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Promoting biodiversity in agricultural landscapes: native windbreaks support greater understory plant diversity in Monteverde, Costa Rica

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Rows of trees bordering agricultural fields, commonly called windbreaks, primarily serve to protect livestock and crops. However, they may also increase biodiversity and serve as foci for regeneration in agricultural landscapes. The effects of windbreak design on restoration potential and conservation have yet to be examined. This study focuses on the differences in understory plant diversity of windbreaks composed of native trees versus exotic trees on a farm in Monteverde, Costa Rica. The following questions are being addressed in this study: Is understory plant diversity greater in exotic or native windbreaks? Is there a difference in soil quality and composition between native and non-native windbreaks, and if so, could this be affecting understory plant diversity? What are the implications of these differences in plant diversity, if any, for biodiversity and forest regeneration? Understory plant species richness and abundance were examined in windbreaks using a randomized plot design. Four windbreaks consisted of planted native trees *Croton niveus* and *Montanoa guatemalensis*, and another four windbreaks were comprised of planted exotic trees *Cupressus lusitanica* and *Casuarina equisetifolia*. The Shannon-Wiener diversity index, which is a measure of species richness and evenness, was significantly greater for native windbreak understories (Hutcheson $t_{(df>50)}=9.35$, $p<.01$). There were significant differences in species composition ([$\chi^2=181.98$, df=36, $p<.01$] [$t_{(df>50)}=9.35$, $p<.01$]). Windbreaks composed of exotic trees contained more invasive individuals. This stark contrast indicates that windbreaks composed of planted native trees could be beneficial for promoting native biodiversity and forest regeneration in agricultural landscapes.

INTRODUCTION

During the months of November through April, the Monteverde region of Costa Rica experiences strong Northeast trade winds and this can take a toll on crop production and livestock wellbeing (Haber et al. 1996; Clark et al. 1999; Harvey 2000_c; Nadkarni and Wheelwright 2000). In the 1980's the Monteverde Conservation League (MCL) started a project to help farmers create windbreaks. Windbreaks are strips of planted or remnant trees that are 2 – 4 rows wide and they help to protect local farms against the ill effects of these winds (Harvey 2000_c; Nadkarni and Wheelwright 2000). Windbreaks effectively decrease mechanical damage to crops and reduce energy loss in cows, thus resulting in an increase in milk yield (Nadkarni and Wheelwright 2000). Initially, the MCL planted non-native species, such as *Cupressus lusitanica*, *Casuarina equisetifolia* and *Alnus jorullensis*, but later switched to native species such as *Croton niveus* and *Montanoa guatemalensis* (Harvey 2000_c; Nadkarni and Wheelwright 2000). As a result, the 180 kilometers of windbreaks in the Monteverde area are composed of both native and exotic species (Harvey 2000_c).

In addition to the benefits windbreaks provide to farmers, they also increase the biodiversity of agricultural landscapes by serving as essential habitat and movement corridors for forest species (Peters and Nibbelink 2011; Harvey *et al.* 2008; Yahner 1983; Harvey and Haber 1999; Corbit 1995; Haas 1995; Beier and Noss 1998). Tree, seed and bird diversities are all higher in windbreaks than in surrounding pastureland (Harvey 2000_a; Harvey 2000_b; Montagnini and Jordan 2005). Given that birds, bats and other animals are the primary seed dispersers for more than 85% of tropical trees, the diversity of trees recruited to windbreaks is greatly affected by visitation of these animals (Harvey 2000_a; Wheelwright *et al.* 1984; Guevara and Purata 1986). Previous studies in the Monteverde area have found greater avian diversity in windbreaks consisting of native trees than those comprised of exotic trees (Nielson and DeRosier 2000; Smith 2010). Increased tree and plant diversities lead to increased structural complexity of windbreaks, which in turn increases the availability of resources for seed-dispersing animals, among others (Peters and Nibbelink 2011; Fukuda *et al.* 2011; Morreale and Sullivan 2010; Montagnini and Jordan 2005). Non-native and native tree species differ in the resources they provide to organisms that utilize windbreaks as habitat (Fukuda *et al.* 2011; Nielson and DeRosier 2000). As a result there is a difference in diversity of visiting species within non-native and native windbreaks. Other factors influencing windbreak diversity include age of the windbreak, proximity and connectivity to forest fragments and the presence of remnant forest trees (Harvey 2000_b, Harvey 2000_c).

Since windbreaks serve as habitat and movement corridors for various species, they have been found to play an important role in forest regeneration when pastures are abandoned (Morse 2009; Harvey 2000_c). At one point 46% of the Costa Rica's land was converted to pastures, however, due to a

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recent forest regeneration initiative, the country is now a successful leader in reforestation in Central America (Morse 2009; Holl 2000; Thacher *et al* 1997). In order to appropriately manage and design windbreaks to maximize reforestation success, it is necessary to learn more about their ecology and how windbreak design and composition affect utilization and diversity (Chazdon *et al.* 2008; Harvey *et al.* 2008). Every region is unique and small-scale studies, such as this one, add to current knowledge that influences restoration strategies for specific regions.

A factor that has yet to be considered when examining diversity within windbreaks is soil quality and composition. Two of the aforementioned widely used exotic tree species, *Cupressus lusitanica* and *Casuarina equisetifolia,* have allelopathic qualities (Harvey 2000_c; Nadkarni and Wheelwright 2000; Singh *et al.* 1999). Allelopathic plants exude chemical substances that may have inhibitory effects on surrounding plant species and can be detrimental to the germination and establishment of recruiting tree species (Rice 1984, Deng *et al*. 1996; Batish and Singh 2000; Piper 2005). The allelopathy of plants has also been linked to decreased soil fertility. Thus these exotic tree species could be decreasing soil nutrient availability of the windbreaks (Inderjit 1994; Michelsen *et al.* 1996; Augusto *et al* 2002)

Taking all these factors into account, it is likely that native windbreaks support greater understory plant diversity, potentially due to better soil quality and composition. This study aims to test this hypothesis, and explore other potential explanations for differences in plant diversity and their implications for forest regeneration and conservation.

MATERIALS AND METHODS

Study Site

La Cruz and the surrounding area is a landscape dominated by pastures and criss-crossed by windbreaks. At 1300 meters elevation with mean annual temperatures of 17 to 24 degrees Celsius and 2000 to 4000 millimeters mean average rainfall, La Cruz is classified as premontane wet forest (Nadkarni and Wheelwright 2000; Holdridge 1967). Soils in this region are Andisols, further classified as Udands, formed from weathered volcanic parent material from the Aguacate and Monteverde formations (Nadkarni and Wheelwright 2000) These soils are darkly colored, high in organic matter and maintain high levels of phosphorous that is not readily available to plants.

This study was conducted in November 2011 on Evelio Vargas' farm in La Cruz, Monteverde within several planted native and exotic windbreaks. The methodology for this study is based on C. Harvey's 2000 windbreak diversity studies (Harvey 2000_a). By including only planted windbreaks on a single farm, potential confounding factors that can affect diversity, such as the presence of remnant trees, differences in elevation, age, and proximity to forest fragments, were removed (Harvey 2000_c). Eight windbreaks on the Vargas farm were randomly selected, four comprised of planted native trees (average area 128.57 ± 22.69m^2) and four comprised of planted exotic trees (average area 237.86 ± 157.38m^2). All were between 25 and 30 years old and were fenced off to protect against cattle grazing which can disturb understory vegetation growth (Stormer and Valentine 1981). The native planted species were primarily *Croton niveus* and *Montanoa guatemalensis* among the wide range of mature native species that had colonized the windbreaks since planting. Although the status of *C. niveus* is somewhat controversial, it is primarily considered native to Costa Rica and a naturalized exotic in the Monteverde area (Nadkarni and Wheelwright 2000). This study considers C. Niveus to be a native species. The trees planted in the exotic windbreaks were *Cupressus Lusitanica* and *Casuarina equisetifolia*, however, several individuals of *C. niveus* had also successfully established and matured in all of the studied windbreaks. These are the four most commonly used tree species in the Monteverde area, thus making the results applicable and translational to many other windbreaks in this landscape (Harvey 2000_a).

Study Design

To examine the understory vegetation of the windbreaks, three one-meter square plots were randomly placed in each of the eight windbreaks and a species inventory was recorded for each plot. The plants were identified to species level with help from expert botanists. Seedlings less than 6 centimeters in height were excluded because accurate identification to species level for these individuals was not possible.

In order to quantify soil nutrient availability and composition within windbreaks, a 500 millileter soil sample was taken from a randomly selected plot within each windbreak to analyze with the LaMotte Basic Soil Test kit. The pH and levels of nitrogen (N), phosphorous (P) and potassium (K) were measured in each sample. The chemicals were disposed of according to LaMotte materials safety data sheet.

Statistical Analysis

The Shannon-Wiener diversity index was used to quantify understory plant diversity of the native and exotic windbreaks. This index is a measure of community diversity that incorporates species richness and evenness; a greater index value represents a more diverse community. Diversity indices were compared using the Hutcheson special t-test (Hutcheson 1970). A Chi-Square test for independence was conducted in order to assess the overall differences in plant species composition of the native and exotic understories. In all statistical tests used, p-value of < 0.5 was considered statistically significant.

RESULTS

The study plots contained a total of 37 species from 23 families overall; 19 species from 15 families in exotic windbreaks, and 30 species from 19 families in native windbreaks (Table 1). One Rubiaceae individual and one Lauraceae individual could not be identified past family level. Only 12 of the total species were found in both types of windbreak. There was a statistically significant difference in overall species composition (χ^2=181.98, df=36, p<.01). *Microstegium vimineum* (Poaceae), *Arachis pintoi* (Fabaceae) and *Rubus robifolius* (Rosaceae) were the only three exotic species found in the understory; all three were present in

Species	Family	# native	# exotic	Dispersal	Habit	Primary/Secondary	Native/Exotic
Viburnum costaricanum	Caprifoliaceae	8	7	bird	woody	mainly secondary	native
Metastelma sepicola	Apocynaceae	2	0	wind	woody	secondary	native
Pouteria sp.	Sapotaceae	1	0	rodents	woody	primary	native
Solanum tuerckheimii	Solanaceae	0	1	bats	woody	secondary	native
Myrsine coriacea	Myrsinaceae	0	1	birds	woody	mainly secondary	native
Myrcia splendens	Myrtaceae	2	0	birds	woody	primary	native
Cestrum near panamense	Solanaceae	2	1	bats	woody	secondary and primary	native
Syngonium sp.	Araceae	1	0	birds	herbaceous	secondary and primay	native
Neea psychotrioides	Nyctaginaceae	1	0	birds	woody	primary	native
Ocotea leucoxylon	Lauraceae	1	0	birds	woody	primary	native
Eugenia monteverdensis	Myrtaceae	8	14	birds	woody	primary	native
Matelea sp.	Apocynaceae	1	0	wind	woody	secondary	native
Pouzolzia phenacoides	Urticaceae	24	95	gravity	herbaceous	secondary	native
Cestrum megalophyllum	Solanaceae	2	1	bats	woody	secondary and primary	native
Monstera adansonii	Araceae	1	0	birds	herbaceous	secondary	native
Unknown	Fabaceae	1	0	unknown	herbaceous	secondary	native
Pseuderanthemum cuspidatum	Acantaceae	0	6	explosive	herbaceous	secondary and primary	native
Paullinia costaricensis	Sapindaceae	4	1	birds	woody	secondary and primary	native
Iresine diffusa	Amaranthaceae	4	0	drop	herbaceous	secondary	native
Croton niveus	Euphorbiaceae	71	6	birds, rodents	woody	secondary	native
Beilschmiedia brenesii	Lauraceae	1	0	birds	woody	primary	native
Palicourea padifolia	Rubiaceae	3	19	birds	woody	secondary and primary	native
Nectandra smithii	Lauraceae	1	1	birds	woody	primary	native
Daphnopsis americana	Thymelaeceae	1	0	rodents	woody	primary	native
Cinnamomm cinnamomifolium	Lauraceae	1	0	birds	woody	primary	native
Neea lanceolata	Nyctaginaceae	3	0	birds	woody	primary	native
Centrosema plumieri	Fabaceae	10	4	explosive	herbaceous	secondary	native
Ilex lamprophylla	Aquifoliaceae	2	0	birds	woody	primary	native
Meliosma idiopoda	Sabiaceae	1	0	rodents	woody	primary	native
Unknown	Lauraceae	1	0	birds	woody	primary	native
Piper amalago	Piperaceae	0	1	bats	herbaceous	secondary	native
Citharexylum costaricensis	Verbenaceae	0	1	birds	woody	secondary and primary	native
Ardisia costaricensis	Myrsinaceae	0	1	birds	woody	primary	native
Hasseltia floribunda	Salicaceae	0	1	birds	woody	primary	native
Rubus rosifolius	Rosaceae	6	0	birds	herbaceous	secondary	exotic
Arachis pintoi	Fabaceae	1	2	other	herbaceous	secondary	exotic
Microstegium vimineum	Poaceae	84	176	other	herbaceous	secondary	exotic

Table 1. A complete table of all plant species found in this study and their characteristics. "#Native" and "#Exotic" columns represent the number of individuals of each species found in plots in native and exotic windbreaks, respectively. "Dispersal" is the predominant dispersal syndrome of each species. "1° / 2°" represents which type of forest the species is predominantly found. "Native/Exotic" represents whether that species is native to Costa Rica.

native sites, whereas only *A. pintoi* and *M. vimineum* were present in the exotic sites. The Shannon-Wiener diversity indice were H'=2.13 and H'=1.46 for native and non-native windbreaks, respectively. This is an extremely statistically significant difference (Hutcheson $t_{(>50)}$=9.35, p<.01). Evenness of native diversity was 0.63 whereas evenness of exotic diversity was 0.49.

A total of 249 total individuals were found in the native windbreak understory, and 339 individuals were found in the exotic understory. The most abundant species in both types of windbreak was *M. vimineum*, which accounted for 34 percent and 52 percent of the total individuals in the native windbreaks and exotic windbreaks, respectively. *M. vimineum*, *Eugenia monteverdensis*, *Pouzolia phenacoides* and *Viburnum costaricanum* were represented in the top five of both types of windbreak (Table 2). Exotic sites contained 6 individuals of *C. niveus*, and it was the second most abundant species in native sites. However, no individuals of *Montanoa guatemalensis*, *Cupressus lusitanica* or *Casuarina equisetifolia* were found at any site. Overall, 27 percent of total species were herbaceous, with 9 herbaceous species comprising 53 percent of total individuals in the native windbreaks, and 6 herbaceous species comprising 66 percent of total individuals in the exotic windbreaks.

Of the 30 species in native windbreaks, 22 produced seeds that were primarily bird dispersed, 3 were rodent-dispersed, 2 were bat-dispersed. Of the remaining, 7 had non-animal dispersers, and one had an unknown vector. In the exotic windbreaks, 10 species were primarily bird dispersed and 4 species were bat-dispersed, while five had a non-animal dispersal method. There were no rodent-dispersed species identified in exotic windbreaks (Figure 1).

The 12 species in the native windbreaks were typically secondary growth forest species compared to nine species in the exotic windbreaks. There were 13 primary growth forest species in the native windbreaks compared to only 4 in the exotic. All the remaining species in both windbreaks can be found in both primary and secondary growth forests. This study defines primary growth species as those found in undisturbed forest. Secondary growth species are those that generally inhabit areas that have experienced major disturbance.

The results for the LaMotte soil test for N, P, and K showed no differences in nutrient levels between any sites. For all eight sites N and K levels were trace, and P levels were very high (Table 3). The average soil pH was 6.5 for both the native and exotic windbreaks.

DISCUSSION

Native planted windbreaks consisting of *C. niveus* and *M. guatemalensis* appear to provide habitat for a greater number of plant species and support higher levels of plant diversity in comparison to windbreaks composed of the exotic planted trees *C. lusitanica* and *C. equisetifolia*. The Shannon-Wiener diversity index was significantly higher for the understory of native windbreaks due to both a greater species richness and a greater degree of evenness (E=.63 for native compared to E=.49 for exotic). These stark differences in diversity and species composition could potentially be attributed to differential utilization of windbreaks by seed dispersers and other animals, allelopathy of *C. lusitanica* and *C. equisetifolia* or the greater invasion of the exotic grass *M. vimineum* in non-native windbreaks.

Although none of the planted windbreak tree species included in this study produced fruit that attracted frugivores (Harvey 2000_a), the greater species diversity observed in native windbreaks could both be a cause and result of differential use of native and exotic windbreaks by local wildlife. A variety of animal species utilize windbreaks as corridors between forest fragments in agricultural landscapes, however, they have a tendency to preferentially visit windbreaks comprised of native species as native windbreaks provide familiar habitat and resources (Fukuda *et al.* 2011; Nielson and DeRosier 2000; Smith 2010). Furthermore, windbreaks which are more complex in structure and species composition, often due to increased animal visitation, in turn provide more potential habitat and resources which deems them more attractive to a wider variety of animal species (Peters and Nibbelink 2011; Fukuda *et al.* 2011; Wheelwright *et al*. 1984; Guevara and Purata 1986; Harvey 2000_a; Montagnini and Jordan 2005). Overall, a greater number of animal dispersed species were found in the understory of native windbreaks and this indicates greater visitation by seed dispersing animals to these sites. This could be a result of the wider variety of resources provided by plants in the native

Windbreak	Species	Family	Individuals	W / H	1° Disperser	1° / 2°	N / E
Native	*Microstegium vimineum*	Poaceae	84	herbaceous	other	Secondary	exotic
	Croton niveus	Euphorbiaceae	71	woody	bird	Secondary	native
	Pouzolzia phenacoides	Urticaceae	24	herbaceous	other	Secondary	native
	Centrosema plumieri	Fabaceae	10	herbaceous	other	Secondary	native
	Viburnum costaricanum	Caprifoliaceae	8	woody	bird	Secondary	native
	Eugenia monteverdensis	Myrtaceae	8	woody	bird	Primary	native
Exotic	*Microstegium vimineum*	Poaceae	176	herbaceous	other	Secondary	exotic
	Pouzolia phenacoides	Urticaceae	95	herbaceous	other	Secondary	native
	Palicourea padifolia	Rubiaceae	19	woody	bird	Primary/Secondary	native
	Eugenia monteverdensis	Myrtaceae	14	woody	bird	Primary	native
	Viburnum costricanum	Caprifoliaceae	7	woody	bird	Secondary	native

Table 2. Top five most abundant plant species in the understory of native and exotic windbreaks. Species are listed in order of decreasing abundance. Viburnum costaricanum and Eugenia monteverdensis are included in the same cell since they have equal abundances in native windbreaks.

understory. In turn, the higher visitation of seed dispersers is most likely contributing to the increased understory diversity, in a manner similar to a positive-feedback loop.

Another factor potentially decreasing the diversity in the exotic windbreaks is the allelopathic effects of *C. equisetifolia* and *C. lusitanica*. Both of these species have been proven to exclude understory vegetation in plantations and natural forests by decreasing seed germination and seedling survival (Suresh and Rai 1988; Michelsen *et al*. 1996; Batish *et al*. 2001). The allelopathic effects of *C. lusitanica* have also been linked to decreases in both soil fertility and nutrient concentrations (Michelsen *et al*. 1996). In this case, the allelopathy does not appear to be affecting the tested aspects of soil nutrients since concentrations of N, P and K were similar in both exotic and native windbreaks. However, the soil analysis kit used for this study could neither detect the more subtle differences in nutrient composition, nor the additional nutrients that affect plant germination and growth. Despite having no detectable effect on N, P and K concentrations, the allelopathic effects of both trees may still be detrimental to the understory diversity of the exotic windbreaks in this study.

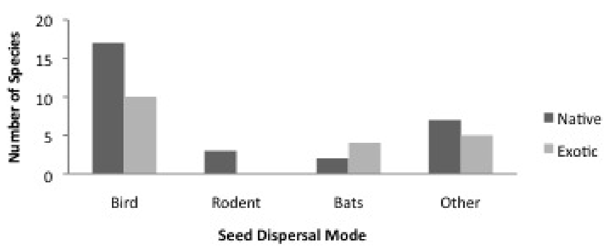

Figure 1. Primary seed dispersal mode of all plant species found in the windbreaks grouped by windbreak type. “Other” refers to a non-animal dispersal method. Native windbreaks had more species with animal dispersed seeds than exotic windbreaks (Willow Zuchowski, pers. comm. 2012).

Another plant that could be negatively affecting the diversity of exotic windbreaks is the highly invasive grass *M. vimineum*, originating from Asia (Gibson *et al.* 2002). It was by far the most prevalent plant species in both native and exotic windbreaks, but it comprised a greater proportion (52%) of the total individuals in the exotic windbreaks. *M. vimineum* is extremely shade tolerant and can rapidly invade disturbed, shaded areas such as planted windbreaks (Bardin 2000). Invasion of patches by *M. vimineum* has been linked to declines in plant diversity and can have long-term effects on community structure (Adams and Engelhardt 2009). Thus, the greater presence of *M. vimineum* in the exotic windbreaks could be an additional reason behind the higher diversity observed in the native windbreak understory due to these invasive individuals outcompeting native species. Despite *M. vimineum* comprising a lower total proportion of individuals in native understories (34%), it is likely that this species is negatively affecting plant diversity in native windbreaks as well. In order for proper forest regeneration to occur in these and similar pastures the growth of *M. vimineum* would have to be controlled through active management in both native and exotic windbreaks alike (Flory and Clay 2010, Beasley and McCarthy 2011).

Windbreak	Nitrogen	Phosphorous	Potassium	Average pH
Native	trace	trace	very high	6.5
Exotic	trace	trace	very high	6.5

Table 3. Average soil concentrations of N, P and K and pH for both windbreak types. Nitrogen and Phosphorous levels were trace at all sites, and Potassium levels were very high at all sites. Average soil pH was 6.5 for both native and exotic sites.

The potential change in species composition of the windbreaks is an important factor to be considered in future management of these and similar windbreaks in the area. No individuals of *C. lusitanica*, *C. equisetifolia* or *M. guatemalensis* were found in the understory. This indicates that these species are neither replacing themselves nor recruiting to other windbreaks, which is similar to previous findings in studies concerned with the colonization of *M. guatemalensis* in windbreaks (Piper 2006). However, *C. niveus* is the second most abundant species in the native windbreak understory, accounting for almost a third (28%) of total individuals, whereas only six individuals were present in the exotic windbreaks. This could foreshadow a transition from multispecies windbreaks to windbreaks dominated by *C. niveus*. The homogenizing of windbreak species could be detrimental to potential forest regeneration and biodiversity by decreasing the variety of resources available to wildlife, thus these and other windbreaks in the Monteverde area should continue to be monitored (Montagnini and Jordan 2005).

A further concern regarding windbreaks serving as foci for future reforestation is the presence of only one species of predominantly primary forest plant among the top five most abundant species in both windbreak types. Not only that, but 90 percent of total individuals found, with the exception of *M. vimineum*, are classified as secondary forest species. In this case the number of secondary growth individuals was about equal for exotic and native windbreaks. This indicates that if these pastures were eventually restored to forested land, the process of succession using both exotic and native windbreaks as foci for regeneration will most likely result in colonization by secondary growth forest species. These restored forests will take a very long time, if ever, to resemble the primary growth forests that once covered these areas (Chazdon 2008; Sader and Joyce 1988). Therefore, although reforestation of agricultural lands is a step in the right direction, it cannot replace conservation of remaining intact forest as the primary strategy to maintain biodiversity in the tropics.

As human practices, such as agriculture and development, continue to put exceeding amounts of pressure on the environment, it is vital to explore any and all methods of preserving ecosystems and maintaining biodiversity. Regeneration of abandoned pastures and agricultural fields is becoming an increasingly enticing option both ecologically and financially (Harvey et al. 2008; Morse et al. 2009; Haggar et al. 1997). As a result, windbreaks in areas where reforestation may occur, such as Costa Rica and the majority of Central America, should continue to be monitored. Small-scale reforestation experiments should be conducted in order to adequately understand the role of windbreaks in pastureland succession and their ability to retain elements of the original forest landscape. Based on the findings of this study I conclude that windbreaks planted in the Monteverde area should consist of native species in order to maximize biodiversity in agricultural landscapes. Native Costa Rican tree species can provide both agricultural and ecological benefits that should undoubtedly be taken into consideration when designing and implementing future windbreaks.

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