CORRIDORS AND PLANT INVASIONS: A COMPARITIVE STUDY OF THE ROLE OF ROADSIDES AND HIKING TRAILS ON PLANT INVASIONS IN MOOREA, FRENCH POLYNESIA

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Abstract. Islands have been shown to be highly vulnerable to the invasion of non-native plant species. The island of Moorea, French Polynesia, is both geographically isolated and lacks a high diversity of native plant species, factors that promote the invasion of non-native plants. Disturbed areas, such as roadsides, have also been closely associated with the colonization and spread of non-native and invasive plants. Roads are particularly important vectors of alien plant invasions, aiding in dispersal and likely serving as starting points for edge effects. The present study considers both the alien and native flora in tropical secondary forests adjacent to paved vehicle roads, dirt vehicle roads, and backcountry hiking trails on Moorea, French Polynesia. The composition of total and alien plant species, level of invasion, and significance of edge effects were analyzed between the three corridor types. Significant differences in the alien plant compositions and level of invasion were found between the corridor types. Dirt roads were found to be the most invaded, followed by paved roads and then hiking trails. Two plant species, *W. trilobata* and *A. falcatoria,* showed dramatic edge effects into the adjacent forest; however, only the spread of *W. trilobata* was significantly affected by corridor type, with paved roads showing the greatest effect.

Key words: invasive species, alien plants, roads, corridors, edge effects, Moorea, French Polynesia

INTRODUCTION

The invasion of alien plant species can threaten and even destroy the integrity of natural habitats because of detrimental effects on native species and ecosystem processes (Pauchard 2004). Though this is an issue of global significance, islands are more susceptible than mainland to alien invasions (Chytry et al. 2007, Sax 2001) and thus warrant particular attention. There is extensive literature on both exotic species and island biology that highlight the vulnerability of islands to invasion (Sax 2001). Much of the literature addresses the characteristics of invading species that make them good colonists and the characteristics of environments that make them susceptible to establishment by aliens (Sax 2001). Common characteristics of successful invaders include: broad ecological requirements and tolerances, r-selected strategies, associations with anthropogenic and naturally disturbed habitats, and origins from large continents with diverse biotas (Rejmanek 1996, Sax 2001). Characteristics of invaded environments often include: low diversity of native species, geographical and historical isolation, human and natural disturbance, and lack of co-adapted enemies (Chytry et al. 2007, Sax 2001).

Given that the general attributes of both invasive species and invaded habitats have been identified and accepted, current research is now focuses primarily on specific sources and vectors of alien propagules, and effective land management techniques that reduce alien invasions. Land use, disturbance, elevation, and climate are all driving factors of alien plant invasions (Pauchard 2004). Anthropogenic land use is of particular concern because it not only disturbs the natural habitat, but typically provides a source of alien propagules that can be distributed in a variety of ways. Invading species are particularly successful in areas with high levels of human activity, such as urban centers, agricultural fields, and roadways (Christen 2006, Sax 2001). These environments are not only novel to native species, but often serve as sources of disturbance-adapted alien and invasive species propagules (Kalwij et al. 2008, Pauchard, Sax 2001). Once colonized in human disturbed areas, these exotic plants may spread from the edges to the interiors of pristine or naturally disturbed environments, known as edge effects (Pauchard 2004). Thus it is not surprising that exotic plants in many geographical regions include a large proportion of 'weeds' that occur in agricultural fields, along roadsides, and around settlements (Sax 2001).

Roads are particularly important vectors of alien plant invasions, aiding dispersal or channeling population expansion, and are likely to serve as starting points for edge effects (Christen 2006, Kalwij et al 2008, Pauchard 2004). Road construction incurs considerable disturbance of natural communities, baring soil, clearing natural vegetation, admitting light to the ground layer, and altering drainage (Christen 2006). Roadsides differ from natural disturbances because of their strong linear structure (Christian 2006). Although the recognizable roadside zone is relatively narrow, it can be quite long, creating continuous disturbed habitat for many kilometers (Christen 2006). Vehicles have been shown to collect and transfer alien species propagules along roads (Kalwij et al. 2008). This often leads to the colonization and eventual dominance of roadsides by disturbance-adapted alien species, bringing reproductive plants into close proximity with natural habitats (Christen 2006, Kalwij et al. 2008). It is therefore reasonable to expect the occurrence of alien flora in natural habitats to be correlated with adjacent roadside corridors (Tyser 1999).

Hiking trails are also human-disturbed corridors of possible importance to the occurrence and spread of alien species (Bright 1986, Tyser 1992). Although hiking trails are narrower than vehicle roads, they too provide long, linear stretches of habitat available for the colonization and movement of disturbance-adapted alien species. Hikers often pick up and deposit seeds that cling to their shoes and clothing, serving as both vectors of current trailside plants and sources of new alien plant propagules (Tyser 1992).

The present study considers the alien flora in tropical secondary forests adjacent to paved vehicle roads, dirt vehicle roads, and backcountry hiking trials on Moorea, French Polynesia. As an island, Moorea is both geographically isolated and lacks a high diversity of native species, making it highly susceptible to alien invasions. This study addresses three specific questions: (1) does the composition of alien plant species differ along different corridor types? (2) which corridor type is least and most invaded? and (3) does the corridor type affect the depth of the edge effect into the adjacent forest?

in length along the corridor and 50 meters deep into the adjacent forest.

METHODS

Study sites

Moorea (GPS location: S 17º 30′, W 149º 54′) is a high volcanic island of the Society Islands archipelago in French Polynesia with a maximum elevation of 1,207 meters. All field work was conducted in the Opunohu Valley, the lesser developed of the two major valleys on Moorea, between October 12, 2008 and November 15, 2008. To determine the effect of corridor type on plant invasions, three corridor types were selected: paved roads, dirt roads, and hiking trails. Three study locations meeting several criteria were chosen for each corridor type. They were initially selected using GoogleEarth because of similarity in isolation from agriculture, housing, and other anthropogenic disturbances and similarity in elevation across the entire site. Preliminary surveys confirmed that each site had similar forest composition and was dominated by *Inocarpus fagifer* or *Hibiscus tiliaceus*, two prevalent tree species in the Opunohu Valley.

The three paved road sites were established along the road leading up to the Belvedere lookout. Two sites were placed in between Lycee Agricole (an agricultural high school) and Marae Tetiroa, while the third was established in between Marae Tetiroa and the Belvedere lookout. Two dirt road sites were selected on roads leading away from Lycee Agricole, while the third was designated along the road connecting the Opunohu and Pao Pao Valleys. Two hiking trail sites were located near Marae Tetiroa. One site stretched from Marae Tetiroa to Marae Ahu o Mahine. Another site was located on the lower Three Pines Trail heading towards Marae Ahu o Mahine. The third hiking trail site was established along a hiking trail leading away from Lycee Agricole. Each site was 75 meters in length along the corridor and 50 meters deep into the adjacent forest.

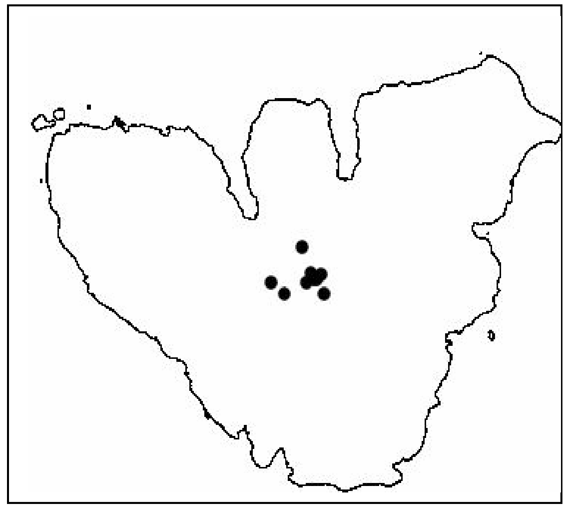

Figure 1: Site Locations on Moorea

Sampling methods

To identify the richness and cover of alien plant species in each site, a set of five 50 meter line transects were sampled at each of the nine study locations (n=45), resulting in a total of 15 transects per corridor type. Each transect was placed perpendicular to the road or trail surface beginning at the corridor edge. The line sampling technique proceeded as follows: (1) samples were recorded every 1 meter; (2) at each sample point a PVC pipe was held perpendicular to the measuring tape; (3) every vascular plant species that intersected the axis created by the PVC pipe was recorded; (4) unidentified species were assigned a number, collected, and later identified. Plant experts including Brent Mishler and Erica Spotswood, the Moorea Digital Flora Project website, *Flora Societies* by Stanley Welsh, *Wayside Plants of the Islands* by Arthur Whistler, and the University of California Herbarium, Berkeley, CA were consulted for plant identification.

Physical data and qualitative observations of each transect were recorded to account for additional factors that could affect plant community structure. Physical data included corridor canopy cover, forest canopy cover, elevation, corridor width, and width of roadside mowing. Qualitative observations included notable features of the road, such as cement culverts, drainage ditches, and the intensity of corridor use. Roads and trails were categorized as high intensity or low intensity use based on the frequency of passing vehicles, bikers, and hikers observed while transects were completed. A voucher specimen was collected for each species and deposited in the University of California Herbarium, Berkeley.

Analysis of corridor plant compositions

To determine if the composition of plant species differed between different corridor types (paved roads, dirt roads, and hiking trails), all species documented in the first five meters of each transect were analyzed. The 15 transects for each corridor type were used to calculate an average percent frequency for each species for that respective corridor type. To test for a statistical difference in total species composition along the three corridor types, a Chi-Square test was performed using the statistical software program JMP 8 (JMP 2007). The native and historically introduced plant species were then removed from the dataset. Plant species were considered native or historically introduced if they were native to French Polynesia or were introduced to Moorea by the ancient Polynesian people. A Chi-Square test was performed on the reduced dataset in JMP 8 (JMP 2007) to test for a significant difference in modern alien species composition along the three corridor types.

To assess for any difference in biodiversity along the different corridors, a Simpson's Index of Diversity value was calculated and the total number of species were summed from the first five meters of each transect for each of the nine sites. The effect of corridor type on the index value and the total number of species were analyzed for each site using an analysis of variance (ANOVA) test in JMP 8 (JMP 2007).

Determination of corridor invasions

Data from the first five meters of each transect were used to determine any difference in modern alien plant invasions along the three corridor types. The total number of transect points containing modern alien species were compared with the total number of transect points containing native or historically introduced species for each site. An ANOVA test was performed in JMP 8 (JMP 2007) on both categories of plant species and compared.

Analysis of edge effects

Ordination, a multivariate analysis technique, was used to reveal patterns of edge effects and community structure in forests adjacent to corridors. The specific ordination technique, Detrended Correspondence Analysis (DCA), was applied to the total species dataset in the computer software program Pcord (McCune et al 2002). The site factors analyzed included adjacent corridor type, intensity of adjacent corridor use, elevation, road canopy cover, interior canopy cover, road width and drainage type. Rare species were downweighted. Transect zones were used as the sample units (including all three corridor types n=139). All 50 meter transects were divided up into three zones. Zone 1 stretched from meter 0-15, Zone 2 stretched from meter 16-30, and Zone 3 stretched from meter 30-49. The species found in each zone were reported as a percentage of the total points in that zone. Species patterns found using DCA were then further analyzed with 2-way ANOVA tests in JMP 8 (JMP 2007).

RESULTS

Corridor Plant Compositions

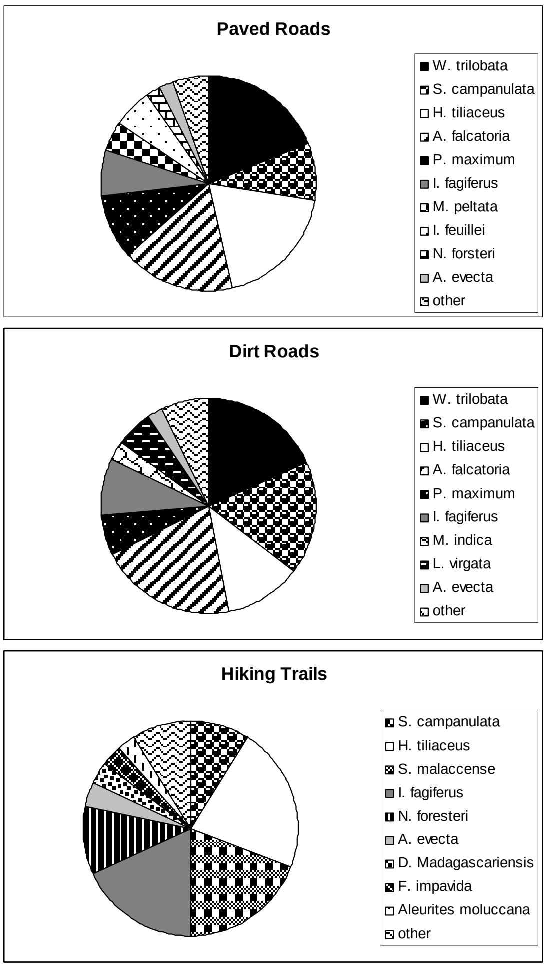

Figure 2 (a, b, c): Percent of total species observations made from the first five meters of each transect (n=15 per corridor type) at one meter intervals

The total number of recorded species different along each corridor type (Figure 2). 14 species were observed along paved roads, 17 species along dirt roads, and 17 species along hiking trails. Several physical factors of the three corridor types also differed. The average width of each corridor differed, averaging 4 meters for paved roads, 2.7 meters for dirt roads and 1.3 meters for hiking trails. The average percent canopy cover was 40% on paved roads, 55% on dirt roads, and 93% on hiking trails. On average, paved roads contained cement drainage culverts, dirt roads contained natural drainage ditches, and hiking trails contained no drainage structures.

The difference in species compositions were found to be statistically significant among the three corridor types (Figure 2) (X^2=346, df=20, p<.0001). Paved roads were dominated by *Wedelia trilobata, Hibiscus tiliaceus,* and *Albizia falcatoria*. Two of these three species, *W. trilobata* and *A. falcatoria* are modern aliens to Moorea. Dirt roads were dominated by *W. trilobata, Spathodea campanulata,* and *A. falcatoria*. All three species are modern introductions. Hiking trails were dominated by *H. tiliaceus, Inocarpus fagiferus,* and *Syzygium malaccense*. These three species are either native to Moorea or introduced by the Polynesians.

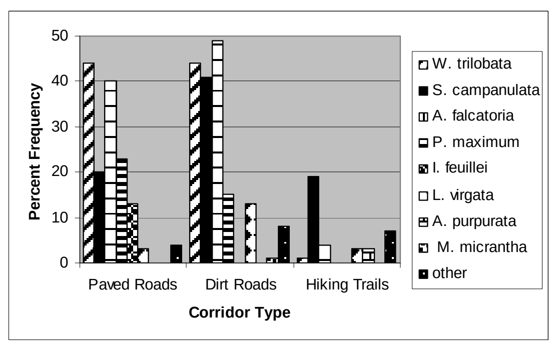

Figure 3: Percent frequency of only modern alien plant species observations made from the first five meters of each transect (n=15 per corridor type) at one meter intervals

Of the 25 plant species observed along corridors, 12 were determined modern introductions, 9 were native or historically introduced, and 4 were unidentifiable. The difference in species compositions of these modern alien plants were also found to be significantly significant among the three corridor types (Figure 3) (X^2=93.45, df=18, p<.0001). *W. trilobata* and *A. falcatoria* dominated both paved roads and dirt roads, but were virtually nonexistent (1% and 4% respectively) along hiking trails. *S. campanulata* was the only species that occurred prominently along all three corridor types, though it showed much greater abundance along dirt roads (49%). Hiking trails were dominated by *S. malaccense* while this species was virtually absent (1%) along both paved and dirt roads.

Corridor Type	Site #	Diversity Index	Total Species
PR	1	0.78	65
PR	2	0.88	74
PR	3	0.78	44
DR	1	0.83	64
DR	2	0.74	58
DR	3	0.74	46
HT	1	0.87	62
HT	2	0.73	35
HT	3	0.80	54

Table 1: Simpson's Index of Diversity and total number of species calculated per site along the three corridor types (PR=paved roads, DR=dirt roads, and HT=hiking trails)

No significant effect was found from corridor type on either plant diversity (Table 1) (F ratio=0.41, df=2, p=.68) or the total number of species (F ratio=0.50, df=2, p=.63) found at each site. All observed plants were included in these calculations including unidentified species.

Corridor Invasions

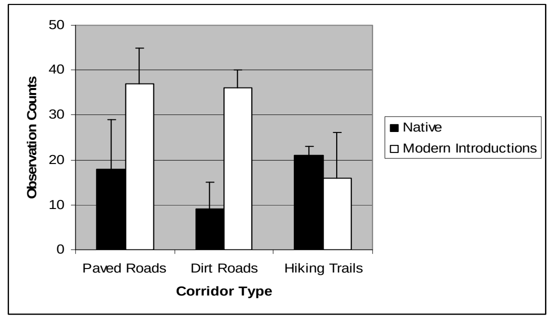

Figure 4: Average number of observations of native (or historically introduced) and modern alien plants found along the three corridor types (paved roads, dirt roads, and hiking trails) with standard deviation bars accounting for site differences

Dirt roads were the most invaded corridor type, with modern introductions comprising 80% of the total plants identified (Figure 4). Paved roads and dirt roads were the second most invaded, with 70% of the plants species identified as modern introductions. Hiking trails were the least invaded corridor type, with only 42% of the identified plant species coming from modern introductions. The corridor type showed a significant effect on the modern alien plant counts (F ratio=7.11, df=2, p=.0261), but no significant effect on the native (or historically introduced) plant counts (F ratio=2.20, df=2, p=.1919). The four unidentified plant species were not included in these calculations.

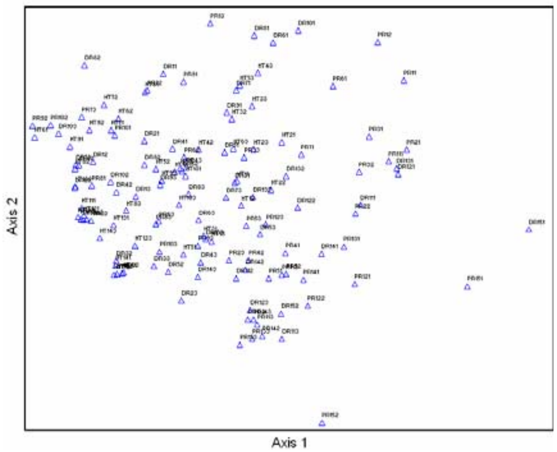

Figure 5: Distribution of sample units in ordination space along Axis 1 and 2

The DCA ordination scatter plot was used to explore the depth of the edge effects of various species (Figure 5). This ordination analysis explained 30% of the variance in Axis 1 and 56% of the variance in Axis 1, 2, and 3 combined. Road type and transect zone were the major two site factors that explained the distribution of species in ordination space along Axis 1. Other site factors were difficult to associate clearly with particular axes or species. *I. fagifer* was found in greatest abundance in forests adjacent to hiking trails but was not clearly associated with any particular zone. The following species were chosen for further analysis as they showed correlations with specific road types and zones: *W. trilobata*, *A. falcatoria*, and *S. campanulata.*

The difference in *W. trilobata* was found statistically significant in the three transect zones (Figure 6) (F ratio= 4.627, df=2, p=.01910) and along the three corridor types (F ratio=3.767, df=2, p=.0354). The highest percent frequency of *W. trilobata* was found in Zone 1 (nearest the corridor) and then

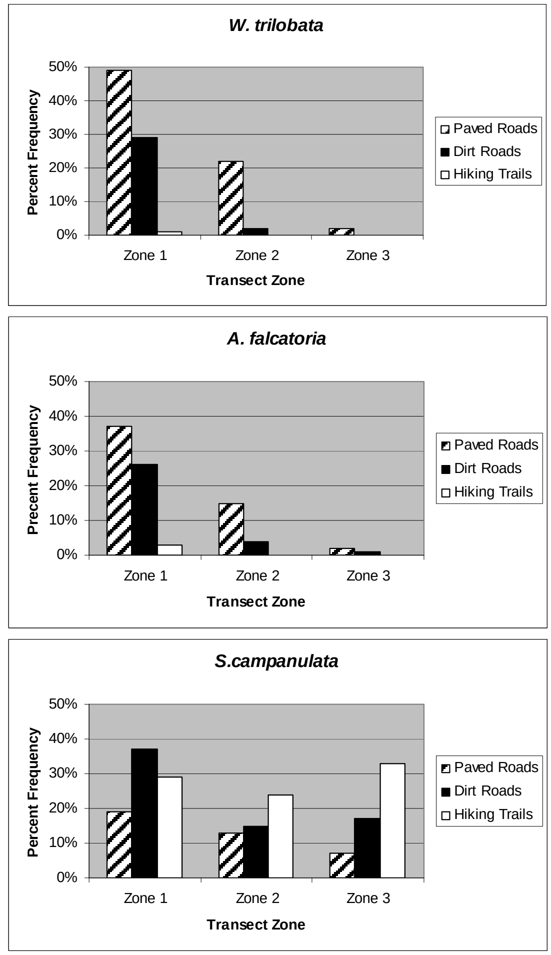

Figure 6 (a, b, c): Percent frequency of *W. trilobata*, *A. falcatoria*, and *S. campanulata* along the three corridor types (paved roads, dirt roads, and hiking trials) and divided into three transect zones (Zone 1=meter 0-15, Zone 2=meter 16-30, Zone 3=meter 30- 49).

decreased as the distance from the road increased. The highest percent frequency was also found in forests adjacent to paved roads, dirt roads, and hiking trails respectively. Similar results and patterns were found for *A. falcatoria*. Transect zones had a significant effect on the percent frequency (F ratio=5.822, df=2, p=.0093), however adjacent corridor type did not (F ratio=2.678, d=2, p=.0910). The highest percent frequency was observed in Zone 1 (nearest the corridor) and decreased with increased distance from the corridor edge. Though *A. falcatoria* showed the greatest percent frequency in forests adjacent to paved roads and then dirt roads, this result was not statistically significant. *S. campanulata* showed the greatest abundance along hiking trails and dirt roads and a generally greater abundance in Zone 1, yet these observations were not statistically significant (Corridor Type: F ratio=0.4976, df=2, p=.6148; Zone: F ratio=1.0628, df=2, p=0.3626).

DISCUSSION

When the total species found along corridors (Figure 2) are compared with the modern alien species found along corridors (Figure 3), it is evident that the majority of dominant species along corridors are from modern introductions. *I. fagifer*, *H. tiliaceus*, and *S. malaccense* are the only prominent species that are native or from Polynesian introductions. This is likely due to the fact that many non-native species are disturbance adapted and are more successful than natives in disturbed areas like roadsides.

The difference in composition of total plant species observed along paved roads, dirt roads, and hiking trails were shown to be statistically significant. These differences may be accounted for by many factors including road width, intensity of road use, and roadside clearance. Paved roads were on average the widest of the three corridor types, experienced the highest volume of foot and vehicle traffic, and contained several meters of mowed clearing on each roadside. Dirt roads shared similar characteristics as paved roads but were found to be slightly smaller, experienced less foot and vehicle traffic, and contained no additional manmade clearance on the roadsides. Hiking trails differed most significantly from the other two corridor types. They were much narrower (less than half the paved road length on average), had no vehicle traffic, higher foot traffic, and had no additional manmade clearing.

The large disturbed areas created by paved and dirt roads made them ideal places for the disturbance adapted species *W. trilobata*, which is known to be a noxious weed in agricultural areas, open lots, waste places, and garbage dumps, along roadsides and trails, and in other disturbed sites (Thaman 1999). *A. falcatoria*, an invasive species that has become a serious problem in Hawaii, was also abundant along paved and dirt roads. It is a nitrogen-fixer and can grow very rapidly even in nutrient-poor soils. Nitrogen-fixation has been shown as a physiological trait that may enable a single species to control characteristics of a whole ecosystem (Vitousek and Walke 1989). It may even stimulate the growth of non-native plants that respond better to increased soil nitrogen (Motooka *et al*., 2003). These synergistic interactions among invaders create a positive feedback system and may well lead to accelerated impacts on native ecosystems, known as an invasional "meltdown" process (Simberloff and Von Holle 1999). *A. falcatoria* is often used in ornamental and forestry plantings (C. W. Smith, 1985) and has likely spread from areas in which it was once planted on Moorea. *S. campanulata* was present along all three road types, but more abundant along dirt roads. *S. campanulata,* commonly known as the African Tulip Tree, is a shade-tolerant evergreen tree that invades both abandoned agricultural land and closed forest (Smith 1985). It is highly invasive in Tahiti up to 1300 meters in cloud forests (PIER 2008). Shade-tolerance likely contributed to its success along dirt roads above paved roads, since on average a greater percent canopy cover was found along dirt roads. The tree propagates primarily from wind-dispersed seeds. Corridors have been shown to aid in dispersal through both increased air flow and vehicle tires (Christian 2006). Dirt roads create better wind funnels than hiking trails due to increased disturbance, and have the added effect of vehicle traffic. These improved dispersal mechanisms help explain the higher abundance on *S. campanulata* along dirt roads edges. *I. fagifer*, *H. tiliaceus*, and *S. malaccense*, none of which are modern introductions, were the dominant species found along hiking trials. All three are believed to be either native or Polynesian introductions that have naturalized to the lowland secondary forests of Moorea. *H. tiliaceus* was found in abundance along all three corridor types, while *I. fagifer* and *S. malaccense* were found in much greater abundance along hiking trails. *I. fagifer* is associated with stream banks and marshes, which were more plentiful near hiking trails. *S. malaccense* is thought to have been planted at sacred sites by the ancient Polynesians (Fuchs 2005). Two out of the three hiking trail sites were near maraes, ancient Polynesian sacred sites, accounting for the abundance of *S. malaccense* along this corridor type.

Diversity is one indicator of community health and resistance to invasion. Highly invaded areas typically have low biodiversity since many species have been replaced by invasives. Though the composition of species differed significantly along different corridor types, the species diversity and total number of species did not. The difference in Simpson's Index of Diversity values did not prove to be statistically significant between the three corridor types. This indicates that there is not a significant difference in overall diversity and no corridor type was completely dominated by one or two species. However, findings from the Simpson's Index of Diversity do not indicate if a difference occurs in the proportion of modern alien plants to native or historically introduced plants.

The difference in proportion of modern alien plants to native or historically introduced plants along different corridor types was found to be statistically significant (Figure 4). Dirt roads showed the highest proportion of alien species, then paved roads, and lastly hiking trails. This seems counter intuitive since paved roads create the greatest disturbance and therefore seem the most vulnerable to disturbance adapted species. However, roadside mowing and better controlled runoff along paved roads sites may have improved their resistance to non-native plant invasions. All paved road sites contained two to five meters of mowed land along each roadside. Mowing can be an effective part of cohesive roadside management programs (Tyser 1999) since it controls the growth, maturation, and spread of alien plant species that colonize road verges. This mowing along the paved roads likely reduced the invasion of non-native plants on the roadsides. The cement drainage ditches found along paved roads may have also reduced the invasion of non-natives by siphoning off road water that may have contained propagules deposited from vehicle tires. Dirt roads contained small natural ditches or no drainage ditches at all. Runoff from these roads was more likely to deposit propagules along the roadside as the water seeped into the ground rather than washed down a culvert.

From the DCA ordination, *W. trilobata, A. falcatoria, and S. campanulata* were identified as species containing associations with certain road types or zone types. These three species are all modern introductions and had high percent frequencies observed along certain corridor types (Figure 3). Both *W. trilobata* and *A. falcatoria* showed the same patterns, with the greatest frequency found in forests adjacent to paved roads and in Zone 1, the zone closest to the corridor edge. The edge effects for *W. trilobata* and *A. falcatoria* were most drastic in paved road sites (Figure 6), where these species spread from the corridor edge well into Zone 2 (meter 16-30). As previously noted, *W. trilobata* is a disturbance adapted weedy species and *A. falcatoria* is a nitrogen-fixer. Both showed a strong ability to out-compete native species along roadsides. However, these two species have not stayed contained on roadsides, but have actually spread quite deep into the natural forest adjacent the road. Although *S. campanulata* showed a greater percent frequency along dirt roadsides, this trend did not extend into the entire adjacent forest, as no significant edge effects were observed. This species was found in greater abundance in forests adjacent to hiking trails and dirt roads (Figure 6), yet this was not found to be statistically significant.

I. fagifer was found in greatest abundance not only along hiking trails, but also in the adjacent forests surrounding hiking trails. This was shown by the clustering of *I. fagifer* species and hiking trail plots in ordination space. Hiking trails were also shown to have the lowest total percent of non-native plant species and showed no edge effects into the natural habitat. This leads to the question of whether the lack of non-native species was actually due to the less intrusive corridor type, or simply a factor of the *I. fagifer* community structure that makes it resistant to alien invasion. Though this question exceeds the scope of this study, it is an interesting question for future research. Likely both factors had some impact on the lower proportion of alien plants in these forests.

This comparative study focused on the role of roadsides and hiking trails on the spread of non-native plant species has found several interesting results. (1) Different corridor types contained different compositions and abundance of modern alien plant species. This can be explained by the differences in disturbance and dispersal properties of the three corridor types. (2) Dirt roads were the most invaded by modern alien species. Paved roads were the second most invaded and hiking trails were the least invaded. Similar disturbance and vehicle effects as paved roads, yet lack of proper roadside management, such as mowing and drainage structures, were probable factors that made dirt roads more vulnerable to non-native plant invasions. (3) The two modern alien species, *W. trilobata* and *A. falcatoria* showed significant edge effects in which they spread from the roadside edge into the natural adjacent forest. Both of these species are well adapted to disturbed areas and show dangerous abilities to out-compete native species. *W. trilobata* reproduces vegetatively, re-rooting easily from the stem (PIER 2008). This leads into question the full effect of roadside mowing. It is apparent that the mowing helped reduce the invasion of paved roadsides, yet if mowed clippings are scattered into the forest rather than bagged and properly disposed of, this management technique may actually increase the spread of *W. trilobata* into the adjacent forest. This is an important question whose findings could help prevent the continual spread of this potentially detrimental plant species. As a nitrogen-fixer, *A. falcatoria* has the ability to facilitate the spread of additional non-native plants and contribute to an invasional "meltdown." Future studies could examine the effects of this species on the growth of other non-natives in both a laboratory and field setting. Findings to this study would demonstrate any synergistic effects of this species on other invasives and larger effects on entire ecosystems. Both proposed studies could help inform management policy and identify the most effective mechanisms for impeding the spread of invasive plant species on Moorea.

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