordination was assessed by plotting the χ^2-value for each species's association with pigs versus the species's ordination score. An obvious trend indicates that the species ordination is somehow related to pig disturbance. No trend indicates that the ordering of species has no relationship to pig activity. A relationship does not necessarily indicate cause and effect (see Discussion).

Raw χ^2-values were used to measure the strengths of the associations throughout. Determination of statistical significance of any specific association employed a hypercritical χ^2 (Pielou 1974). An association was considered significant if the generated χ^2 exceeded 15.0. This corresponded to an alpha equal to c. 0.00011 and kept the experimentwise error rate below 0.05 (i.e., 0.00011 × 325 possible pairwise comparisons = 0.036).

Results

Table 1 contains the calculated χ^2-values for all possible combinations of the 25 alien plant species. The strongest negative association ($\chi^2 = -167.5$) occurred between *Ehrharta stipoides* (meadow ricegrass) and *Andropogon virginicus* (broomsedge). *Andropogon* is one of the most common species, occurring in 67.1% of the plots, but *Ehrharta* was also well represented (28.1%). These two grasses formed the endpoints for the polar ordination (Table 2).

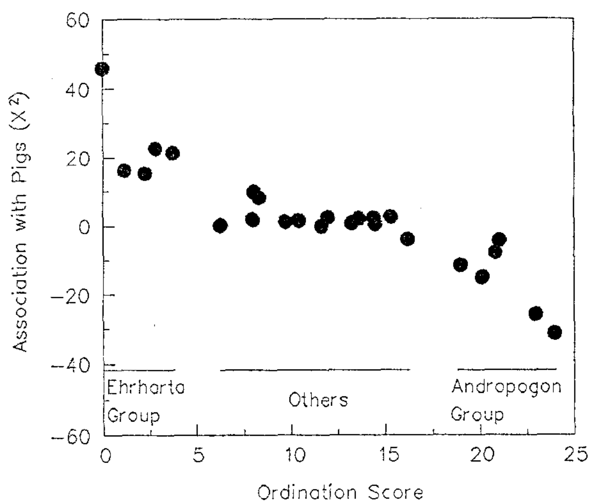

Fig. 1. Relationship of alien plant ordination score to each species's association with pig-induced soil disturbance. The trend suggests a correlation between the composition of the alien portion of the plant community and pig activity. Assignment to groups was based on visual discontinuities in the one-dimensional polar ordination.

The twenty-five species were subjectively broken into 3 groups based on the clustering evident in the ordination diagram (Fig. 1, Table 2). The first group consisted of those species that were significantly positively associated with *Ehrharta*. Included were *Hedychium gardenerianum* (kahili ginger), *Myrica faya* (firetree), *Paspalum urvillei* (Vasey grass), and *Setaria palmifolia* (palmgrass). This group was a diverse assemblage including three grasses, a tree, and a perennial herb. Origins were also vastly different and included Australasia (*Ehrharta*), tropical Asia (*Setaria*), the Himalayas (*Hedychium*), the Canary Islands and Azores (*Myrica*), and the New World tropics (*Paspalum*) (Wagner *et al.* 1990).

A second group comprised those species clustered near the *Andropogon* end of the ordination. These species were significantly associated with *Andropogon* and included *Cyperus halpan* (umbrella sedge), *Holcus lanatus* (velvet grass), *Kyllinga brevifolia* (kili'o'opu), *Schizachyrium condensatum* (bush beardgrass), and *Sporobolus africanus* (African dropseed). All were grasses or grasslike plants. Origins included southeastern North America (*Andropogon*), the New World tropics (*Schizachyrium*), Europe (*Holcus*), and Africa (*Sporobolus*). The two sedges are considered to be pantropical (Wagner *et al.* 1990).

The third group consisted of the remaining 14 species. This was an extremely diverse group and included grasses, annual forbs, herbaceous perennials, shrubs, and a tree (*Psidium cattleianum* (strawberry guava)). Six of these were of New World origin, three were European, four were Asian, and *Sacciolepis indicus* (Glenwood grass) was of paleotropic origin (Wagner *et al.* 1990). Nine of the species were relatively infrequent (freq. $<15\%$), and *Anemone hupehensis* (Japa-

Table 1. Frequencies of the 25 common alien plant species encountered during the study and chi-squared statistics describing the strength of the association between all possible pairs of species.

	EHST	SEPA	HEGA	PAUR	MYFA	PSCA	HYMU	ANAR	YOJA	ANHU	COBO	PHTA
Freq.	0.28	0.14	0.04	0.44	0.60	0.04	0.07	0.05	0.07	0.85	0.03	0.05
EHST												
SEPA	30.7											
HEGA	29.7	3.01										
PAUR	121.0	53.7	2.70									
MYFA	55.9	0.91	12.8	30.5								
PSCA	2.15	0.85	0.97	0.35	−2.03							
HYMU	0.22	0.24	1.69	0.03	0.01	3.39						
ANAR	0.70	2.04	0.04	11.2	18.5	5.57	3.53					
YOJA	0.98	1.09	0.24	1.29	10.9	0.03	13.5	62.9				
ANHU	2.32	15.6	0.04	17.3	9.57	1.58	0.50	4.07	6.10			
COBO	3.34	2.17	0.74	7.96	5.52	2.04	0.09	9.00	17.1	3.52		
PHTA	2.00	1.35	0.00	0.08	2.46	7.45	0.55	4.12	2.02	3.18	11.5	
FRVE	0.02	16.7	2.17	19.7	0.70	1.32	3.54	5.16	14.8	15.2	1.55	3.23
RUAR	−8.05	6.31	0.11	−6.05	2.27	0.59	1.27	0.01	0.94	0.03	0.07	0.02
AGRI	0.33	17.0	0.75	14.7	0.20	1.31	2.04	10.9	6.93	11.4	2.44	2.25
SEGR	0.66	−31.8	−11.6	0.00	9.19	0.03	1.57	11.4	1.47	18.7	2.60	−4.51
CEFO	−8.33	0.56	1.24	1.50	0.62	6.25	1.71	67.5	57.0	5.92	17.6	4.68
SAIN	0.03	1.64	−26.0	3.37	21.4	0.32	0.16	8.53	6.33	42.6	9.59	0.19
HYRA	−10.1	−4.60	0.93	−4.30	3.94	10.1	12.7	0.08	1.05	2.33	0.80	3.39
CYHA	−14.3	−12.3	2.75	1.35	−2.52	3.13	−3.32	0.61	−5.71	0.12	0.64	3.63
SPAF	−17.4	−10.5	−4.97	0.03	0.05	1.74	0.03	0.19	1.42	5.07	0.86	1.16
HOLA	−28.5	0.78	−28.9	6.29	5.72	0.10	0.31	2.52	4.80	63.7	3.91	2.83
KYBR	−39.5	−8.40	1.87	−13.7	0.78	3.66	1.56	2.33	8.16	5.89	2.02	13.2
SCCO	−78.0	−30.4	−10.2	−75.1	−3.36	−6.36	−4.39	−0.31	0.34	0.52	3.98	−5.92
ANVI	−168.0	−35.0	−31.6	−30.6	−4.40	0.44	0.26	0.85	1.03	6.74	7.30	7.45

nese anemone) was nearly ubiquitous (freq. = 85%). *Sacciolepis* and *Setaria gracilis* (yellow foxtail), two common grasses, fell into this group, though they were also significantly associated with *Andropogon* (Table 1).

These three groups were determined based solely on visual discontinuities in the ordination of alien plant species without consideration of their relationship with disturbance. The link between pig-induced soil disturbance and alien plant community organization was investigated by plotting each species's association with recent pig activity against its ordination score (Fig. 1). The obvious downward trend suggests a strong relationship between the ordination and pig activity. All and only members of the *Ehrharta* group were significantly positively associated with pig disturbance ($\chi^2 \geq 15.0$), whereas members of the *Andropogon* group showed negative association with pig activity. *Andropogon*, *Schizachyrium*, and *Sporobolus* were significantly negatively associated with pig disturbance. None of the members of the third group showed a significant positive or negative association with pig activity.

Discussion

The alien plants encountered in this study appear to segregate into distinct assemblages that are related to the presence or absence of pig-induced soil disturbance (Fig. 1). The *Ehrharta* group is much more likely to be found in association with soil disturbance than is the *Andropogon* group. The third group occurs with no affinity for disturbed or undisturbed sites. The strength of the relation described in Figure 1 supports an association between alien plant community composition and pig disturbance.

The next step in this analysis would be the

Table 1. (Continued)

FRVE	RUAR	AGRI	SEGR	CEFO	SAIN	HYRA	CYHA	SPAF	HOLA	KYBR	SCCO	ANVI
0.15	0.11	0.25	0.52	0.05	0.56	0.04	0.10	0.17	0.59	0.14	0.30	0.67
0.14												
13.4	0.72											
1.28	8.08	0.10										
15.8	0.81	36.8	12.2									
46.4	4.64	16.0	70.2	11.6								
3.33	12.1	13.2	10.5	6.73	10.7							
−7.00	2.01	0.94	3.13	0.69	8.31	1.13						
−4.52	−4.51	1.91	26.1	0.02	5.57	3.20	65.7					
37.3	30.6	36.3	5.01	9.89	123.0	6.93	0.17	0.24				
9.14	1.03	13.7	3.09	18.3	14.9	14.4	3.00	0.43	31.8			
−11.2	0.90	−4.53	29.4	0.20	1.75	−3.96	32.1	50.2	0.18	0.22		
2.44	3.14	9.17	51.5	3.40	30.1	7.29	34.5	51.3	43.2	22.2	114.0	

Table 2. Results of the rank-based polar ordination and calculated χ^2 values describing the strength of each species's association with pig-induced soil disturbance. The lines indicate the breaks between the three alien plant groupings observed in the ordination diagram (see Fig. 1).

Acronym	Species	EHST Assoc. Rank	ANVI Assoc. Rank	Ordin. Score	Chi-sq. with Pigs
EHST	*Ehrharta stipoides* Labill.	1	25	0.00	45.90
SEPA	*Setaria palmifolia* (J. Konig) Stapf	4	24	1.17	16.20
HEGA	*Hedychium gardenerianum* Ker-Gawl.	5	23	2.25	15.33
PAUR	*Paspalum urvillei* Steud.	2	22	2.83	22.63
MYFA	*Myrica faya Aiton*	3	21	3.75	21.30
PSCA	*Psidium cattleianum* Sabine	8	19	6.27	0.28
HYMU	*Hypericum mutilum* L.	7	20	8.00	1.37
ANAR	*Anagallis arvensis* L.	11	18	8.06	9.95
YOJA	*Youngia japonica* (L.) DC	10	17	8.35	8.34
ANHU	*Anemone hupehensis* Lemoine	14	13	9.75	1.95
COBO	*Conyza bonariensis* (L.) Cronq.	6	11	10.44	1.57
PHTA	*Phaius tankarvilleae* Blume	9	10	11.65	0.02
FRVE	*Fragaria vesca* L.	16	16	12.00	2.48
RUAR	*Rubus argutus* Link	17	15	13.25	0.93
AGRI	*Ageratina riparia* R. King & H. Robinson	13	9	13.67	2.30
SEGR	*Setaria gracilis* Kunth	12	3	14.44	2.50
CEFO	*Cerastium fontanum* Baumg.	18	14	14.50	0.56
SAIN	*Sacciolepis indica* (L.) Chase	15	7	15.33	2.69
HYRA	*Hypochoeris radicata* L.	19	12	16.23	– 3.83
CYHA	*Cyperus halpan* L.	20	6	19.00	– 11.50
SPAF	*Sporobolus africanus* Robyns & Tournay	22	4	20.15	– 7.74
HOLA	*Holcus lanatus* L.	21	5	20.85	– 15.00
KYBR	*Kyllinga brevifolia* Rottb.	23	8	21.06	– 4.13
SCCO	*Schizachyrium condensatum* (Kunth) Nees	24	2	23.00	– 25.60
ANVI	*Andropogon virginicus* L.	25	1	24.00	– 31.20

elucidation of the mechanisms behind this pattern. However, cause and effect are irresolvable through this type of analysis. Association analysis can only resolve the pattern; it cannot address, for example, whether the species in the *Ehrharta* association were present *because* of pig disturbance, or whether the pigs were drawn to those species. As the following discussion shows, alien community composition may be both cause and effect.

Several members of the *Ehrharta* group are typically found in mesic to wet forest environments (Wagner *et al.* 1990), and *Myrica* can form dense, nearly monospecific stands (Whiteaker and Gardner 1985). In contrast, members of the *Andropogon* group are restricted to more open sites (Wagner *et al.* 1990). Thus, the positive association between pig activity and the *Ehrharta* group simply may reflect a shared affinity for shade.

Additionally, *Myrica* has been shown to produce high-quality litter (Vitousek & Walker 1989), which increases population levels of earthworms (Aplet 1990), a favored food of pigs, and the resource presumably sought during digging (Diong 1983). Conversely, Rice (1972) reports that *Andropogon* can be allelopathic toward nitrogen-fixing bacteria. With low nitrogen levels in the soil, population levels of the soil-dwelling organisms pigs seek may be greatly reduced. Thus, the presence of *Myrica faya* or *Andropogon virginicus* may indirectly influence pig rooting activity.

The vegetation also may affect directly the quality of the observation. The ability to detect pig disturbance and small, inconspicuous plant species is hampered in the dense grass canopies created by *Andropogon* and *Schizachyrium*. This may contribute to the significantly negative associations between pig disturbance and some members of the *Andropogon* group.

Alternatively, the strong association of pig digging activity with certain species suggests that alien species assemblages may be the *result* of localized soil disturbance. Many weedy species require soil disturbance for establishment (Baker & Stebbins 1965; Baker 1974), and *Ehrharta*, *Paspalum*, and *S. palmifolia* are known to invade disturbed sites in Hawaii (Smith 1985; Wagner *et al.* 1990). *Myrica*, though capable of rapidly invading open forest in Hawaii (Vitousek & Walker 1989), is primarily an invader of disturbed sites (Whiteaker & Gardner 1985). In contrast, Smith (1985) does not link disturbance to the spread of *Andropogon* or *Schizachyrium*.

In addition to creating good seedbed conditions, pigs may act as seed dispersers. All five of the species in the *Ehrharta* group are animal dispersed (Smith 1985). *Ehrharta* produces awned fruits which are easily dispersed on animal fur. *S. palmifolia* is passively dispersed, and *Paspalum conjugatum* Bergius (Hilo grass), a congener of *P. urvillei*, is animal dispersed. Stomach contents of feral pigs have also been found to contain significant quantities of *Myrica* fruit (Whiteaker & Gardner 1985), and preliminary germination results indicate that pigs can pass viable seed (G. Aplet unpublished data). Though *Hedychium* is thought to be dispersed by alien, and perhaps native, birds (Smith 1985), its red fruits also may be attractive to pigs. In contrast, the species in the *Andropogon* group are primarily wind dispersed (Smith 1985).

In general, our results concur with previous work. With the exception of *Ehrharta* itself, Stone (1985) (citing unpublished data by J. K. Baker) lists all members of the *Ehrharta* group as beneficiaries of pig disturbance. Also included on his list, however, are *Psidium cattleianum*, *Anemone hupehensis*, *Phaius tankervilliae* (Chinese ground orchid), *Rubus argutus* (prickly Florida blackberry), and *Ageratina riparia* (Hamakua pamakani), none of which shows an affinity to pig disturbance in this study. He also lists *Andropogon* spp. (including *Schizachyrium*), which are highly negatively associated with pigs in this study. In addition, *Holcus* and *Kyllinga* have been found to heavily colonize pig-disturbed sites in upper montane and subalpine grasslands in HVNP and Haleakala NP (Spatz and Mueller-Dombois 1975, Jacobi 1981). Their association with *Andropogon* rather than pigs in this study suggests that they may respond differently in rainforest or submontane environments. Alternatively, *Holcus* and *Kyllinga* may so rapidly colonize new disturbances in the *Andropogon* grassland that they obscure the freshness of the sign, and their association with pig activity may be difficult to detect.

Conclusions

The root causes of the associations among alien plants and between plants and disturbance are likely very complex and may reflect cause, effect, and/or coincidence. For instance, some members of the *Ehrharta* group may benefit from pig activity, some may encourage it, and some simply may prefer the shade which the pigs also seek. Alternatively, some members of the *Andropogon* group may discourage pig activity while others benefit from undisturbed conditions. The complexity of the interrelationships among invaders, disturbance, and disturbance agents thwart any attempts to generalize about the causes of biological invasion in this system.

Nevertheless, the strength of the measured associations between alien plants and pig activity suggest the possibility of using alien plant species composition to gauge pig activity. An increase in abundance of the *Ehrharta* group would suggest increased pig activity. Likewise, an increase in the *Andropogon* group relative to the others might suggest reduced pig influence in an area. Understanding cause and effect is not necessary for the application of this approach; all that is required is an established association of plant species with pig activity, which we have demonstrated. This approach may have utility to managers who lack the resources to independently monitor both plant and animal populations.

In conclusion, the argument over cause and effect notwithstanding, alien plants of the Thurston-Puhimau Pig Control Area appear to sort into distinct assemblages which exhibit different relationships with pig-induced soil disturbance. Thus, we can expect each of these groups to respond differently to manipulation of pig population size. While pig disturbance may favor the plants of the *Ehrharta* group, our results suggest that pig removal may have a negligible impact on members of the other two groups. Except where native plant recovery leads to the decline of alien species (e.g. Katahira 1980), feral pig control can be expected to have little effect on the predominant alien plant assemblage within the study area.

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