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The role of abiotic and biotic factors in limiting Piper abundance and distribution in a lowland Costa Rican wet forest

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The role of abiotic and biotic factors in limiting *Piper* abundance and distribution in a lowland Costa Rican wet forest site

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THESIS ABSTRACT

Niche theory proposes that species are able to coexist because each specializes on a certain portion of the habitats available. Both abiotic resources and the presence or the absence of biotic factors likely influence habitat specialization, although very few previous studies of plant distribution have considered both sets of factors. I conducted an observational study in the primary forest of the La Selva Biological Station in Costa Rica in which I sampled plants of the genus *Piper* greater than 1 cm at ground level on two different soil types along 26 transects, each 100 m long and 2 m wide. I measured light and herbivory for each individual encountered, as well plant size. I found that herbivory and soil type predict *Piper* species composition within patches. Moreover, for the most frequent and abundant species of *Piper*, light is an important predictor of *Piper* presence and absence. Abundance across the genus was not affected by soil type but mostly by plant size, which could be an indirect effect of competition between seedlings and small juveniles with older and larger plants. Generally, *Piper* plants suffered more damage by insect herbivores in small patches. However, when these plants are on alluvial soils and at high light levels they suffer less herbivory compared to plants in larger patches but in lower light levels and on volcanic soils. In looking at the distribution of individual species, it does not appear that the most common *Piper* species differ in their light requirements or in their resistance to herbivores. Thus, although the response to some factors was species-specific, in general the common *Piper* species seem to be sharing the same niche. I conclude that there is an important role for both abiotic and biotic factors in determining distribution of these understory habitat specialists as a group but not individually. Herbivory, patch size and light levels seem to be determining the habitat in which certain *Piper* species are able to establish and grow.

CHAPTER 1

ABIOTIC AND BIOTIC FACTORS AS DETERMINANTS OF PLANT
ABUNDANCE AND DISTRIBUTION

INTRODUCTION

Ecologists have long been concerned with the question, "What determines
distribution and abundance of plant and animal species?" (Pickett & Bazzaz, 1978;
Louda,1982). The answer to this question may lay in niche theory. According to that
theory, species can only coexist: 1) by specializing on a subset of conditions within a
given location (its "niche"), or 2) if trade-offs exist, such that allow one species is a
specialist on one resource and its competitor specializes on another resource.

Some researchers, however, do not believe that niche theory is sufficient to answer
this question. More specifically, niche theory is concerned with competition for
resources whereas neutral theory concerns itself with species extinction, migration
rates, and random forces that contribute to species distribution (Silvertown & Law,
1987; Hubbell, 2001). Neutral theory addresses the issue of how there can be far more
species in one place than available resources that can be partitioned; neutral theory
does this by focusing on individuals rather than on species. After one takes into
account proximity to a colonization site and the local abundance of all species, neutral

theory assumes that there is a certain randomness to who wins. More recent theories have unified niche theory and neutral theory (Tilman, 2004).

In support of niche theory, species distribution and abundances show patterns of habitat specialization. As has been known for some time, plants divide their habitat by the abiotic resources therein (Tilman, 1994; Rees et al., 2001). Species often aggregate along soil nutrient gradients. There is habitat specialization according to soil gradients in moisture and nutrient availability, including nitrogen, calcium and potassium (Palmiotto et al., 2004; de Oliveira et al., 2014). This pattern can be observed at different spatial scales (Clark et al., 1998; Clark et al., 1999; John et al., 2007). Moreover, plants also may partition habitats based on gradients in light availability, either by growing in different light gradients under closed canopy or within forests gaps (Rüger et al., 2009). Abiotic factors have long been considered as important factors guiding plant distribution and habitat specialization.

However, what of biotic factors? Researchers have realized for some time that biotic factors, such as herbivores, have the ability to limit plant species to a certain habitat. Herbivores by consuming seeds and therefore affecting the size of the dispersing seed pool, by determining whether seedlings can establish, and by modifying competition between plants can shape recruitment and seed production (Louda & Potvin, 1995; Morris, 2004; Becerra, 2007). Ecologists now need to test how abiotic and biotic factors together may be affecting species abundances and distribution. A few studies have shown interesting results, where the effect of herbivores and the environment together promote habitat specialization (Fine et al., 2004, Salgado-Luarte & Gianoli, 2010). However, more research needs to be

conducted to more accurately assess under what conditions herbivores and the environment are working in concert to determine a plant's current location.

In this review I will focus on how these factors promote species coexistence, habitat specialization, and species diversity of **plants**. I emphasize the importance of incorporating both abiotic and biotic factors in testing for local adaptation and habitat specialization. Species live in communities where they not only utilize the environment's resources but interact and form links with all species living in each particular community. Thus, it is importance that we give more attention to how these different links affect communities and how the former contribute to shape the latter.

I. THEORIES OF SPECIES COEXISTENCE

NICHE THEORY AND SPECIES COEXISTENCE

The definition of the **niche** as conceived by Hutchinson in 1957 is an n-dimensional hypervolume defined by axes of resources or environmental conditions that a species requires to exist in a particular location. This idea has been furthered developed into **realized** and **fundamental niche**. In the absence of competitors a species would be able to exist throughout its fundamental niche, while competitive interactions with other species force it to occupy only its realized niche.

Different theories of coexistence based on niche theory have been developed (e.g. Tilman, 1997). The classic and most simplistic approach begins with the Lotka-Volterra competition model, where it is understood that intraspecific competition must be stronger than interspecific competition for species to coexist. However, one of the major criticisms of the Lotka-Volterra model is that resources are not taken into

consideration. It was Tilman who first provided empirical results for a competition

model that included resources (Mittelbach 2012). Tilman's competition model (1994)

included species interactions in the form of trade-offs. He considered that the ability of

two species to coexist through **trade-offs** and a **limiting similarity** (i.e. species must

not be completely similar to each other). This means, for instance, that species A is a

better competitor for resource A but not a good one for resource B. This tradeoff

allows another species to utilize resource B to greater effect. These tradeoffs

ultimately allow species to coexist in space and time by their differential ability to

obtain resources from the environment (Tilman, 1977 & 1994; Rees et al., 2001).

Tilman (1982) also suggested that species living in a heterogeneous habitat might

show niche differentiation by adapting to specific habitats. Arguing that a

heterogeneous habitat is the basis for coexistence, and therefore habitat specialization

by plants, Pickett and Bazzaz (1978) proposed two types of niches: alpha and beta

niche; species have alpha and beta traits as well. Co-occurring species together with

the local resources determine the alpha niche, and the alpha traits makes this local

coexistence possible through either differences in phenology or microhabitat. The beta

niche, in contrast is within a regional environmental gradient that varies continuously.

It is the space where the species can be found and is determined by climate and abiotic

requirements, e.g. soil type, fire frequency. Beta traits make it possible for a species to

survive in different microhabitats. It is, therefore, possible that the alpha niche is

nested within the beta niche (communicated by R. Jörgen). The important difference

between Hutchinson's definition and Pickett and Bazzaz's is that the latter is based on

environmental heterogeneity. Nevertheless for these definitions, the realized and

fundamental or the alpha niche and beta niche, coexistence is determined by species traits and their fundamental trade-offs.

Much empirical work gives evidence for niche differentiation by species (see reviews: (Silvertown, 2004; Stubbs & Wilson, 2004; Tilman, 2004; Harpole & Tilman, 2007; Noble & Fagan, 2015). Species coexistence, according to niche theory, is a consequence of interspecific differences in traits that determine resource use, spatial heterogeneity in resource supply, and a limited supply of resources.

THE UNIFIED NEUTRAL THEORY

The neutral theory was proposed to answer questions, that for some researchers, niche theory seems to leave unanswered. For example, there exist only a limited number of resources to compete for in a particular area, but there are far more species coexisting in one place than there are resources to subdivide. Additionally, how much can species keep on subdividing their habitat and resources to result in current community structures? How are resources divided to produce observed patterns in nature such as rarity in plants?

The unified neutral theory by Hubbell (2001) arose as a contradiction to the ecological niche theory by favoring **speciation** and **extinction** rates, **dispersal** and **random forces**, yet ignoring species differences in traits or rather questioning how important these differences are in structuring a community. Hubbell's theory is mainly based on individuals rather than on species and their level of saturation in a particular area. The idea is that as the abundance of one species increases, it will reduce the

abundance of another. As an individual disappears, through death or migration, a new individual must replace it. Hubbell argues that this replacement will be from a random draw of individuals surrounding that area. All individuals of all species have the same opportunity to conquer space through birth, migration, speciation or dispersal. However, abundant species have a higher probability of filling the space. In contrast, niche theory suggests this replacement occurs via competition because not all species are equal in resource use.

Norris (2003) explains this by imagining the community as a checkerboard with individuals occupying each square. All individuals have equal probabilities of giving birth, dying or migrating, however this does not mean that all species have equal chances of filling an empty square. The species that will occupy an empty square are the ones that are more abundant and/or are closer to the space that was recently vacated. Hubbell paid particular attention to dispersal limitation. Indeed if a patch has been vacated, individuals need to be able to reach the unoccupied site. In fact, Ehrlén & Eriksson (2000) observed this situation in a temperate forest; in their experiment the authors found that while patches were suitable for a particular species to grow, those species nevertheless were not present. Moreover, none of the abiotic factors tested explained differences in emergence between patches. Ultimately patch occupancy was determined by the dispersal ability of the species and seed size, as larger seeds were dispersed shorter distances.

Since Hubbell's book was published, a number of authors have concluded that neutral theory has a place in the natural world. Relaxing some of the assumptions of the original theory has proven to be a good match for sampled data on species

abundances. For example, relaxing the assumption of the conservation of community size and yet still assuming that all individuals are demographically identical, He (2005) was able to fit his modified neutral model accurately to the data collected on tree abundances on BCI. He concludes that demographic processes, such as birth and death rates, included in neutral models explain patterns of species abundances. This conclusion is not far from that of Shinen & Navarrete (2014): barnacle species appear to coexist due to their similarities rather than trade-offs, owing their distributions to dispersal and random arrivals into a vacant space more than to competition.

Furthermore, most scientists conclude that the neutral theory is a good null model for testing hypotheses of species' relative abundances (Alonso et al., 2006, Etienne et al., 2007; Rosindell et al., 2010 & 2011). The theory has therefore great merit in the scientific community, it has allowed for new debates and it has made scientists aware of the importance of demographic processes.

However there are others that disagree. McGill & Collins (2003) was unable to fit empirical data to the 'zero-sum multinomial distribution' that neutral theory claims species abundance distributions follow. Furthermore, the slow replacement of species by drift does not match how fast species change in a given community, the observed regional species turnover and observed patterns of community structure (Ricklefs, 2003; Adler, 2004; Wootton, 2005). Again McGill et al. (2006) reviewed and tested different theories of neutrality and concluded that there is little empirical support for the theory and suggests that neutral theory works better as a null hypothesis. More recently, using empirical data, Chu & Adler (2015) found strong niche differences in their studied plant community, concluding that these species follow non-neutral

dynamics. All in all, the demographic parameters so important in neutral models may play a role in community structure but species differences and their response to environmental disturbances have an undeniable role in nature.

STOCHASTIC NICHE THEORY

A more recent approach to the question of species coexistence considers the combination of niche trade-off theory and neutral processes. It is likely that both trait differences and chance contribute to coexistence (Tilman, 2004; Gravel et al., 2006; Matthews & Whittaker, 2014). Tilman (2004) proposed unifying the importance of competition and resource partitioning with ecological drift, i.e., any species could occupy an empty space in part due to random processes, however more abundant species have a greater likelihood to fill that space. He assumes that arrival at a particular location depends on the rarity of the species and the effect of drift; establishment depends on the species limiting similarity, and growth and reproductive success comes from the differential use of resources. Gravel and colleagues (2006) incorporated dispersal and migration in their model. It turns out that migration and dispersal limitation in a community with high levels of niche overlap maintain species by way of constant immigration. A number of studies conclude that together niche and neutral theories most accurately predict species abundances (Brokaw & Busing, 2000; Chisholm & Pacala, 2010; Noble and Fagan, 2015).

Nevertheless, before scientists decide that a union between theories is the best predictor of species abundances, there is still much to decide regarding niche theory, especially niche-based habitat specialization. In this regard, for example, plant ecologists tend to focus on the fundamental niche: assigning axes of environmental

variables to plant species. In contrast, plant-herbivore ecologists tend to emphasize the role of herbivores at reducing plant fitness and growth (Crawley, 1989; Doak, 1992). Others, however have observed the herbivore's role in setting the limits of the realized niche (Parker & Root, 1981; Louda, 1982; Lau, et al., 2008). Research should consider both abiotic and biotic factors in determining niche based species distributions.

II. EVIDENCE OF SOME NON-NEUTRAL FACTORS CONSIDERED TO AFFECT PLANT DIVERSITY, ABUNDANCE AND DISTRIBUTION

Plant distribution and restriction to certain habitats could be due to abiotic factors, biotic factors, or both, if indeed communities organize following niche-assembly rules and have evolved habitat specialization. Traditionally, it was thought that species distribution was mostly due to climatic conditions (Merriam, 1898; Gleason, 1926). Later on, species interactions were included in most theories (Tilman, 1976). Currently researchers are aware that patterns of species distributions are controlled by abiotic conditions and interspecific interactions.

ABIOTIC

1. Light availability

Although plants require light to survive and grow, light is not always a constant resource within forests and therefore may be a factor by which species partition their habitat. Light regimes in forests are heterogeneous because light incidence changes between seasons, latitude, under the forest canopy, within tree gaps and in open spaces (Denslow, 1987; Canham et al., 1990a; Clark et al., 1996). In fact, the amount of photosynthetically active radiation (PAR) that comes through a fallen-

tree gap is more than double the usual amount under the forest canopy (Canham et al., 1990b). Particularly for rainforests, the PAR may vary throughout a gap space of 1-10 m in size (Canham et al., 1990a). Plants growing in forest gaps coexist, at least during the first successional stages, by taking advantage of the heterogeneity of light availability within the gap. There is evidence for differences in seedling establishment, recruitment and distribution on a gradient in light availability that suggests that forest gaps may be influencing the diversity of plants found in the understory (Denslow et al., 1991; Clark et al., 1996; Montgomery & Chazdon, 2002; Rüger et al., 2009). The high diversity of species in tropical forests may be explained by resource heterogeneity in light (Tilman, 1982; Tuomisto et al., 1995). The gap heterogeneity hypothesis states that forest gaps create changes in different physical factors at the forest floor, generating opportunities for species to colonize these areas (Ricklefs, 1977). As an example, Ricklefs (1977) mentions that the amount of light coming in through gaps may influence the water availability in the soil, which in turn may have an effect on what species occur in gaps. As supportive evidence, Anderson and Leopold (2002) found that the differences between gap and non-gap areas are due not only to the increase in light availability, but also the water table fluctuation through time. Moreover, this fluctuation was positively correlated with species richness within gaps.

Canopy openings provide a resource that many plant species are able to use. Tropical rainforest plants, for example, can be arranged along a continuum in use of available light within and outside forest gaps (Denslow, 1987; Montgomery and Chazdon, 2002; Rüger et al., 2009). Lusk et al. (2006) found that half of the tree

species studied showed a preference for particular amounts of light penetration, which may ultimately play a role in determining the species presence in a particular location. Growth responses of understory trees vary depending on the amount of light received. Van Pelt & Franklin (1999) showed how differences in light availability affect budbreak, growth and leave retention. They made artificial gaps in a forest encompassing a range of light conditions. During three consecutive springs they measured budbreak of the understory trees, growth and mortality and took hemispherical photographs along the main axis of the plots and beyond the gap edge and in control plots. At the beginning of the study, diffuse light had the most influence on budbreak and growth. On the contrary, an assortment of trees located in the north end of the gap receiving direct sunlight for long periods did not survive. After a short period of adjustment, the remaining trees and species in the gap center had growth rates much higher than those that were not exposed to high amounts of light. Moreover, Rüger and colleagues (2009) found that 87% of their species studied benefited from high light levels. Nevertheless, they found that species are spread throughout a light continuum, with few species recruiting at low light levels, others having the highest increase in recruitment at medium light levels, and finally others requiring high light levels to have the most recruitment. However, some species of plants have different light requirements at different life stages. Poorter et al. (2005) investigated how tree species partition vertical light gradients at different life stages and heights. They found that few species actually conformed to the notion of life-long shade-tolerance or intolerance. This means that as a seedling grows, the amount of

light it receives and needs for its success varies until the individual reaches the forest canopy.

Lastly, heterogeneity at the forest floor in light level may cause a particular forest structure by promoting trade-offs. For instance, in a deciduous forest in Japan, topography influences the trade-off gradient between light and nitrogen (N) availability (Tateno & Takeda, 2003). As topography changes, a negative trend between N and light appears; an abundance of soil N causes more species to be present in that particular area triggering competition for reduced light availability. Therefore, shade tolerant species have an advantage. Enoki & Abe (2004) had similar results; the difference in species distribution was due to a trade-off in soil nutrient and light availability. These trade-offs permit coexistence of species because of their specialization to particular environments.

2. Soils

One of the many factors considered contributing to species partitioning of resources and the ability of plants to coexist in one locality is soil composition. Soil composition and structure contribute to habitat specialization as well as to the spatial distribution of plants. Specialization of vegetation to particular soil types is well-documented (Ashton, 1969; Gartlan et al., 1986; Tuomisto & Ruokolainen, 1994; Oliveira et al., 2014). Studies have found that vegetation patterns are influenced by soil moisture (Sollins, 1998), drainage (Teer Steege, 1993; Tuomisto and Ruokolainen, 1993), and chemical factors such as Al toxicity, P availability and micronutrient availability (B, Zn, Mn, Fe, Cu, Cl [Sollins, 1998; John et al., 2007]).

Authors have also found niche differentiation due to a combination of soil and topography (Clark et al., 1998 & 1999).

Some researchers might consider variability in soils as an important contributor to species coexistence and have proposed mechanisms behind the observed patterns. In a review by Laliberté et al. (2013) five potential factors are mentioned: 1) Nutrient availability and soil stoichiometry, or in other words, the balance between organisms and their effect on soil chemistry and vice versa. This is a potential effect because nutrient availability changes as soils age. 2) Diversity, i.e. variety of the chemical forms of nitrogen and phosphorus found in the soils. The authors propose that plants may partition resources according to the different chemical forms in which N and P are found in the soil, promoting species coexistence. 3) Soil spatial heterogeneity; spatial differences in nutrient availability might influence the number of species that can coexist. If there are different amounts of nutrients throughout space, plants may partition the habitat by specializing on certain nutrient availability. 4) Aboveground heterotrophs; herbivore biomass may be affected by soil fertility indirectly through plant consumption; as soil fertility decreases, there is less herbivory. However, plants in turn are affected by soil fertility in their ability to replace lost tissue. 5) Belowground heterotrophs; soil biota help resource partitioning by aiding in consumption and mobilization of certain nutrients (e.g., the role of mycorrhizae in aiding plants at obtaining certain soil nutrients).

Differences in plant distribution in relation to soil heterogeneity have been tested at landscape scale ($>1,000$-$10,000$km^2), mesoscale (1-100 km^2) and local scale (<1 km^2) (Newbery et al., 1986; Clark et al., 1998 &1999; Tuomisto et al 2003; Costa

et al., 2005; Paoli et al., 2006; John et al., 2007; Oliveira et al., 2014), supporting the hypothesis that vegetation does have a strong association with soil characteristics and nutrients. Phillips et al. (2004) concluded that at the **landscape** scale, species tend to respond to edaphic gradients even within small variation within the soil. In a more recent study where the authors not only studied soil, but also climate effects, they found that although climate is a strong driver of species distribution, soil also has a strong influence (Toledo et al., 2012). At a **mesoscale**, the findings of Clark et al. (1998) are particularly interesting because they tested the distribution of nine different tree species among soil types that do not possess sharp distinct characteristics. Yet they observed these trees had a non-random distribution according to soil type. The authors suggested the need for transplant experiments to test these differences in distribution of trees in varying soil gradients. In a prominent study, Palmiotto et al., (2004) found that the main factor determining the clustering of dipterocarp tree species was soil type. By means of a transplant experiment, the authors observed a difference in growth and mortality of the plants. Research has found community assemblage associations with edaphic habitat heterogeneity at **local** scales (e.g. Gentry, 1981). John and colleagues (2007) found a strong association between edaphic gradients and tree distribution in forest plots in Ecuador, Colombia and Panama. Oliviera et al. (2014) found that habitat specialization by edaphic gradients in a restinga forest explains species coexistence. They found plants to be more similar within same habitat type than between different habitats. These authors also found phylogenetic overdispersion within this forest. This denotes that species that are more

closely related tend to occur in different habitats whereas species in the same habitat are more distantly related.

Although an undeniable soil-vegetation pattern is observed, it has been suggested that at a small scale there is little or no association between soil and vegetation. Therefore other factors such as tree gaps, natural history, low dispersal and disturbance may be affecting species composition (Newberry et al., 1986; Hart et al., 1989; Pitman et al., 1999; but see Tuomisto & Ruokolainen, 1993).

BIOTIC

1. Herbivores

Plant consumers are ubiquitous in almost all environments. Herbivore effects on plants range from subtle to conspicuous, and have the potential to alter plant diversity, abundance and distribution. The detrimental effects of herbivores on plant performance are well known. Damage by insects impacts flowering, fruit production, growth, and seed and seedling mortality (Doak, 1992; see reviews by Crawley, 1989; Marquis, 1992). Long-term studies on the effects of herbivores have shown an influence on plant population and community dynamics (Huntly, 1991; Augustine & McNaughton, 1998; Olff & Ritchie, 1998; Gómez, 2005). In his 1970 paper, Janzen suggested that seed and seedling predators, rather than competition with other plants, prevent a single plant species from dominating a location. Huntly's review (1991) addresses the numerous ways by which herbivores may affect plant communities, specifically by altering the environment and therefore the resources used by plants, by promoting apparent competition or through density-dependence in plants.

Consumers are capable of affecting plant diversity (Lubchenco, 1978; Olaff and Ritchie, 1998; Marquis, 2004; Maron & Crone, 2006a). Herbivores are thought to positively affect plant diversity by their effect on plant competition. If herbivores consume the competitively dominant species, new opportunities arise for the less dominant species. However, this effect is not always positive and it depends on the abiotic environment. Herbivores affect plant competition by differences in plant's palatability and tolerance to herbivores, which in turn might depend on the habitat characteristics and herbivore size (Lubchenco, 1978; Olaff and Ritchie, 1998). Differences in soil nutrients, water and light change the plant's response to grazing and their competitive ability, therefore the effects of herbivores on diversity.

Plant consumption by herbivores can also limit abundance and distribution (Parker and Root, 1981; Louda, 1982; Maron and Crone, 2006). Gómez & Hódar (2008) found that fenced holm oak seedlings under pine trees were more abundant than in unfenced plots where wild boar and other ungulates would eat them. The ability of herbivores to limit plant distribution is clearly seen in an experiment done by Parker and Root (1981), wherein the authors measured mortality and fecundity of plants unexposed and exposed to herbivores in sites where the plant species does not typically occur. Exposed plants were completely defoliated which increased plant mortality. However fecundity of protected individuals matched those found in their natural range where the herbivores rarely occurred. The authors concluded that herbivore pressure limits this plant's distribution.

Researchers are now well aware of these effects. Therefore, in this review I will consider only the following five major factors (see also Marquis, 2005): 1) their

effect on seed dispersal, 2) effect on apparent competition, 3) the effect of plant apparency and the resource concentration principle, 4) their effect on phylogenetic community composition, and 5) the interaction of herbivores and the environment (section III).

1. The impact of herbivores on seed dispersal

The dispersal process begins when fruits are still on the parent plant and ends with seedling establishment. During this time, dispersal might be affected by factors such as the number and distance of **suitable sites, capacity** to disperse to these sites (i.e. dispersal limitation) and pre-dispersal and post-dispersal **predation**, which in turn are influenced by habitat heterogeneity (Nathan & Muller-Landau, 2000; von Euler et al., 2014). The dispersal of seeds to a suitable microhabitat may influence distribution and abundance patterns. However, if plants are limited by their ability to disperse rather than site limited, dispersal limitation results. For example, Ehrlén & Eriksson (2000) found that for the seven herbaceous species, site availability was not a problem. Soil factors and competition with other plant species seemed not to affect the arrival of seeds, because at the end of their experiment, suitable unoccupied patches had not been colonized. The authors concluded that the pattern of natural abundance of these plants was not related to the availability of suitable sites. The authors instead suggest that these plants are limited by their capacity to disperse (e.g., most seed stay close to parent plant) and by seed limitation that can be enhanced by **seed predation** at a more local scale. Dispersal limitation has important consequences for the distribution and abundance of species, but is out of the scope of this review (see Dalling, 1998; Levine & Murrell, 2003).

Herbivores are capable of reducing the population size of their host plants and their host's spatial range (Louda & Potvin, 1995). For example, seeds might be able to reach suitable habitats but their post-dispersal predators might not allow them to germinate. Crawley (1989, 1992), Hulme (1996b) and others (Andersen, 1989) emphasize that the effect of herbivores on seeds will not be important if plants 1) regenerate mostly by vegetative means and 2) are safe-site limited rather than limited by their herbivores. A number of studies have shown that plants are safe-site limited. For example Crawley & Long (1995) in their long-term study found that even with the artificial addition of acorns the oaks did not have a higher rate of recruitment. Other studies had similar results (Green & Palmbald, 1975; Hulme 1996a; Barberá et al., 2006). Crawley (2000) explains different situations in which herbivores might or might not have an effect on a plant's population abundance: In a low seed input situation, herbivores are most likely to consume all available seeds and have a strong effect; in a mid-seed input, the species is likely to be site-limited yet, seed herbivores might have their highest influence. Conversely, at high densities of seeds, plants are site-limited and herbivores have almost no effect on plant abundance and or population dynamics. Seed herbivores, as well, may enhance local species diversity, only if predators differentially attack seeds of competitively dominant plants (Green and Palmbald, 1975; Samson et al., 1992; Hulme 1996b).

Seed predators are usually divided in two types, pre-dispersal and post-dispersal predators. Pre-dispersal herbivores are those that consume seeds when they are still attached to the plant. This type of herbivore tends to be specialists and small in size. Their effect on the seeds is also different than the effect post-dispersal seed

predators have on recruitment because seeds are still attached to the parent plant and are able to use its resources for defense. Post-dispersal herbivores consume seeds when these have already been dispersed. These herbivores are usually generalists, bigger in size and have high mobility. When herbivores attack dispersed seeds, the latter only have the resources available within the seed for defense (Crawley, 2000).

Pre-dispersal herbivores. The effect of herbivores that is usually measured for pre-dispersal predation is amount of damaged seeds. Pre-dispersal predation has been shown to reduce the number of seeds that are dispersed and ultimately, germinate (Green and Palmbald, 1975; Rice, 1987; Wood & Andersen, 1990; Louda & Potvin, 1995; Fröborg & Eriksson, 2003; Maron & Crone, 2006; von Euler et al., 2014). Together, seed herbivores and a heterogeneous environment, both spatial and temporal, may affect abundance and distribution patterns observed in nature (e.g., Louda, 1982; Kolb et al., 2007b see reviews by Crawley1992 and Kolb et al., 2007a). Interestingly, Kolb et al. (2007b) found that, along a light gradient, a pre-dispersal seed predation gradient was observed that ultimately changed the population's growth rates. Yet, they noticed that not only does the amount of seed predation matter, but the sensitivity of population growth to seed predation. In levels of high seed predation intensity, sensitivity decreased. The authors believed this happened because herbivores are not the most dominant stress factor, as the plants are microsite limited and compete for light. In a metaanalysis, Kolb and colleagues (2007) found that pre-dispersal seed predation negatively affects population growth by reducing recruitment. However the variability of predation through years and places allows seeds to escape predation in

some years and in specific places, influencing plant recruitment and therefore abundance.

   Post-dispersal herbivores. After seeds have left the parent plant they may be subjected to intense herbivory, which can have a strong effect on species abundance, and seedling recruitment and distribution (Reader, 1993; Wenny, 2000; Orrock, 2006; Zwolak et al., 2010; Pearson, 2013). The types of herbivores that attack seeds at this stage have different effects, especially when it interferes with seed establishment. Studies in oaks have found that insect parasitism generally does not allow the seed to emerge and in the rare cases where germination occurs, seedlings have fewer numbers of leaves and slower growth (Dixon et al., 1997; Lombardo & McCarthy, 2009; Dalgleish et al., 2012) which might have an effect on seedling competitive ability. The effects of mammals can be different as well, especially if their behavior is scatterhoarding. Some forgotten seeds may have the opportunity to emerge, if left in suitable places; spatial distribution of plants may be affected by this spatial inequality and possibly promote species coexistence (Harmon & Stamp, 1992; Hulme, 1998). Moreover, if seeds compete for site availability, seed herbivores may determine which species establish in available sites, thus influencing distribution (Brown & Heske, 1990; Hulme, 1996a; Maron & Crone, 2006).

   Pre-dispersal and post-dispersal predation may be linked, together influencing seedling recruitment. If floral herbivores negatively affect inflorescences and reduce seed numbers before dispersion, post-dispersal herbivory could probably have a higher effect on recruitment, and ultimately on plant abundance. Louda and colleagues (1990) investigated the combined effects of pre-dispersal, post-dispersal predation and

seedling competition on Platte thistle populations in Nebraska. They found that, in general, seed predation and competition both had a negative effect on seedling recruitment. Pre-dispersal seed predators had a much higher impact on seedling recruitment than post-dispersal predators. However, post-dispersal predators add to the overall negative impact to seedling recruitment. Additionally, seedling competition with other plants greatly contributed to the low seedling recruitment observed.

It is possible to conclude that seed herbivores do have an adverse effect on plant diversity, abundance and distribution. This would be particularly true when herbivores prefer particular types of seeds and abundantly consume them, and the parent plant is not limited by site availability.

2. Apparent competition

Another way herbivores may exert their effects on plants is through apparent competition. By means of real competition species compete directly for resources, such as nutrients, light, food; apparent competition, on the other hand, is indirect. Apparent competition arises when two or more species indirectly affect each other's abundance negatively through a shared predator (Holt, 2012). The predator population must have a numerical response to its prey, which means that as prey abundance is reduced, the predator is as well. However, when there is an alternative prey, it allows predator populations to be maintained, which in turn may increase the attack rate on both or on one prey population (Holt, 1977; Holt & Lawton, 1993; Abrams & Matsuda, 1996; Wootton, 1994; Cronin, 2007; Holt, 2012). An herbivore (predator), through apparent competition, may place constraints on the type and number of the plants (host) it feeds on and allow for two possible outcomes: extinction of a host

population or coexistence between host populations. Thus, two type of responses to a shared predator are possible: 1) Negative, when the increased abundance of one host species increases the attack rate on the alternative species, or 2) positive, when the increase in one host species warrants switching or satiation of the predator and reduces attack rate on the alternative host species (Abrams & Matsuda, 1996).

It is argued that apparent competition has an important effect on community structure, species abundance, distribution and diversity (Holt & Lawton, 1994 and citations therein). Shared herbivores may influence the direct competitive effects of plants on each other (see Marquis, 2005). Denslow et al. (1991) planted seedlings of two *Inga* species under the shade of palms or in areas with no palms. They found that seedlings near palms had almost no growth. However, this was not due to competition between seedlings and palms for resources, but to a higher rate of herbivore attack under the shade of the palms greatly affecting the distribution of *Inga* throughout the forest. Herbivores have the ability to modify plant traits that help them acquire resources and make them better competitors (Louda et al., 1990 and citations therein). In their review Louda et al. (1990) synthesize the different field and laboratory experiments demonstrating that addition of herbivores changed the outcome of plant competition by reducing the dominant species' ability to obtain resources. Herbivores may be affected by host palatability and tolerance to herbivory, which will affect herbivore preferences (Olaff & Ritchie, 1998).

Apparent competition in plants mediated by their herbivores sometimes is labeled as an indirect effect, which can be anything from indirect mutualisms to trophic cascades (Strauss, 1991; reviewed by Wootton, 1994 and White et al., 2006).

Moreover, apparent and direct competition may have similar results, and therefore misguidedly arguing for direct competition when it is not the case (Reader, 1992). One exception are studies that report the effects of invasive species on native flora (reviewed by White et al., 2006). These studies have found alarming results of the effects of apparent competition between invasive and native plant hosts with either the mediator or predator being an exotic herbivore species or native herbivores. It is usually found that the presence of the invasive plant increases the abundance of the exotic herbivore. Thus attack on the native plant by herbivores increases, reducing the native plant's abundance or even excluding it from the system (Sessions & Kelly, 2002; Rand & Louda, 2004; Lau & Strauss, 2005; Malmstrom, 2005). The presence of an invasive plant species and the increases in food supply it provides for native herbivores, also negatively affects neighboring native species richness (Orrock, 2015). The presence of a shared predator (either native or non-native) could aid in excluding the native species or drastically reduce its abundance. The predator has a positive numerical response to the increase in abundance of prey species, in this case the exotic species that can sustain the predator population without reducing its numbers. The native species now may suffer higher rates of predation because of the predator's higher abundance, experience a reduction in fitness and ultimately might be excluded from the area.

There are studies documenting the effects of apparent competition on native communities as well. These studies have found that the presence of a particular plant species increases the abundance of the shared predator and therefore not only reduces abundance of the second plant species but it limits its distribution to ranges where the

first plant species is rarely or completely absent from the site (Thomas, 1986; Veech, 2000; Rand, 2003; Rooney & Waller, 2003; Dyer et al., 2010). Interestingly ecologists have found that generally this increase in herbivory and abundance of the second prey species is not correlated to with density (e.g. Rand, 2003). Apparent competition may also occur through a trophic cascade interactions. One interesting example found that the addition of a top predator of ants that defend its plant species against herbivores, increased herbivore consumption of the focal and neighboring species. Moreover, neighboring plant species richness decreased with the addition of the focal plant infested with its herbivore (Letourneau and Dyer, 2005). The explanation is that when the top predator of the ants was present, it reduced ant numbers and therefore allowed herbivores to increase in numbers in the focal species. The predators are generalist species and therefore this increase in predators spilled over to neighboring plants, increasing their attack rate and reduced neighboring species richness. These studies suggest that the abundance of a plant species may increase the shared herbivore abundance. As a result the deleterious impacts of the herbivores increase on a second species, in some cases reducing its abundance and limiting its distribution.

Apparent competition as an indirect interaction has enormous consequences on populations, however these effects are usually unnoticed or blend in with other types of interactions. Nevertheless it shows strong patterns of herbivore impact on neighboring species and it is particularly important in structuring community dynamics with invasive species. It appears that spatial patterns and the density of neighbor's species affect the community and we should pay attention to how apparent

interactions affect the abundance and limit or perhaps even enhance species distributions.

3. Spatial considerations: Resource concentration principle and plant apparency

The resource concentration hypothesis (RCH) states that the **size of a patch** of host plants influences the likelihood that herbivores find and remain in the patch. Moreover, the denser one species is and the less diversity there is within a patch, the more its specialist herbivores will be found in that particular patch (Tahvanainen & Root, 1972; Root, 1973). Thus, the RCH usually measures the relationship of two variables: **a)** absolute density of the host plant, and **b)** the relative density of non-hosts. Different studies have found support for the resource concentration hypothesis, including those that have revealed that the particular biology of the herbivore species and their ability to migrate around patches, as juveniles and adults, is important (Bach, 1980; Maguire, 1983; Andow, 1990; Grez & González, 1995; Östergård & Ehrlén, 2005; Kim & Underwood, 2014). With this is mind, the resource concentration hypothesis hypothesizes that herbivores that respond to plant patches may have strong effects on host plant populations (Stephens & Myers, 2012).

Patch size and host plant absolute density, as mentioned earlier, are not the only concern of the RCH. These and other studies have also found that the influence of non-host neighbors within a patch is also important because it reduces abundance of herbivores and therefore, damage (reviewed by Barbosa et al., 2009, Alaloun et al., 2014). The effect of non-host plants on the abundance of herbivores on diverse patches could be two fold: **1)** by way of chemistry, such as volatiles and post-contact

deterrents and/or **2)** visual traits. Chemical traits **(1)** of neighbors have been shown to aid host plants to reduce herbivore damage by obtaining cues from volatiles that allows neighbors to start producing their chemical defenses or by post-contact deterrents, i.e. plant defenses that are used when the herbivore lands or feeds on the plant (Tahvanainen & Root, 1972; Karban & Maron, 2002; Engelberth et al., 2004; Barbosa et al., 2009; Zakir et al., 2013). Visual traits **(2)** of neighboring plants may confuse or distract herbivores from reaching their preferred host type by shading and hiding the host plant, impeding movement of herbivores towards the host plant or acting as attractants and retaining the herbivores (Holmes & Barrett, 1997; Finch et al., 2003; Tillman, 2006; Dulaurent et al., 2012).

These neighbor effects may, as well, be interpreted in the light of plant apparency. The **plant apparency** hypothesis proposes that most conspicuous and long-lived species will suffer greater herbivory than unapparent and annual host species (Feeny, 1976). In diverse patches, apparent plants may be located by their herbivores and in some cases allow neighboring plants to escape herbivore damage (Chew & Courtney, 1991; Floater & Zalucki, 2000; Castagneyrol et al., 2013; Louthan et al., 2014). More apparent plants, therefore, may deter herbivores from arriving to their neighbors and may have strong community effects. For example, if herbivores continuously oviposit in the most conspicuous plants and the larvae feed on flower heads or seeds, then those plants will experience a reduction in fitness and consequently in abundance.

According to the resource concentration hypothesis small patches of a single host plant will have fewer specialist herbivore species than larger patches of a single

host plant, although some studies have found no relationship (Futuyma & Wasserman, 1980; Grez & González, 1995; Rhainds & English-Loeb, 2003). Nevertheless, part **(b)** of this hypothesis is suggests a role for plant density relative to other plant species (i.e. patch diversity). A patch with only one plant species is more susceptible to damage by specialist herbivores because there are no other plant species that chemically or visually can help deterred these herbivores. However, large host plants might be visible to herbivores even with potentially helpful neighbors, perhaps these host plants are inevitable going to be found by their specialist herbivores (e.g. Sholes, 2008). The spatial distribution and abundance of plant species may affect the amount of damage a neighboring plant species may experience; in the end, this may have repercussions in plant species coexistence.

4. Herbivores drive phylogenetic community composition

Host patch diversity may decrease the abundance and damage of herbivores not only by masking host chemicals or by visual deterrence, but also by differences in phylogenetic relatedness of hosts within a patch or community. Phylogenetic distance between plants within a community is now believed to have a strong effect on the community structure of herbivores and the damage they may cause to their neighbors (Jactel & Brockerhoff, 2007; Gossner et al., 2009; Yguel et al., 2011). It is commonly believed that closely related plant species share similar chemical and physical characteristics that allow an herbivore to attack more easily plants that are closely related (Gilbert et al., 2012). Therefore, species susceptible to one type of herbivore or pathogen tend to be more closely related; this susceptibility decreases as phylogenetic

relatedness decreases between neighboring plants (Gilbert & Webb, 2007; Harvey et al., 2012).

Researchers have indeed noticed that in phylogenetically diverse communities associational resistance (AR) is more likely to occur. AR occurs when a patch of a focal plant (host) species is surrounded by non-host plants and allows the focal species to escape with little or no predation. Castagneyrol et al. (2013) found that a focal species within a plant community with high phylogenetic diversity had less herbivore damage compared to communities with closely related species. The authors argued that this is because as phylogenetic distance between the host plants increases the herbivores feeding on them suffer a fitness reduction. It has been frequently shown that as the phylogenetic distance between a new host plant and the typical host increases herbivores are not able to adapt to the new host (reviewed by Bertheau et al., 2010). However, if the plant host is attacked by generalist herbivores (polygophagous) it is more likely the host will suffer more damage since these herbivores do not experience a fitness reduction as strong as specialist (monophagous) herbivores would (Jactel & Brockerhoff, 2007; Yguel et al., 2011; Castagneyrol et al., 2014).

Niche theory explains that highly distinct species would grow together because there exists little or no niche overlap between species and therefore they are less likely to compete for resources. However, competition for resources may not be the only reason why similar species should may not be found growing together. Phylogenetic distance between hosts and their particular herbivores may affect the distribution and abundance of species as well; parallel diversification of hosts and herbivores may occur and lead to phylogenetic conservatism (Farrell & Mitter, 1990; Dinnage et al.,

2012) where only specialist herbivores are able to highly damage their host. By keeping their particular host rare, species coexistence between different hosts would be promoted, either by existing in patches of distantly related plant species or patches where particular leaf chemical compounds (e.g. defense compounds) are overdispersed throughout the plant phylogeny. As herbivores and pathogens exert selective pressures on defense compounds, leaf chemistry may tend to be more dispersed throughout the plant phylogeny within a patch or community, even though the plants themselves are may be closely related. Consequently, plant-herbivore interactions may be a force that determines species composition by promoting coexistence (Coley & Kursar, 2014).

The evolutionary arms race between plants and their herbivores has most probably led to the wide array of secondary compounds in plants (Becerra et al., 2009). Moreover, it has been shown that herbivore colonization of a host depends mostly on leaf chemistry and may even be independent of plant phylogeny. In a Mexican dry forest, the tight relationship between the plant genus *Bursera* and its chrysomelid beetle *Blepharida,* shows that leaf chemistry is partially unrelated to plant phylogeny; the most closely related species within the genus have the most different leaf chemistry. Furthermore, *Blepharida* spp. host use depends on host chemistry and is independent of plant phylogeny; herbivores only colonized species of chemically similar plants that are not necessarily the most closely related. These results demonstrate that patterns of host shifts are controlled by chemical similarity and that plant chemistry has played an important role in the evolution of host shifts (Becerra, 1997). Ten years later, the same author found that local, low elevation, and highly specialized communities of *Bursera* and *Blepharida* were chemically overdispersed.

Plants in those communities differed greatly in leaf chemistry. Phylogenetic distance, on the other hand, was not as expected: these communities harbored more closely related species than expected by chance. However, at higher elevations where communities are more diverse and there is a decrease in herbivore specialization, communities were not chemically different from random communities (Becerra, 2007).

This result suggests that evolutionary pressure that herbivores exert on plants results in divergence in chemical profiles. Closely related species are sometimes not similar in defensive chemistry. Hence, in certain plant communities it is possible to find closely related species growing together that differ greatly in their chemical compounds. Coexistence and species diversity are therefore managed by providing associational resistance to neighbors due to insect specialization of plants with particular chemical characteristics. Recently, it has been found around the world that as the strong influence of insect herbivory, and particularly specialist herbivores, increases, plant species richness increases (Becerra, 2015). Antagonistic interactions are capable of driving a specific phylogenetic community composition either by enhancing phylogenetic diversity or chemical diversity, consequently shaping abundance and distribution of these communities.

III. INTERACTION BETWEEN THE ABIOTIC ENVIRONMENT AND HERBIVORES

As I have reviewed, plants respond to abiotic factors that contribute to habitat heterogeneity, such as light and soil, to form clumped distributions at their favored

sites, in this way contributing to habitat specialization and species coexistence. Nonetheless, plant species are also limited by herbivores, affecting dispersal, competition and selecting for specific community composition. I have described how herbivores contribute to species diversity, abundance, distribution and coexistence in local communities, as well as throughout environmental gradients. Moreover, researchers have also found that herbivore abundance may depend on patch diversity (Maron & Crone, 2006b; Becerra, 2015).

Additionally, abiotic conditions such as water limitation, light availability and soil nutrients in an area may influence plant's vulnerability to herbivore attack (Gershenzon, 1984; Marquis & Braker, 1994; Endara & Coley, 2011). For example, nitrogen and sulfur deficiencies generally reduce the production of secondary compounds, but in conditions of plant stress where these two nutrients are not limiting, secondary compounds increase (Gershenzon, 1984). However, these responses depend on herbivore feeding habits and the amount of plant stress (Jactel et al., 2012). The plant stress hypothesis suggests that abiotic stressors increase the susceptibility of plants to herbivore attack (Jactel et al., 2012). This could be by decreasing plant's defenses or by gathering necessary nutrients that are attractive to herbivores. For example, one study measuring changes in plant chemistry and herbivore responses to drought found that in general secondary metabolites decreased with increasing drought stress. Herbivores response, however, was mixed; the specialist herbivore preferred well-watered plants while the generalist herbivore preferred feeding under drought stress (Gutbrodt et al., 2011). Another study using drought stress found that healthier saplings tend to be more attack by bark beetles than

stressed individuals. However, stressed individuals suffered from girdling damage

when un-stressed individuals did not (Sopow et al., 2015).

Light also has an effect on the amount of herbivory on plants. In a study of

palms and their orthopteran consumers, it was found that palms in small gaps had

higher levels of herbivory than plants living in the understory (Braker & Chazdon,

1992). Other studies have shown that plants under shade may suffer more herbivore

consumption and pathogen invasion than plants under higher light levels (Denslow et

al., 1991; Salgado-Luarte and Gianoli, 2010, Goodale, 2014). Soil nutrients may also

be responsible for the amount of damage received by plants. The resource availability

hypothesis (RAH) states in one of its predictions that plants in soil rich nutrient

habitats would sustain higher levels of herbivory because plants invest more resources

on rapid growth, therefore investing less in secondary compounds for defense. The

cost of losing tissue to herbivory is not high in these plants (Endara & Coley, 2011).

On the other hand, plants growing in nutrient-poor soils, invest more in defenses

because the loss of vegetative tissue is costly (reviewed by Endara & Coley, 2011).

This particular hypothesis agrees with Gershenzon's (1984) studies and review.

Nonetheless, a study of soil fertilization in different species found that the increase in

nutrients did have an increase in growth, but this was not at the expense of secondary

compounds. On the contrary, for almost all species the amount of phenolic production

increased (Braker & Chazdon, 1992). Another study with red mangroves found that

the addition of fertilizers did not increase or decrease leaf herbivory. However, the

effects of a specialist herbivore that feeds on apical buds significantly increased in

enriched trees compared to control trees. The same result was obtained for another

specialist herbivore on the red mangrove, the presence of this leaf miner was much higher than in non-fertilized trees (Feller, 1995).

Interestingly, much less is known about how ***both*** abiotic and biotic factors affect plant distribution and abundance. As mentioned before, we know that the strength of the effect of herbivores may depend on the habitat characteristics, such as soil fertility and water availability (Menge & Olson, 1990; Olff & Ritchie, 1998). Additionally, stressful environments (*e.g.* drought) potentially increase herbivore damage and modify plant's habitat selection (Menge & Olson, 1990; Louda & Rodman, 1996; Harley, 2003).

Abiotic factors and herbivores may hamper plant success in part of their range, limiting their distribution. A study by Louda and Rodman (1996) found that the local distribution of their focal plant species is limited to shaded areas because plants in the sunlight suffer higher levels of herbivory, which decreases plant growth and reproduction. Plants grown in the sun but protected from herbivory, on average, grow and produce fruits just as much as plants in the shade (Louda & Rodman, 1996.). Along the same lines, a more recent study tested plant tolerance to herbivory along a light gradient. The authors believed that herbivory is contributing to the exclusion of tree species from the shade. However they found that herbivory increased in the sun and seemed not to be due to a reduction in plant defenses, but rather to the abundance of herbivores in open sites. Nevertheless, plants in the shade had reduced tolerance and resistance to herbivory and decreased seedling survival and growth, which did not appear to happen in the sun (Salgado-Luarte & Gianoli, 2010). Others have tested habitat specialization in plants in the tropics; studied abiotic factors like light and

flooding contributed, along with herbivory, to seedling establishment to a tropical tree species *Calophyllum brasiliense* (King, 2003). A study in the Amazonian forest between two soil types (white-sand soils and clay soils) with different nutrient availability, found that clay specialists are able to grow in white-sand soils if protected from herbivory, but when unprotected, mortality increased significantly resulting in the exclusion of those species from the white-sand soils (Fine et al., 2004). In a continuation of this study, Fine and colleagues (2006) tested the growth vs. defense hypothesis to observe if defense strategies and growth are affected by soil characteristics and therefore contribute to the observed pattern of herbivore consumption. They found that, indeed, differences in defense strategies are affected by soil, which then contributes to the effect herbivores have on plants and ultimately promotes habitat specialization (Fine et al., 2006).

Herbivores do seem to have an important role in promoting habitat specialization. As mentioned earlier, herbivores, as well, are influenced by abiotic factors such as soil characteristics (Abdala-Roberts et al., 2014). We already know that environmental heterogeneity and herbivores acting independently have a strong influence of plant diversity. We should ask now how these effects might be affecting species coexistence by acting together.

CONCLUSION

Naturalists and ecologists have long noticed patterns in plant distributions and have strived to understand their relationships with the environment in which they are found. Perhaps the most clear relationship and with obvious consequences is with the abiotic environment. Indeed, plant species grow along gradients of soil nutrients, soil

moisture and utilize different light gradients throughout canopy understory. However it is known that biotic forces also regulate plant's distribution and abundance. Plants are limited by the herbivores they encounter in a community. However herbivores do not act alone, in fact, as McNaughton (1983) argues in his study of grassland Savannas, herbivores, fires and soil ***interact in complex ways*** to cause the current spatial patterns of grasslands we observe. This situation is probably not unique. Undoubtedly interactions between herbivores and abiotic factors in different places may contribute to the plant diversity observed today. Nonetheless few studies have been done and thus, it is difficult to make general statements. It is therefore necessary to contribute with studies of how abundance and distribution is limited by herbivores and abiotic factors. The few studies have been done with different genera or with one particular species. However, the tropics are home to super-diverse genera, with all species coexisting in the same habitat or even in the same patch. How are these species specialized to their habitat and therefore coexist? Are abiotic factors like soil and light affecting these plants' interactions with their particular herbivores and therefore affecting abundance and community composition? It is now time to accept the important role of herbivores, although not alone, but ***working in concert*** with the abiotic environment and how these factors may be causing patterns of plant abundance, distribution and diversity.

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CHAPTER 2

THE ROLE OF ABIOTIC AND BIOTIC FACTORS IN LIMITING *PIPER*

ABUNDANCE AND DISTRIBUTION

INTRODUCTION

A long-standing challenge in ecology is to identify the factors that determine which species can co-occur together (Gleason, 1926; Picket & Bazzaz, 1978; Louda, 1982; Fine et al., 2004). Gleason (1926) believed that the abiotic environment is the main factor determining where species are found, with little or no influence of co-occurring species. When Tilman proposed the hypothesis of coexistence (1982, 1994) he focused on the role of interspecific competition, concluding that differences in the abiotic environment allow different species to coexist via tradeoffs in resource use along resource gradients. These ideas are based on niche theory (Hutchinson, 1957), which proposes that species align along axes of environmental conditions that are required for their existence resulting in predictable associations with particular habitats or microhabitats.

Much evidence indeed demonstrates that species specialize on a limited portion of available gradients in abiotic resources, and that there are tradeoffs in the ability of species to use those resources. For example, certain understory tree species vary in their growth depending on the amount of light received (Lusk et al., 2006; van Pelt & Franklin, 1999). The underlying mechanism is that differences in light

gradients under the forest canopy influence a species distribution and abundance by creating opportunities for plant establishment and recruitment by affecting plant growth, mortality, and seedling establishment (Denslow, 1987; Montgomery and Chazdon, 2002; Rüger et al., 2009; Goodale et al., 2014).

In addition to light, plant distribution and abundance are also influenced by edaphic patterns. Differences in soil nutrients and moisture influence species growth and survival in a particular area (Tuomisto and Ruokolainen, 1994; Sollins, 1998; John et al., 2007; Toledo et al., 2012; De Oliviera et al., 2014). Plant species respond to changes in soil characteristics at different geographical scales, both large and small (John et al., 2007; Oliviera et al., 2014). Vegetation is non-randomly associated with soil type at both a local scale of <1 km^2 and at a scale of 1-100 km^2 even when soils do not possess sharp differences in their composition (Clark et al., 1998; Palmiotto et al., 2004, John et al., 2007). Studies at landscape scales ($>1,000$-10,000 km^2) have found the same response (Phillips et al., 2004; Toledo et al., 2012). Palmiotto and colleagues (2004) found that although most of the variation in species distribution was explained by soil type, they were unable to distinguish a mechanism for some of the species studied. For these species soil nutrients and phosphorous availability did not co-vary with distribution. The authors believed that water availability or mycorrizhae were probably responsible. It is not unreasonable to think that other biotic contributing factors, such as herbivores, might be important.

Herbivores greatly influence species abundance, distribution and diversity by impacting flowering and fruit production, growth, seed and seedling survival (Parker and Root, 1981; Louda 1982; reviewed by Crawley, 1989, Doak, 1992, Marquis 2005, 2010, Maroon and Crone, 2006). For example, herbivores affect seed dispersal by consuming seeds still attached to the parent plant (pre-dispersal seed predation) and by feeding on seeds that have already been dispersed (post-dispersal seed predation). This effectively reduces species abundance, particularly when the species already produces few seeds (in other words, is seed limited [Louda & Potvin, 1995; Orrock et al., 2006; Pearson et al., 2013; von Euler et al., 2014]). Herbivores are also capable of decreasing plant abundance through apparent competition (Holt, 1977), as observed most prominently from exotic plant invasions (Morris et al., 2004; Lau & Strauss, 2005; Cronin, 2007; Blitzer & Welter, 2011). Another way that herbivores affect plant distribution and abundance is via associational resistance and its alter ego, associational susceptibility (Barbosa et al., 2009; Stephens & Myers, 2012; Louthan et al., 2014). These phenomena are often apparent when one takes into account the effect on neighbor identity of the amount of damage received by focal individuals. Herbivores also affect plant community composition by influencing the phylogenetic relatedness within a patch (Castagneyrol et al., 2014; Harvey et al., 2012; Castagneyrol et al., 2013). Therefore, patches of tree species that are closely related with leaf chemical characteristics that differ more than what would be expected by chance can be found (Becerra, 2007). Thus, herbivores can drive phylogenetic community composition, limiting a species place in space and their abundance in at a location.

There is much room for a more integrated view for the factors that determine plant species distributions. Plant ecologists tend to ignore the effects of herbivores on plant distributions, while herbivore ecologists often omit abiotic factors. This is exemplified in previous work in the tropical regions and at La Selva Biological Station, Costa Rica, which focused on soil type as the main driver of plant distribution (Clark et al., 1998 & 1999, John et al., 2007, Toledo et al., 2012), while others focused on the role of herbivores (reviewed by Marquis and Braker, 1994 and citations therein). Only a few studies have examined a possible interaction of the two (Denslow et al., 1991; King, 2003; Fine et al., 2004), although it is known that abiotic environmental factors influence a plant's vulnerability to herbivore attack (Marquis and Braker, 1994 and citations therein).

I conducted an observational study using the genus *Piper* (Piperaceae), a diverse genus of shrubs, vines, and small trees, at the La Selva Biological Station in Costa Rica, to investigate the possible contributions of both abiotic and biotic factors for determining *Piper* distribution and abundance. *Piper* was chosen as it contains ~50 species coexisting at the study site. Additionally, this genus displays some evidence of abiotic niche partitioning: species germinate differently at different light levels (Vazquez-Yanes et al., 1990) and vary in cloning ability (Greig 1993). The La Selva Biological Station has two main soil types (alluvial and volcanic) and I measured abundance, light, and herbivore damage for plants in both types. I hypothesized that herbivores, interacting with soil and light, significantly affect *Piper* distribution and abundances of particular *Piper* species across soil types. Furthermore, the size and diversity of the patch can affect herbivore damage. The resource concentration

hypothesis suggests that in a small patch with low plant diversity herbivore damage will be higher than in a patch of higher diversity (Root, 1973). My sampling design and methods were designed to answer the following questions and predictions:

1) Do soil type and herbivore damage influence *Piper* distribution and community composition? I predicted that species that are soil specialists will be more abundant and suffer less herbivore damage on their "preferred" soil type than when found in the habitat where they are not specialists. Evidence of adaptation would be more individuals on one soil than the other, but if herbivores are driving this adaptation, they should also have less herbivory.

2) How do light and soil predict the local presence/absence of *Piper* within a transect? I predicted that *Piper* would be present at high light levels because of the necessary of light requirements for germination (Vazquez-Yanes et al., 1990); however soil may change at what light levels *Piper* would be present because of the difference in soil nutrients.

3) How do soil and light affect the abundance of individual *Piper* species? I predicted that *Piper* would be more abundant on alluvial soils and at higher light levels.

4) Do soil type, plant size, patch size, light and species richness have an effect on the percentage of herbivore damage at the individual plant level? *Piper* herbivore diversity is not affected by differences in soil type or light availability (Marquis and Braker, 1994). I predicted, then, that plants in alluvial soils should suffer more herbivore damage than plants in volcanic soils; the resource availability hypothesis

states that plants in more nutrient-rich soils would invest less in defense and therefore

would be more damaged by herbivores. I also predicted that herbivory will be

negatively correlated with light exposure, because herbivores often prefer leaves

grown in shade (Goodale et al., 2014). Moreover, I predict that plants in small patches

with low number of species would have more herbivore damage as predicted by the

resource concentration hypothesis. However, damage changes with ontogeny (Boege

and Marquis, 2005), therefore I predict that older (larger) plants would show less signs

of herbivore damage.

METHODS

Study area

The La Selva Biological Station, Heredia, Costa Rica, is located at 10° 26' N,

83° 59' W. The study site, owned by the Organization for Tropical Studies, is situated

approximately at 50-1000 masl with an average of 4,200 mm annual rainfall (Dyer and

Palmer, 2004). Close to the Caribbean side of Costa Rica, it is surrounded by two

major rivers and has 1,600 hectares of tropical wet forest (McDade, 1994).

La Selva's soils have two major factors that contribute to its formation and

therefore its differences: parent material and soil age (Sollins et al., 1994). The parent

material at La Selva consists of lava flows that covered the entire area over millions of

years of volcanic activity. At lower elevations, alluvial deposits from nearby rivers

have covered the volcanic lava. The residual soils that have remained volcanic are rich

in organic matter, are strongly acidic and are limited in potassium (Sollins et al.,

1994). Volcanic soils also have high rates of nitrogen mineralization and low

phosphorus availability (Vitousek & Denslow, 1986), have high drainage and low base saturation. Alluvial soils, in contrast, vary from extremely acidic to moderately acidic. These soils have higher levels of base saturation and have moderate amounts of organic matter (Sollins et al., 1994). Approximately one third of the property consists of alluvial soils. In general, alluvial soils are more fertile than volcanic soils (Parker, 1994).

 Study species

      Piper species typically grow in humid and warm rainforest and can be vines, herbs or shrubs (Greig, 2004). La Selva has approximately 50 species of *Piper* that occur throughout the forest (Dyer & Palmer, 2004) and are found in patches throughout the site. *Piper* herbivore species range in the degree of their host specialization from those that only feed on one *Piper* species (specialists) to those that feed on more than one in the genus (generalist) (Marquis, 1991). The genus *Piper* produces amides (nitrogen-based chemical defenses) as secondary compounds directly (Scott et al., 2007) but some species (*P. cenocladum* at La Selva) have mutualisms with ants (Greig, 2004), which act as an indirect defense. In Costa Rica, *Piper* species form patches that differ highly in their chemical characteristics (secondary compounds). It seems that for a new *Piper* species to coexist with others in that cluster, its chemical characteristics should differ from those already present (D. Salazar, unpublished data). *Piper* species at La Selva are mostly dispersed by bats, which forage throughout the station (Salazar et al., 2013) and presumably do not discriminate between soil types. Therefore equal dispersal is assumed for *Piper* species throughout the area.

Field work

I selected sites using La Selva's soil maps and grid system. Half of the 26 transects were in alluvial soils and the other half on volcanic soils based on soil maps of the La Selva. All transects were 100 m long and two meters wide and ran either north to south or east to west. Transects were at least 50 m away from forest edges and at least 50 m away from each other. I sampled only in primary forest to limit the amount of variation due to succession and differences in land use. For each transect, I laid down a 100 m measuring tape and I measured all *Piper* plants 1 cm or greater in diameter at ground level that were encountered. For each individual, I recorded distance from the start of a transect, species identity, height, and number of leaves.

Light sampling/canopy openness

I measured canopy openness with a concave densiometer at 1 m intervals. Densiometer measurements have been shown to be positively correlated with measurements taken by hemispherical photography; moreover, densiometer measurements can be more precise in their estimation of light availability than hemispherical photography in places of high canopy cover (Bellow & Nair, 2003). I took four measurements at each meter, facing north, west, east and south and counted the number of dots that fell in open spaces. These four measurements were averaged per location and multiplied by 1.04 to obtain the percent overhead area not occupied by canopy (Lemmon, 1956).

Herbivore consumption

To measure leaf area lost to herbivores, I photographed leaves, using a graph paper background for scale (Panasonic DMC-ZS1). For plants with 10 or fewer leaves, I photographed all the leaves. For plants with more than 10 leaves, I systematically sampled 10 leaves throughout the plant. I used graph paper underneath the leaf for every picture taken to be able to scale the picture. I used the software ImageJ (1.48v) to measure total leaf area and area lost to herbivores. Using the graph paper as a reference, I scaled each photograph and then total area of the leaf was drawn and measured. If the leaf was incomplete, I drew it according to the type of leaf. After this, I measured all area missing. The type of damage or the herbivore identity was not considered in these analyses.

Statistical Analysis

Sampling of *Piper* species was done within 100 m transects. However, I noticed that *Piper* forms patches and was not evenly spread throughout transects. I calculated a Morisita's index to test this observation. The results show that clumping of all species among transects was significant (88.6% of the 26 transects had a p-value <0.001). Consequently, subsequent analyses use patch as sampling unit, unless otherwise specified. Patches were defined as contiguous meters that had at least 1 *Piper* within it. I analyzed herbivory measurements as percentages so that herbivory would be comparable between different leaf sizes. I built statistical models for all species encountered, one for just the most frequent species collectively, and a model for each of the most common species.

1. **Do soil and herbivory influence *Piper* distribution and community composition?**

I performed a permutational multivariate analysis of variance (PERMANOVA) for each of the six most frequent species (*i.e. P. trigonum, P. garagaranum, P. holdridgeanum, P. cenocladum, P. multiplinervium* and *P. urostachyum)* to test if species occurring primarily in one soil type would be more abundant and suffer less herbivory in that soil. Moreover, to observe niche differences between species I made kernel density graphs along light and herbivore damage axes.

I also compared plant species composition by constructing distance matrices with Jaccard's dissimilarity index and subsequently using Non Metric Multidimensional Scaling (NMDS) weighted by the size of a patch. To assess if community composition varied across patches I used a PERMANOVA that included soil, herbivory and light as explanatory variables. Analyses were done with the vegan package in R (R Development Core Team, 2015).

2. **Do the effects of soil and light predict the presence or absence of *Piper* plants?**

To test this, I performed a logistic regression. I used presence/absence of *Piper* in plots of 1 x 2 m throughout the 100 m transect. Plots were used instead of patches in this case because there is no simple way to define empty space within a transect. Most importantly, patches can be more than 1 m long and could have more than one plant. A 1 x 2 m plot allowed us to define empty plots.

My logistic regression model had fixed effects of soil and light and transect as a random effect. I used the binomial distribution for the response variable and p-values

for the estimates were obtained by using a likelihood ratio test. I applied this model to the presence/absence of *Piper* with all species present (model 1), a model using only the six most frequent species in the study (model 2) as well as a model for each of the six most frequent species (models 3-9). To observe niche differences between species, I graphed abundance per species across all levels of canopy openness (%) using kernel density estimation.

3. **Do soil, light, species richness and plant height affect the abundance of *Piper* at the study site?**

To test this I used generalized linear mixed effect models (GLMM). GLMMs were evaluated for all *Piper* species pooled (model 1), for the six most frequent species pooled (model 2) and for each of those most frequent species individually (models 3-9). For all models performed, I constructed a full model with all effects included and then used multiple model comparisons between models that differ in fixed effects. I used Akaike's criterion (AIC) values to select the best model (only keeping a variable if the AIC was raised by 1 or more units). For all models, I used the negative binomial distribution for the response variable, as it accounts for overdispersion, common in abundance data. P-values for estimates were obtained with likelihood ratio tests. Fixed effects for the full model included soil, light (as polynomial, *i.e.,* it does not follow a linear response), species richness per patch, average height of individuals per patch and a two-way interaction of soil and light. For all models, transect and patch were considered to be random effects. For models 1 and 2 species identity was included as a random effect. Analyses were done in R with the package glmmADMB (R Development Core Team, 2015).

4. Do soil type, plant size, plant height, species richness and light predict percentage of herbivore damage?

To test this, I used a GLMM with percent herbivory per individual plant as the response variable. Again, GLMMs were evaluated for all species sampled (model 1), for the six most frequent species pooled (model 2) and for each of those most frequent species individually (models 3-9). First, I constructed a full model that included the fixed effects of soil, light (as a polynomial), plant size (the number of leaves of an individual divided by height), species richness per patch, patch size (number of meters that a patch is formed of), the three-way interaction of patch size, soil and light. For all models, patch nested within transect was added as random effect, for models 1 and 2 species identity was used as random effect. I then used multiple model comparisons and AIC values to select the model that best fit the data. I used the negative binomial distribution for the response variable in all models as it accounts for count data that is overdispersed. P-values for estimates were obtained with chi-square likelihood ratio tests.

Lastly, to observe niche differences between species, I graphed abundance per species across all herbivory levels using kernel density estimation. All analyses were done in R with the package glmmADMB (R Development Core Team 2015).

RESULTS

I found 828 individuals from 24 *Piper* species in the 26 transects. Ten species had at least 15 individuals each: *P. artecuminatum, P. auritifolium, P. cenocladum, P. colonense, P. garagaranum, P. holdridgeanum, P.multiplinervium, P.*

pseudobumbratum, P. trigonum and *P. urostachyum.* These species represent 91% of all individuals sampled. *Piper trigonum* was the most abundant species in the study, representing 27% of all individuals and 30% of the ten most abundant species (Fig.1). The most frequent species, *i.e.,* species that were found in at least 15 of transects, were *P. cenocladum, P. garagaranum, P. holdridgeanum, P. multiplinervium, P. trigonum* and *P. urostachuym.* They were found in more than 58% of the transects; *P. trigonum* was found in all transects. Table 1summarizes information on mean herbivore damage (%), mean leaf area and mean percent (%) canopy openness per species. Species were mostly found in a percent canopy openness 2-10% and a percent herbivore damage varied between 0-45%.

1. Do soil and herbivory influence *Piper* distribution and community composition?

Results for *Piper* distribution show that three of the six most frequent species were significantly more abundant on one of the two soil types (Fig. 2). *Piper cenocladum* and *P. holdridgeanum* conform to my prediction of greater abundance and lower herbivory on the preferred soil types. *P. cenocladum* is more abundant in volcanic soils ($P = 0.03$) and shows less herbivory in that soil, however this is not a significant trend. *P. holdridgeanum* is more abundant in alluvial soils (marginally significant, $P = 0.09$) and suffered less herbivory on that soil type ($P = 0.02$). Although *P. trigonum* and *P. urostachyum* show this same trend, it is not significant. On the other hand, *P. garagaranum* is more abundant in alluvial soils ($P = 0.02$) and suffers more herbivory on that soil ($P = 0.03$). Only *P. multiplinervium* shows no signs of a trend in either direction (Fig. 2).

The community composition analysis for all sampled species shows that soil, herbivory and an interaction between soil and light all have an effect (Fig. 3, PERMANOVA: F = 2.61, P = 0.004; F = 2.95, *P* = 0.010; F = 1.67, *P* = 0.068, respectively). An NMDS and PERMANOVA performed on the six most frequent species shows that soil, herbivory and an interaction between soil and light significantly predict community composition (Fig. 4, PERMANOVA; F = 3.79, P = 0.007; F = 4.47, *P* = 0.002; F = 2.49, *P* = 0.046, respectively). Although the NMDS plots do not show strong patterns, the results of PERMANOVA suggest that community composition is influenced by both soil and herbivory.

2. Does the effect of soil and light predict the presence or absence of *Piper* plants?

I predicted that *Piper* would generally be found in high light levels and that soil type may influence the presence of *Piper*. However, for all species sampled (model 1), neither light nor soil had a significant effect on the presence of *Piper* (Table 2). Nevertheless, for the most frequent species pooled (model 2), light is a good predictor of *Piper* presence (Table 3). These six species prefer light levels between 3-8%, however no niche separation by species is particularly obvious (Fig. 5).

The individual species models show varying results (models 3-9). *Piper trigonum*'s presence is significantly affected by soil type, light and an interaction between soil and light (significance levels are shown in Table 4). The results of the logistic regression for *P. cenocladum* show a marginally significant effect of light (P = 0.09, Table 5) and light significantly predicted the presence of species *P.*

multiplinervium and *P. holdridgeanum* (Table 6 and 7, respectively). However, for *P. urostachyum* and *P. garagaranum* there was no effect of either soil or light.

The niche separation graph shows that in general, *Piper* species do not show signs of niche differences in light availability (Fig. 5).

3. Do soil, light, plant height and species richness affect the abundance of *Piper* at the study site?

I predicted that *Piper* species would be more abundant in high light areas in alluvial soils. However, there seemed to be no influence of soil for all *Piper* species pooled (model 1); the only significant effects were species richness and plant height (Table 8). Nevertheless, abundance is higher at intermediate levels of plant size (60-110 cm) and lower when plants are short (≤ 10 cm), small (>10 and ≤ 60 cm) and large (>110 cm, Fig. 6A). Species richness also predicts abundance in a patch: the more species, the greater number of plants (Table 8, Fig. 6B).

The results for the most frequent species (model 2) only show species richness as a significant variable (Table 9, Fig. 7). The models per species (3-9) showed that species richness positively predict the abundance of *P. trigonum, P. cenocladum, and P. urostachyum* (Table 10). However, analysis of *P. garagaranum, P. multiplinervium* and *P. holdridgeanum* abundances revealed no significant variables.

4. Do soil type, plant size, species richness and light predict percentage of *herbivore* damage?

For all species sampled (model 1), plant size was the only significant predictor of herbivory (GLMM, levels of significance in Table 11). Larger plants with numerous leaves suffered less herbivory than small plants (Fig. 8). For the most frequent species (model 2) the best-fit model included soil, light, patch size (small ≤ 2m, medium > 2 m and large > 4 m), the interaction between light and soil, and the three-way interaction of soil, light and patch size. However, according to the likelihood ratio tests the only significant predictors of herbivory are patch size (GLMM, Table 12), the interaction between light and soil (GLMM, Table 12) and the three-way interaction of light, soil and patch size (GLMM, Table 12). These results suggest that the larger the patch, the more herbivory was suffered by plants (GLMM, $P = 0.09$, Fig. 9). When the interaction between light and soil is considered, plants at low light levels (<3.5% of canopy openness) suffered more leaf area loss in volcanic soils than in alluvial soils (Fig. 10). The latter results are contrary to my prediction that in alluvial soils there would be higher amounts of herbivory. The more complex result, the three-way interaction, shows some uniformity across all light and patch size levels, but small patches at lower light levels and in volcanic soils suffer more herbivory than plants in patches of the same size but at higher light levels (Fig. 11).

The best-fit GLMM models for each of the six most abundant species (models 3-9) included many different variables (Table 13). However, for all species except *P. holdridgeanum*, these variables were not significant (Table 13). Results for *P. holdridgeanum* show that significant predictors of herbivory are soil, plant size, patch size, the interaction between patch size and soil type and the interaction between soil and light (GLMM, Table 14). Marginally significant is the three-way interaction

between soil, light and patch size (GLMM, Table 14). *P. holdridgeanum* plants suffer

more herbivory in volcanic soils (13.1 ± 1.2, mean$\pm$SE) where it is less abundant

(PERMANOVA, $p = 0.09$) than in alluvial soils (08.7 ± 01.1, mean $\pm$SE).

In general, smaller patches of *P. holdridgeanum* have plants with higher

amounts of herbivory than larger patches, as I predicted (Fig. 12). Nevertheless, when

including interactions with light, soil and patch size, results change. For example,

when considering the interaction between soil type and patch size, plants in alluvial

soils suffer less herbivory at any patch size than in volcanic soils, except in large

patches where the percent area removed seems to be equal in both soils (Fig.13). In the

three-way interaction of soil, light and patch size, plants in alluvial soils generally had

less herbivore damage than plants in volcanic soils (Fig. 14), contrary to my

predictions regarding soil type. However, in alluvial soils and high light levels, plants

suffer less herbivory than plants in alluvial soils but in medium levels of light (Fig. 14

and 15). These results suggest that plants of *P. holdridgeanum* would suffer less

herbivory when in alluvial soils and at higher light levels regardless of patch size. But

when there is no interaction of soil and light, plants in small patches suffer more

herbivory than plants in larger patches, as predicted. Lastly, large plants of *P.*

holdridgeanum suffer less herbivory than small plants (Fig. 16).

The niche separation graph shows that in general, *Piper* species do not show

signs of niche differences in herbivore damage (Fig. 5).

Discussion

Habitat specialization of species may be due to both abiotic and biotic factors, which in turn affect species abundance and distribution. In general, *Piper* species presence in this study responds to light availability and abundance and is mostly predicted by plant size and patch species richness. However, plants in general are also limited by the amount of damage that herbivores inflict on them. Species, therefore, would most likely be found where there is low herbivore attack (Parker & Root, 1981). In this study, *Piper* is generally more damaged when in small patches. However, this can also depend on the amount of light received by the patch and the soil type (Fig. 11). Plants in small patches at low light levels and in volcanic soils receive more herbivory than small and larger patches at higher light levels and in alluvial soils (Fig.11).

1. Is *Piper* distribution and community composition influenced by soil and herbivory?

I predicted that the distribution of a species on a soil type, and therefore its habitat specialization, would depend herbivore damage. If soil type is driving this habitat specialization, then the species abundance is a proxy for adaptation to that soil. But if herbivores are also responsible, herbivore damage would be less on the preferred soil type.

The results show that of three of the six most frequent species show a significant difference in abundance between soils: *P. cenocladum* is more abundant in volcanic soils, while *P. holdridgeanum* and *P. garaganum* in alluvial soils (Fig. 2). However, levels of herbivory are not lower for all species that are more abundant in a particular

soil. *Piper trigonum* and *P. urostachyum* show a non-significant trend of being slightly more abundant on alluvial soils where they have less herbivore damage, as predicted. *Piper cenocladum* is concentrated in volcanic soils and shows less herbivore damage, and thus conforms to the resource availability hypothesis (Endara & Coley, 2011) that specifies that species growing in nutrient-poor soils would invest more in defense. Moreover, Letourneau and Dyer (2005) found that plants in rich-nutrient soils (alluvial) had more herbivore damage than plants in volcanic soils at La Selva; this study included *Piper cenocladum.* However, contradicting my results, the authors also found that in alluvial soils the abundance of *P. cenocladum* is explained by soil nitrogen: the more nitrogen in the soil more plant abundance (Letourneau & Dyer, 2005). Nevertheless, according to Vitousek & Denslow (1986), volcanic soils have higher nitrogen concentration than alluvial soils at La Selva; this might be the reseason for the higher abundance of *P. cenocladum* in volcanic soils in this study. Also, *Piper* species secondary compounds are mostly nitrogen-based (Scott et al., 2007), which could explain the lower levels of herbivory at volcanic soils in this species. On the other hand, *Piper garagaranum,* is more abundant in alluvial soils and shows more herbivory in that soil. It is probable that *P. garagaranum* prefers nutrient-rich soils to grow and invests less in n-chemical defenses as predicted by the resource availability hypothesis (Endara & Coley, 2011) and therefore suffers more herbivore damage in that soil.

I predicted that *Piper* species composition is probably influenced by soil type and herbivory. The results show that herbivory and soil are the most important predictors (and not light) of *Piper* community composition. One potential mechanism behind this

result is the differential palatability of the plants in a community. Herbivores

preferences for particular species may influence species composition (Fenner 1999).

Moreover, studies have shown differences in plant secondary metabolites at the

seedling stage (Elger et al., 2009), and that herbivore preference for specific seedlings

affect community composition (Hanley et al., 1995; Hanley & Sykes, 2009). This

situation is also enhanced by environmental factors, like soil (Fine et al., 2004).

Therefore, it is possible that herbivores are differentially attacking *Piper* species

within patches, contributing to differences in community composition

In this study, soil also influences community composition, however not as strongly

as herbivory. Through the incredible amount of studies done in the tropics and in

temperate forests we know that soil influences plant distribution. The response to soil

in this study might be species-specific as I described above and as Condit et al. (2013)

found in their study of the distribution of 550 tree species in the Panama isthmus along

environmental gradients of soil chemistry and drought. If the response of species to

soil gradients is species-specific it would allow for differences in species distribution,

altering community composition and promoting diversity (Wright, 2002).

There appears to be much niche overlap between these abundant species, whether

that niche be defined by light or herbivory (Fig. 5, *P. trigonum, P. urostachyum, P.*

garagaranum, P. holdridgeanum, P.cenocladum and *P. multiplinervium).* These

species share the same understory light levels, although there seems to be weak

differences in abundance peaks between the species at the different soil types. Density

curves at different light levels in alluvial soils seem to separate. However, these

differences do not look strong enough to conclude that there are niche differences

between species and between soils. These results are consistent with Masaki et al. (2015). In their study of habitat association with tree species and at different life stages, they found weak differences in niche associations along soil conditions and no niche differentiation along the light environment. It is possible that the weak light differentiation among the species I sampled is because the majority of my sites were sampled under understory light conditions. Therefore light may have low predictive power in species distribution in this study. The same result applies to density curves for amount (%) of leaf area removed. Interestingly and different from the light density curves, it was observed that in alluvial soils all species density curves seem to overlap perfectly compared to volcanic soils, where abundances between species somewhat differ.

Piper distribution in this study is predicted by soil and herbivory, although a weak signal can be observed in the small differences in plant density along the light and herbivory axes. Future studies should perform transplant experiments with different combination of species in both soil types and with treatments of herbivore exclusion. This would directly test the role of soils and herbivores in the species richness and diversity of an area. Additionally, studies of seedling palatability, through chemical analyses or feeding trials should aid in discerning the effect of herbivores at the seedling stage and their effect on adult community composition.

2. Is the presence or absence of *Piper* plants predicted by soil and light?

I predicted that *Piper* species would be found at higher light levels and the type of soil may influence at which light levels *Piper* will be present. Although light and soil

are not good predictors of *Piper* presence when all species are considered, light availability is important for the six most frequent species for the logistic regression. These species are more abundant at ranges of canopy openness from 4% to 8%. Perhaps the presence of *Piper* is predicted by light because of phototoxic defenses. Downum and colleagues (1991) found that the family Piperaceae possesses toxins that are activated by light and are capable of damaging a wide range of organisms (but non-insects). The investigators found that light levels from 1 to 10% percent are sufficient to activate these toxins. These species are generally found in understory light conditions that range from 2 to 10% open canopy. These defenses are important for plants in the understory, research has found that plants in more shaded areas suffer more herbivory than those at higher light levels (Denslow et. al., 1991; Goodale et al., 2014).

However, only two species of the four affected by light possess these phototoxic chemicals (*P. cenocladum* and *P. multiplinervium*) (Downum et al. 1991). It is probable that for the two species that do not possess phototoxins but whose presence is predicted by light (*P. trigonum* and *P. holdridgeanum*), other plant functions, such as nitrate assimilation and photosynthesis, would require high light levels. Work on other understory *Piper* species and their light acclimation at Los Tuxtlas Reserve, Mexico, showed that species specialized on habitats with high light levels lose more of their carbon reserves through respiration when grown in more shaded areas (Walters & Field, 1987). Possibly distribution (presence/absence) of *Piper* is determined by the amount of light received by the seed after dispersal. Studies with *Piper* and seed germination revealed that *Piper* seeds commonly found in high light sites have a

phytocrome pigment with which they can detect the specific amount of light they require for germination (Vazquez-Yanes & Smith, 1982). This allows for different species to utilize different light levels, therefore permitting coexistence. An investigation by Daws et al. (2002) considered niche differentiation within the light axis by four *Piper* species and found that *Piper* germination rates can be determined by the amount of light received by the seed. For Daws and coauthors (2002) these differences in germination by light availability may explain species coexistence and indicate niche separation due to light. Other studies in the tropics have found that seedling establishment and recruitment is affected by light and that this contributes to niche differentiation (Denslow et al., 1991; Rüger et al., 2009). It is possible that I did not observe a more conspicuous separation of the species by light (Fig. 5) because I did not measure germination rates at specific light differences. It is possible, as well, that *Piper* and in general plants in the understory require different light availability at different life stages, as shown by Poorter et al. (2005). Ultimately, the *Piper* species in this study do not show niche differentiation as adults, which could be because there were no high light specialists represented in this study.

The two species that do not appear to respond to light, *P. urostachyum* and *P. garagaranum*, may be light generalists and therefore are distributed randomly across this environmental axis. Work at La Selva has shown that many different understory tree species are randomly distributed with respect to canopy openness and show overlaps in their use of light (Lieberman et al., 1995).

Light affects distribution (presence) of *Piper,* which agrees with other studies of different plant species in the tropics (Denslow et al., 1991, Clark et al 1996,

Montgomery & Chazdon, 2002, Rüger et al 2009). However, future research should concentrate on performing germination rate experiments with *Piper* frequent species at different light levels. Observe how many and which species' seeds grow at different controlled levels. This would aide in determining the amount of light some species prefer and therefore, where they would be most commonly found in the field.

3. **Is the abundance of *Piper* at the study site predicted by soil, light, species richness and plant height?**

In previous section we obtained results that show that light predict *Piper* presence; does it similarly affect abundance? Abundance was used in this study as a proxy for habitat specialization. Studies have demonstrated that abundance can show strong habitat associations (Valencia et al., 2004; Metz, 2012). I predicted that the abundance of *Piper* would be determined by light and soil type. High light areas in alluvial soils would have more plants than high light areas in volcanic soils because there are more nutrients in alluvial soils. I also predicted that where there is greater abundance there will be less herbivory. My results show that for all species, plant size and species richness are the only predictors of abundance; *Piper* is more abundant at heights of 60-110 cm than in patches with smaller (< 60 cm) and much taller (> 110 cm) plants. Perhaps competition to acquire resources yields this pattern. Possibly the shading by taller plants or browsing or digging by peccaries and other herbivores reduces the abundance of small and large plants. Recently it has been observed that the differential survival and abundance of seedlings is influenced by the heterogeneity of the habitat. Metz (2012) found that seedling survival and abundance changed with differences in the topographic environment, suggesting the niche differences can be observed at an

early plant stage. Moreover, she compared seedling and adult abundances and found they were positively correlated. Although I did not measure survival or differences in abundance at the seedling stage, it is possible that the low abundance of plants of less than 10 cm with four or less leaves reflects this differential survival.

Species richness and abundance were positively correlated for all species (Fig. 7B) and for just the six most frequent species (Fig. 8). Thus as patch species richness increases, abundance increases. This result suggests that herbivores function to maintain species richness. The resource concentration hypothesis predicts that the influence of non-host neighbors reduces the abundance of specialist herbivores and consequently damage (reviewed by Barbosa et al., 2009, Alaloun et al., 2014). Other work has shown that herbivores consume plant species that are closely related (Castagneyrol et al., 2014), and although these species belong to the same genus, there are great physical and chemical differences between species (Dyer & Palmer, 2004).

It is likely that the reason why soil does not predict species abundances is the lack of fine-grained soil characteristics, such as moisture and nutrients. Other studies have shown that species differentiate according to moisture and phosphorus (Condit et al., 2013). *Piper* distribution (presence) does respond to light (question 2), but not its abundance. Light as a resource is ephemeral and changes through time (Wright, 2012); it is possible that when individuals germinated there was enough light availability, but later, the light received in the understory is not enough to sustain high numbers of individuals.

Abundance is affected by plant size and species richness but not soil or light, by

reasons explained above, contradicting my predictions. Measurements of survival rates of seedlings should be performed in future studies in order to observe if species do exhibit habitat association at such an early stage and if it is the habitat associations (*i.e.* niches) that are influencing abundance.

4. Is percentage of herbivore damage predicted by soil type, plant size, plant height, species richness and light?

The best predictor of herbivore damage for all species in this study was plant size. Small, younger plants tend to show more herbivore damage than older plants. It is possible that this result represents a change in defense allocation at different plant stages. Research has shown that herbivore resistance changes with plant ontogeny (Boege & Marquis, 2005). In fact, invertebrate herbivores usually favor younger plants as palatability changes from seedlings to adults (Fenner et al.,1999), which may reflect increased defenses at advanced stages. Toughness, which can be used as herbivore defense, also increases as a plant matures, leaving seedlings weakly defended by this structural trait (Kitajima et al., 2013). Seedlings appear to be the most vulnerable to herbivore attack and this stage may be subject to the strongest selection pressure by herbivores (reviewed by Barton & Hanley, 2013). Interestingly, herbivory during the seedling stage probably affects recruitment in a community (or patch) affecting the success and the establishment of only a few species (Barton & Hanley, 2013). This idea has serious repercussions for plant abundance and distribution. If less defended seedlings are more vulnerable to mortality by herbivores, they would become less abundant. Similarly, if seedlings are surrounded by less palatable species,

herbivores might attack the vulnerable seedlings more than the rest of the community and possibly exclude them from the area.

An example of this mechanism in action may be *P. holdridgeanum*, which is especially vulnerable during what may be the seedling stage (Fig. 16). Barton and Hanley (2013) showed in their review that herbivores target seedlings of different species and ignore others due to seedling palatability and defense. This might determine where *P. holdridgeanum* establishes. *P. holdridgeanum* is also more damaged in alluvial soils than volcanic soils and interestingly, *P. holdridgeanum* plants are denser at high light levels (6%) in volcanic soils than at 4% light in alluvial soils (Fig. 5). Kitajima and colleagues (2013) believe that light-demanding seedlings are constrained from growing in the shade because of their lack of traits to avoid herbivore damage in the shade. This might be important for *P. holdridgeanum*. Although, contrary to my results from *P. holdridgeanum,* Kitajima et al. (2013) found that seedlings suffered more herbivory in gaps than in shade attributing this to the higher abundance of herbivores in gaps. However, other studies have found that plants growing in shade suffer more herbivory (Denslow et al., 1991; Salgado-Luarte & Gianoli, 2010). Though a 2% light difference is not large, it might be enough for *Piper holdirdgeanum* to avoid herbivory at higher light in volcanic soils. Because different species show different sizes at different life stages, I cannot determine seedling stage, however individuals with height of less than 10 cm still show more herbivore damage than larger ones (Fig. 8 and 16).

Other results show an interaction between patch size, light and soil in regards to herbivore damage. It would seem that small patches found at low light levels and in

volcanic soils suffer more damage than plants in patches of the same size but at higher light levels in any soil. These results highlight the importance of light for the majority of *Piper* species. Plants may experience higher levels of herbivore damage when in the shade compared higher light levels (Denslow et al., 1991; Salgado-Luarte & Gianoli, 2010). It is probable that light influences plant allocation to chemical defenses in *Piper* (Dudt & Shure, 1994; Coley & Barone, 1996). It is possible that herbivore damage might influence *Piper* species distributions by restricting the species to places in the understory with high light levels and preferably in larger patches where, in general, *Piper* suffers of less herbivore damage. King (2003) studied the abiotic effects of light, successional stage and flooding with the effects of herbivory on *Calophyllum brasiliense*. Her results showed that plants were mostly distributed where there was high light availability and less herbivory both resulting in higher rates of seedling growth.

When considering only the most abundant species, results show a more complicated relationship between abiotic factors. I had predicted that plants adapted to nutrient–poor volcanic soils should be better defended against herbivores because of the higher investment in defense, while plants adapted to nutrient-rich alluvial soils should suffer higher amounts of herbivory. Although in general, soil had no effect on its own, it did interact with light and patch size. I had predicted that because light is thought to negatively affect herbivory, plants in higher light levels should undergo less herbivory. Plants in volcanic soils and at low light suffer more herbivore damage than plants in alluvial soils and low light levels. This is an interesting result and indicates that factors are interacting to determine herbivore attack. Other work has shown that

soil nutrients, light availability and water limitation may affect tissue quality and plant investment to defenses (Gershenzon, 1984; Denslow et al., 1987; Marquis & Braker, 1994; Gutbrodt et al., 2011; Endara & Coley, 2011).

My finding that more herbivore damage occurs in nutrient-poor soils and at low light levels contradicts the generally-held idea that the amount of secondary compounds increase and damage decreases when plants grow in stressful abiotic conditions (Gershenzon, 1984; Endara & Coley, 2011). In general, however, biotic and abiotic conditions affect herbivore damage, which in turn affect species distribution patterns.

CONCLUSIONS

Distribution and abundance of the genus *Piper* are affected by both abiotic and biotic factors. In this study, the presence of the genus *Piper* is affected by light availability and although none of the understory species show clear niche differentiation, their abundance is clearly associated with 4-6% canopy openness. *Piper* abundance is mainly determined by biotic factors: plant size and species richness. Both of these variables can be indirectly affected by the influence of herbivores and their ability to determine community composition. Though it is not possible to directly determine habitat specialization (*i.e.* niches) with this study, as a first step, it is possible to say that herbivore damage in this genus is highly influenced by the abiotic and biotic characteristics of the environment. This, in turn, can influence the distribution and abundance of individuals. For example, *Piper* presence is predicted by light, and light availability can predict the amount of herbivore damage; plants in more shaded areas are more affected by herbivores. Therefore, herbivores

restrict *Piper* to places with higher light levels. Transplant experiments should be done to directly measure the effect of herbivores and the abiotic environment. These results have important repercussions for plant's niche differentiation and coexistence. Niche axes to which plants can partition their habitat are not only limited to environmental or resource elements, but the influence of biotic factors, like herbivory, can affect distribution of species and ultimately coexistence. Evidence of the independent influence of each factor on plant distribution and coexistence is plenty; it is time to work on studies that consider the impact of these factors when working together.

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TABLES

Table 1. Information per species on occurrence, mean herbivore damage (%), mean leaf area (cm) and percent open canopy separated by soil type.

Species	Response	Occurrence		Herbivory (%)		Leaf area (cm)		% Open canopy	
	Soil type	Alluvial	Volcanic	Alluvial	Volcanic	Alluvial	Volcanic	Alluvial	Volcanic
All species		13	13	11	11.8	76.412	83.59	5.357	5.582
Most abund. species		13	13	12.3	12.4	64.475	84.474	5.434	5.581
P. arcteacuminatum		4	4	7.9	10.4	52.981	63.607	6.532	4.606
P. auritifolium		4	5	6.3	13.2	108.545	162.774	5.958	5.72
P. biseriatum		2	0	15.6	0	102.019	0	4.507	0
P. cenocladum		7	8	9.7	8.7	221.188	187.901	5.128	5.336
P. colonense		7	4	13.5	8.6	62.159	64.394	5.373	4.875
P. concepcionis		3	1	10.3	10.8	73.567	45.319	4.16	4.68
P. darienense		1	1	7.4	22.4	105.195	23.532	2.86	3.9
P. dryadum		3	4	14.6	8.6	41.624	25.502	4.784	5.906
P. equale		0	1	0	3.3	0	37.458	0	6.5
P. garagaranum		10	8	12.8	8.2	32.799	37.845	5.391	4.67
P. glabrescens		2	0	10.3	0	105.266	0	5.59	0
P. holdridgeanum		5	11	8.8	13.2	96.654	91.637	5.361	6.137
P. imperiale		1	0	18.4	0	78.242	0	5.72	0
P. melanocladum		2	6	5	11.7	93.769	67.457	4.767	6.145
P.		9	8	9.8	9.9	37.647	24.757	5.863	6.33

multiplinervium								
P. perbrevicaule		1	1	4	5.8	1.952	23.803	5.46	5.113
P. pseudobumbratum		4	1	10.1	16	151.99	117.05	3.949	5.005
P. reticulatum		3	0	5.7	0	148.094	0	4.88	0
P. santi.felicis		4	1	5.7	5.8	84.17	112.54	5.275	3.64
P. trigonum		13	13	14.1	14.6	44.818	42.602	5.858	5.584
P. umbricola		1	0	8	0	43.529	0	5.46	0
P. urophyllum		1	0	2.1	0	36.616	0	4.264	0
P. urostachyum		9	8	9.5	11.6	87.188	83.253	4.905	5.089
P. xantostachyum		3	2	6.9	2.2	40.747	37.96	4.524	5.07

Table 2. Results of the logistic regression for presence/absence of all *Piper* species

sampled

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	-0.007734	0.067708	0.013	0.909
Soil	-0.024366	0.423341	0.120	0.9417
Light	0.069433	0.048251	3.651	0.161

Table 3. Results of the logistic regression for presence/absence of the six most frequent species.

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	-0.05059	0.07479	0.4521	0.501
Soil	0.39664	0.48013	0.677	0.712
Light	0.15101	0.05482	10.973	**0.004**

Table 4. Results of the logistic regression for *P. trigonum*

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	-0.29625	0.11209	6.977	**0.008**
Soil	1.57808	0.66982	7.020	**0.029**
Light	0.21735	0.07603	8.614	**0.013**

Table 5. Results of the logistic regression for *P. cenocladum*

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	0.15019	0.20207	0.564	0.452
Soil	0.14204	1.30495	2.63	0.268
Light	0.07296	0.17431	4.695	**0.095**

Table 6. Results of the logistic regression for *P. multiplinervium*

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	-0.00493	0.17032	0.0004	0.976
Soil	-0.11402	1.10390	0.113	0.944
Light	0.23802	0.12714	6.961	**0.030**

Table 7. Results of the logistic regression for *P. holdridgeanum*

Fixed effects	Estimates	Std. Error	X^2	P value
Light*soil	-0.03801	0.16658	0.051	0.819
Soil	1.19890	1.16285	2.954	0.228
Light	0.24885	0.14154	8.090	**0.017**

Table 8. Results of the GLMM with abundance as response variable using all sampled species.

Fixed effects	Estimates	Std. Error	x^2	P value
Height	-0.000959	0.000566	3.13	**0.076**
Spp richness	0.550912	0.039401	126.87	**<0.001**

Table 9. Results of the GLMM with abundance as response variable using the six most abundant species.

Fixed effects	Estimates	Std. Error	x^2	P value
Species richness	0.3237	0.0358	62.03	**< 0.001**

Table 10. Results of the GLMM with abundance as response variable

Species	Fixed effects	Estimates	Std. Error	x^2	P value
P. trigonum	Species richness	0.1936	0.0824	4.88	**0.02**
P. cenocladum	Species richness	0.1824	0.1003	2.94	**0.08**
P. urostachyum	Species richness	0.1722	0.0892	3.29	**0.06**

Table 11. Results of GLMM with herbivory as response variable for all sampled

species.

Fixed effects	Estimates	Std. Error	x^2	P value
Size	-0.364	0.164	4.96	**0.02**

Table 12. Results of GLMM with herbivory as response variable for most frequent species

Fixed effects	Estimates	Std. Error	x^2	P value
Patch size	-0.0600	0.0362	6.46	**0.09**
Soil	-0.0559	0.1904	5.28	0.25
Light	-0.1218	0.0766	6.84	0.14
Light * Soil	0.1936	0.1099	3.08	**0.07**
Soil*Light*patch size	0.0649	0.0293	5.1	**0.07**

Table 13. Results of GLMM for five out of 6 most frequent species, no significant

results.

Species	Fixed effects	Estimates	Std. Error	x^2	P value
P. trigonum	Patch size	-0.01441	0.01517	2.168	0.70
	Soil	0.00411	0.02804	1.858	0.76
	Light	-0.00426	0.00827	2.268	0.51
	Patch size * Soil	0.01790	0.01743	1.068	0.30
	Soil*Light*patch size	0.00229	0.00264	1.75	0.41
P. cenocladum	Soil	0.4294	0.4818	2.808	0.24
	Light	0.2447	0.1743	4.546	0.20
	Size	1.0703	1.4985	0.51	0.47
	Patch size	-0.0726	0.0597	5.204	0.15
	Patch size*light*soil	0.0832	0.1069	2.808	0.24
P. multiplinervium	Light	0.05551	0.22664	0.118	0.9427
	Patch size	0.03915	0.19890	0.038	0.981

	Light*Patch size	-0.00877	0.09997	0.006	0.938
P. urostachyum	Light	-0.0251	0.1038	2.976	0.395
	Patch size	-0.2380	0.2077	2.337	0.505
	Soil	-0.1649	0.3606	3.109	0.375
	Patch size*Soil*Light	0.0591	0.0436	2.122	0.346

Table 14. Results of GLMM for *P. holdridgeanum.*

Fixed effects	Estimates	Std. Error	x^2	P value
Soil	-1.9231	1.0566	12.674	**0.048**
Size	2.6509	1.1829	4.984	**0.025**
Patch size	-0.0558	0.1695	8.458	**0.076**
Patch size*soil	0.7162	0.3270	4.814	**0.028**
Soil*Light	0.6446	0.2545	9.792	**0.007**
Soil*Patch size*Light	-0.2227	0.1262	5.242	**0.072**

Figures
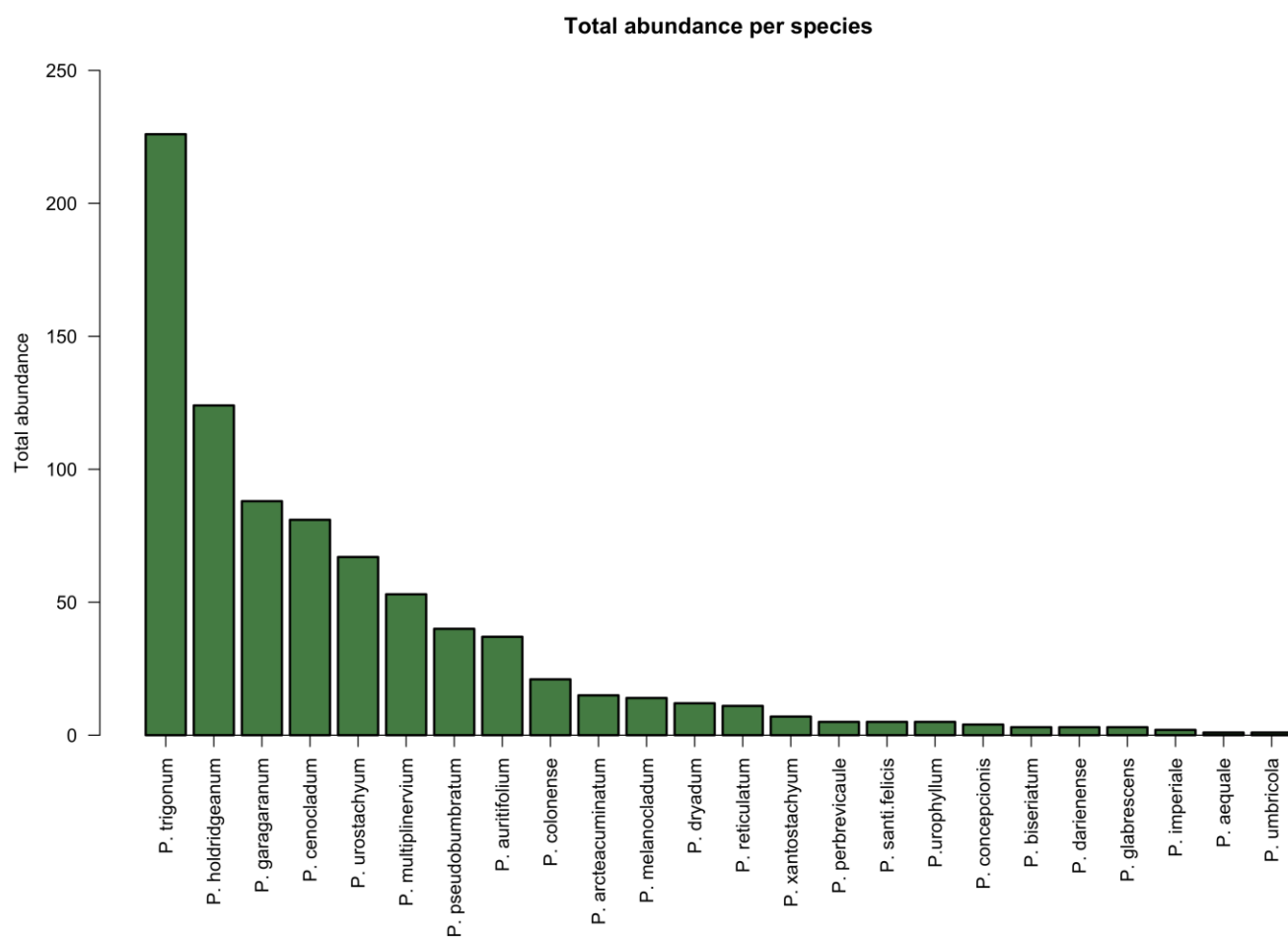
Figure 1. Total abundance of all *Piper* species sampled in transects.
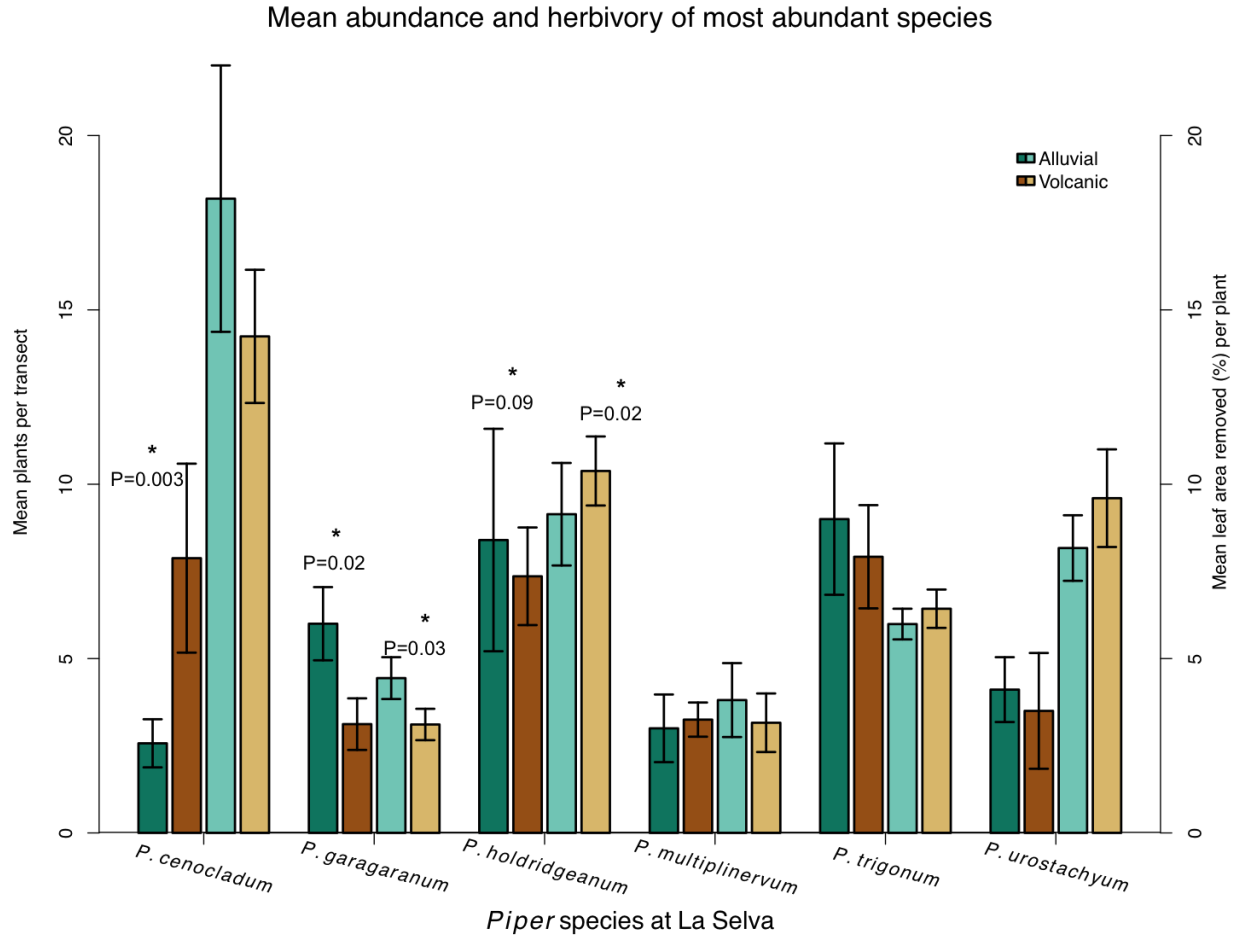
Figure 2 Mean abundance of plants per transect and mean leaf area removed (%) per plant. The two bars on the left side represent abundance and the two bars on the right side represent mean leaf are removed (%) in both soils (alluvial and volcanic). P-values were obtained through a PERMANOVA. Error bars represent standard error.

MDS total abundance communities
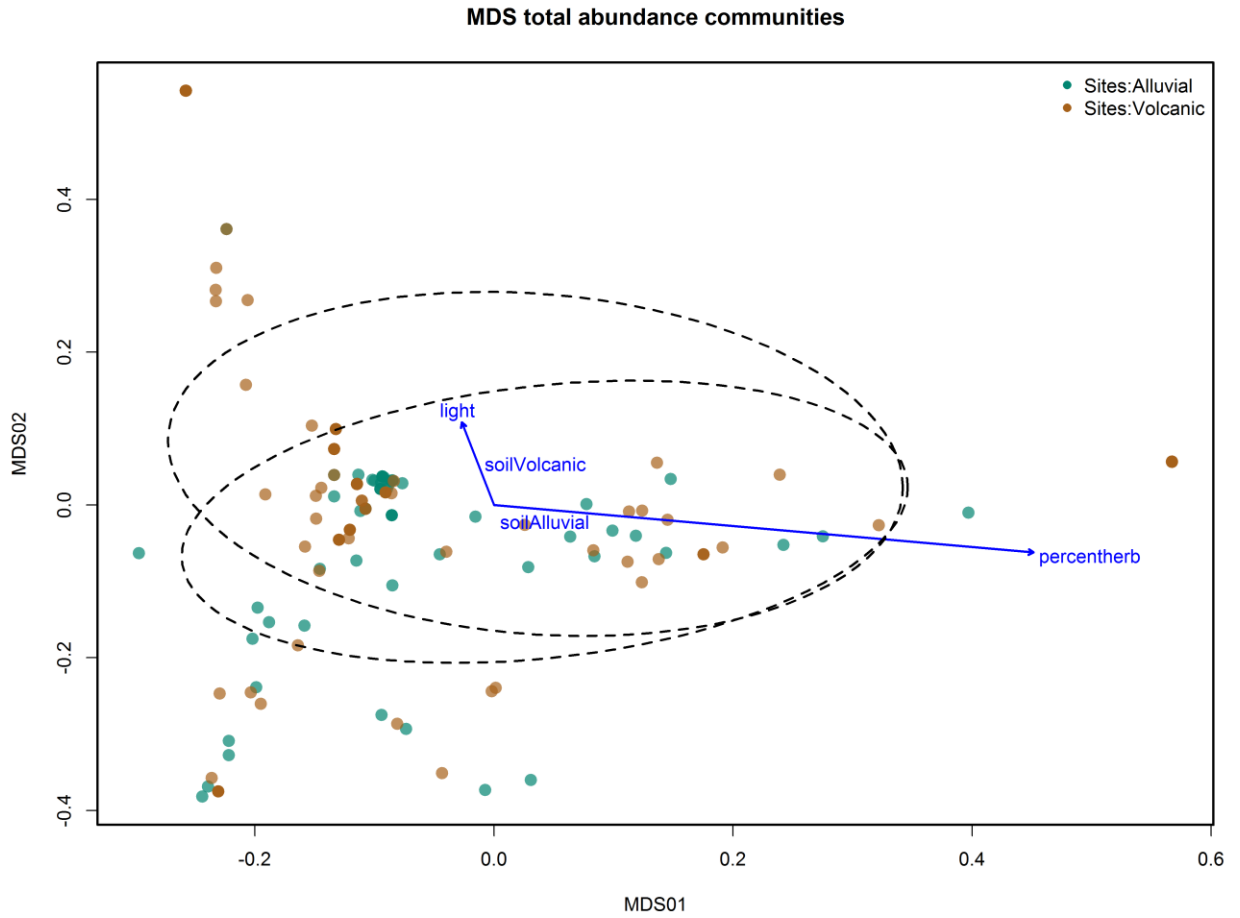
Figure 3. NMDS plot for all sampled *Piper* species. This ordination plot

shows the weak separation of patches between different soil types. The

ordination plot projects the position of sampled patches into ordination space.

Dots represent patches in different soil types; blue dots are alluvial and brown

dots represent volcanic soils. Blue arrows represent the environmental

variables fitted to the NMDS. Ellipses represent the SE of the average scores

(an ordination axis specifying the location of the patches in the ordination

plot).
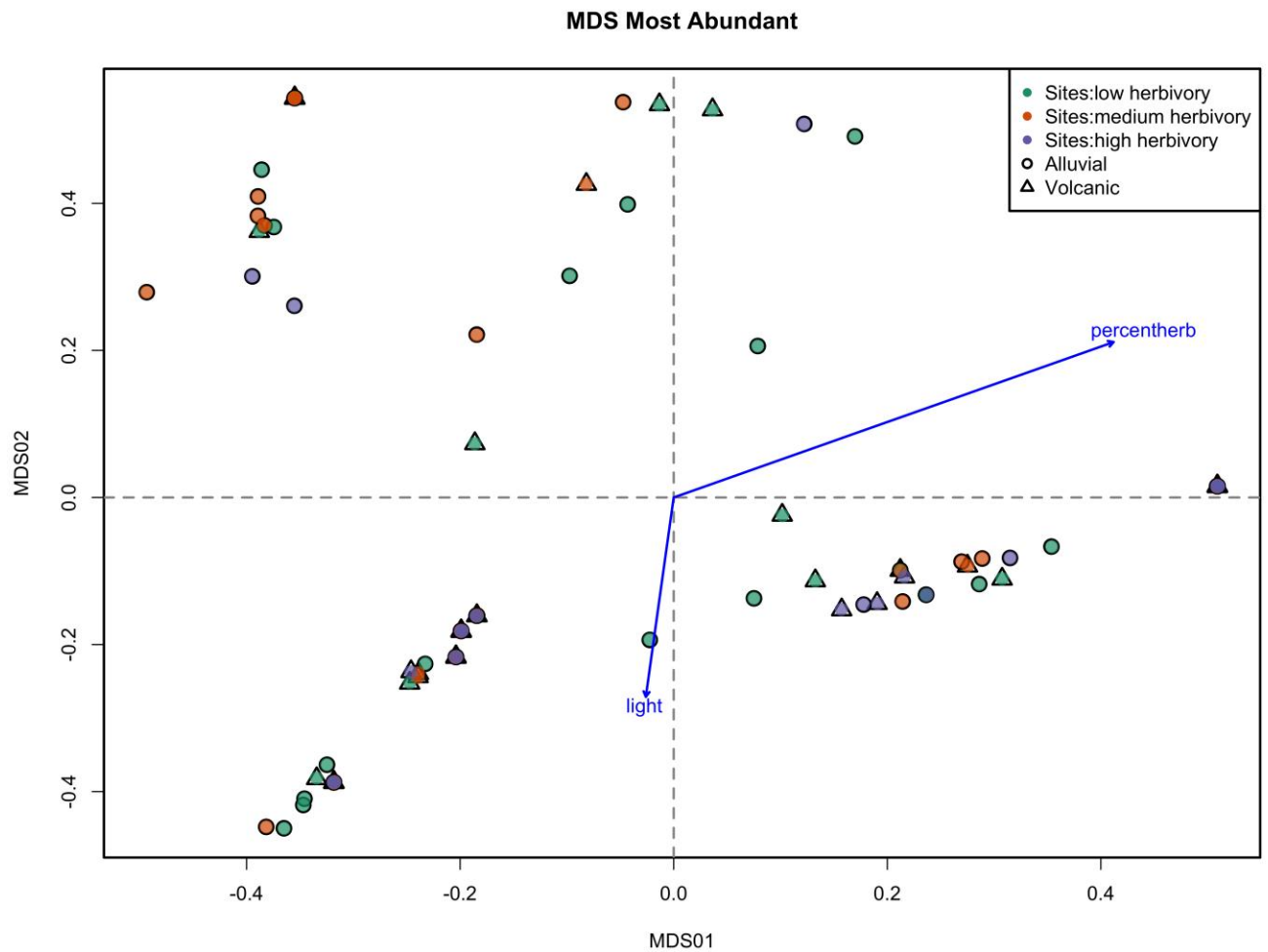
Figure 4. NMDS for the most abundant species. Colors correspond to patches with different levels of herbivory and shapes (circle and triangle) correspond to soil type. Herbivory ranges were chosen by using minimum and maximum quartiles, low herbivory: <10% medium: 10-20% high: >20%. Although some patches cluster, they do not seem to respond to herbivory or soil. However, the PERMANOVA does show these are significant effects.
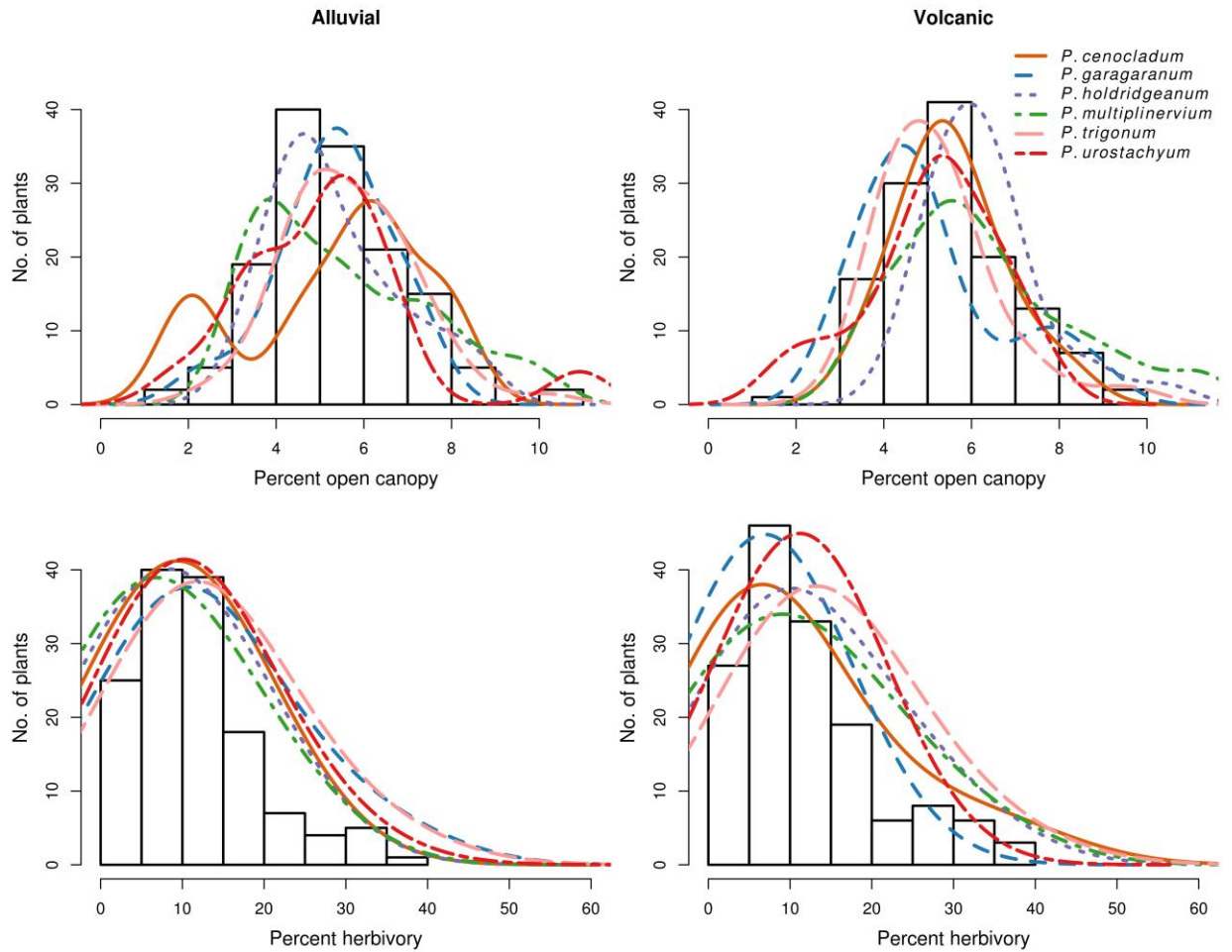
Figure 5. *Piper* abundance along light and herbivory gradients. The first two upper panels show the frequency of individuals of the most frequent *Piper* species across different open canopy levels. The remaining two panels show the frequency of individuals at different levels of herbivory (%). The lines represent the kernel density of individuals as a way to smooth the lines around the frequency histogram.

Patch species richness~abundance

Abundance per patch ~ patch mean height
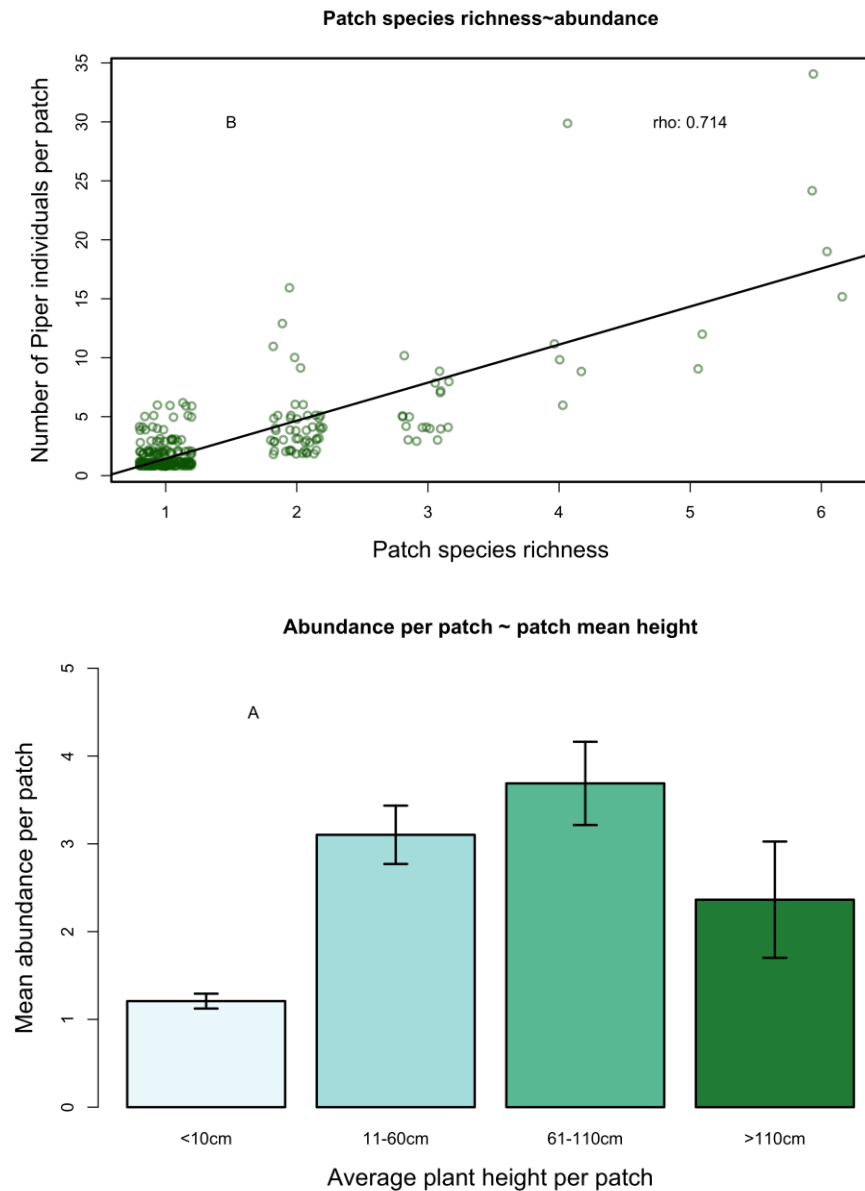
Figure 6. Species richness and plant height predict abundance of *Piper*. A. The differences in plant abundance grouped by plant height. B. Abundance increases as species richness increases. Error bars represent Standard Error.
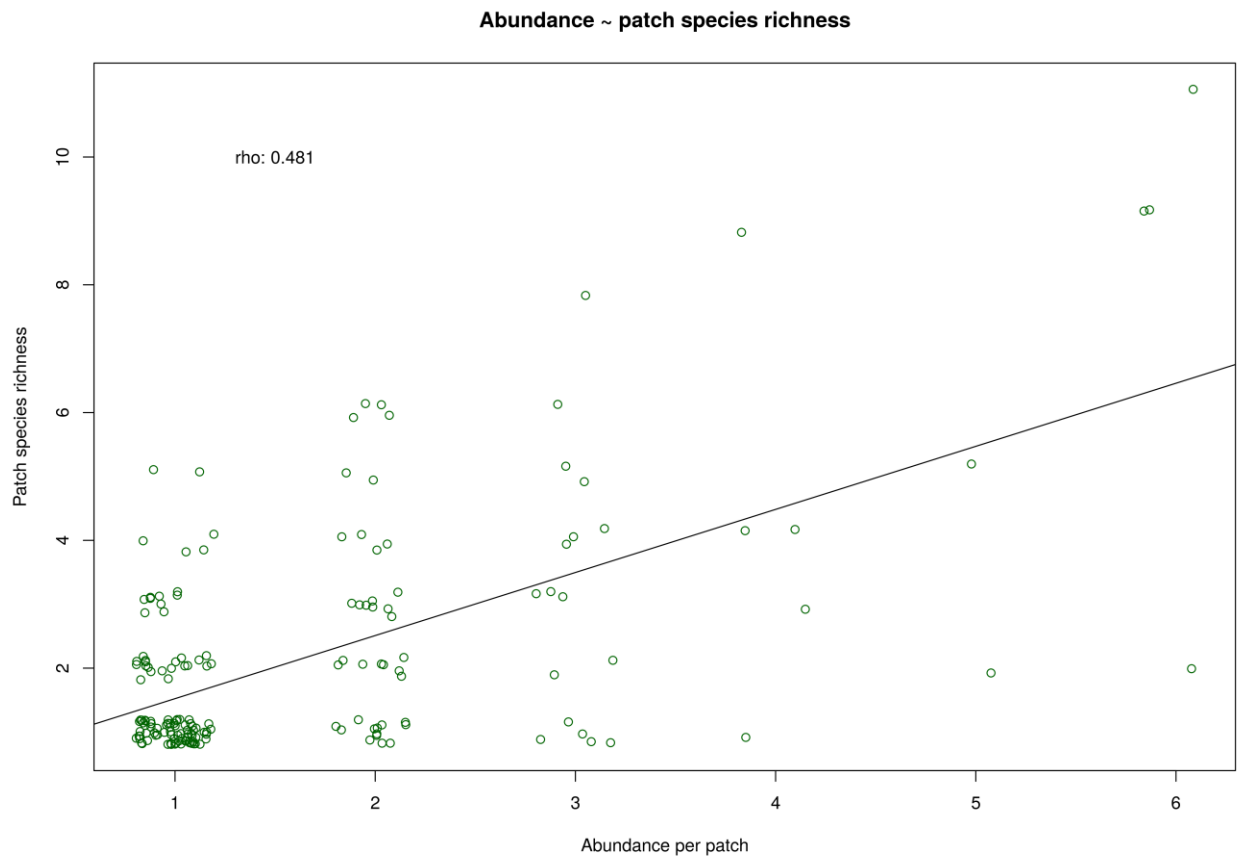
Figure 7. Abundance for the six most frequent and abundant species. Species

richness increases as abundance increases.
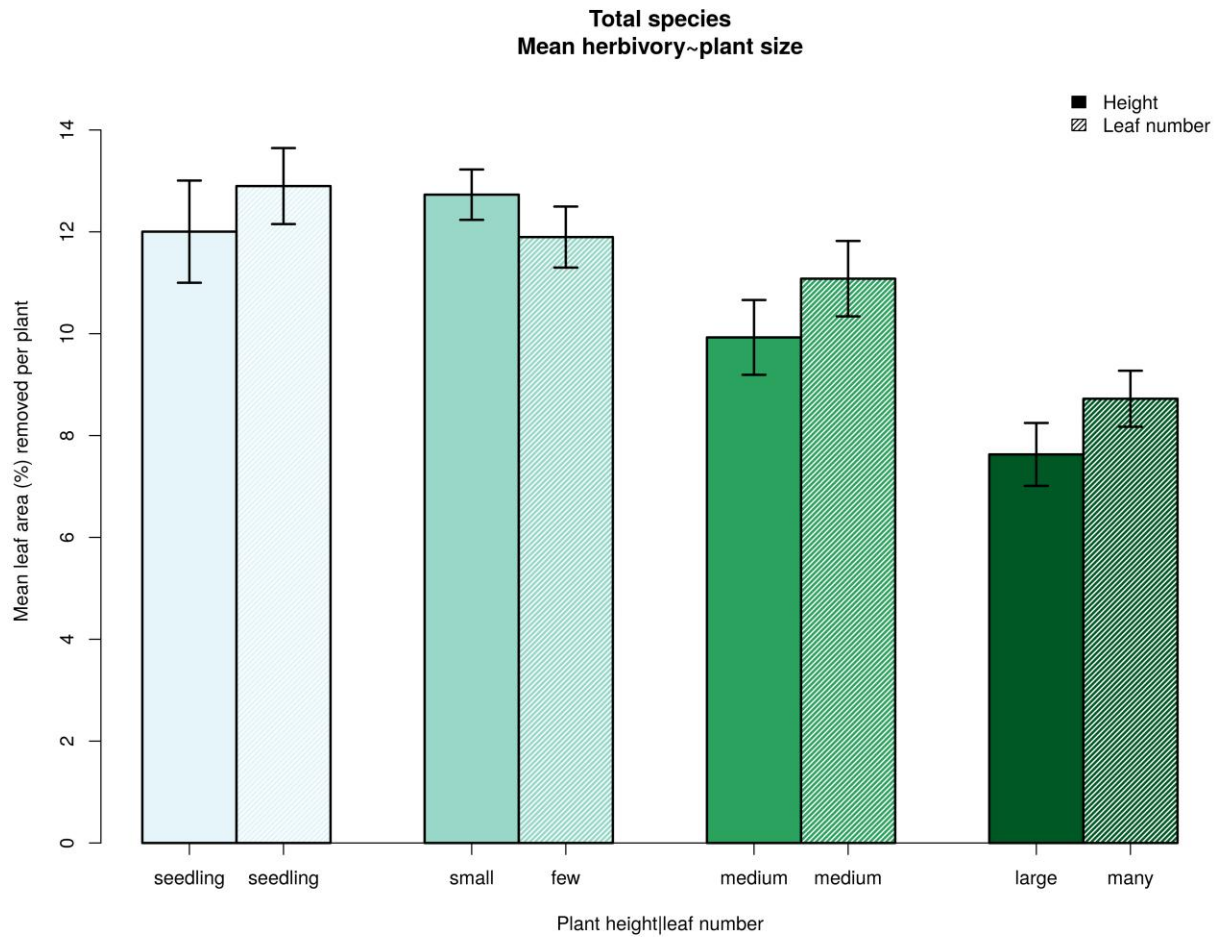
Figure 8. Amount of leaf area (fraction ±) removed is affected by plant size.

There is less herbivory in large plants with many leaves. Lined bars refer to

leaf number and full bars refer to plant height. Height category limits, seedling;

≤10, small: ≤ 60, medium: > 60 and ≤110, large: > 100 cm. Leaf quantity

category limits,, small: ≤ 4, medium: > 4 and ≤ 13, many: > 13. Error bars

represent Standard Error.
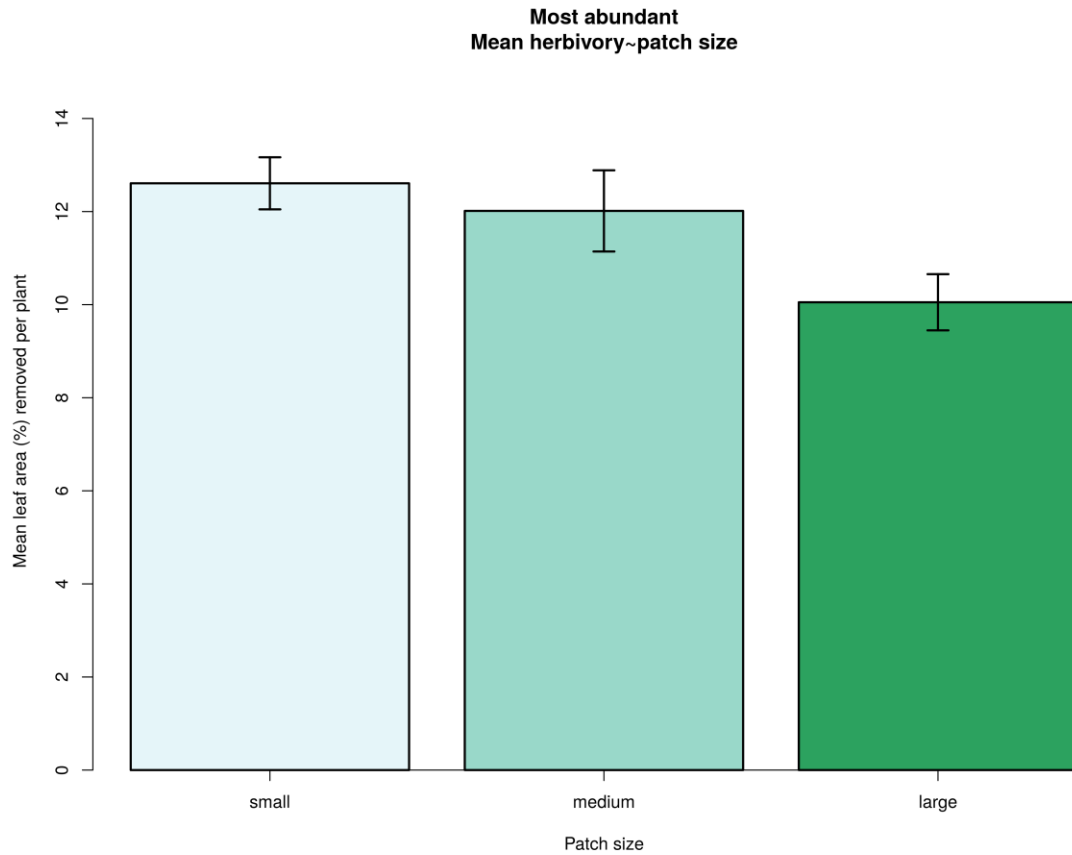
Figure 9. Herbivory decreases as patch size increases for the six most frequent and abundant species (marginally significant; GLMM, *p*=0.09). Patch sizes, small: ≤ 2 m, medium: > 2 and ≤ 4 m, large: > 4 m. Error bars represent Standard Error.
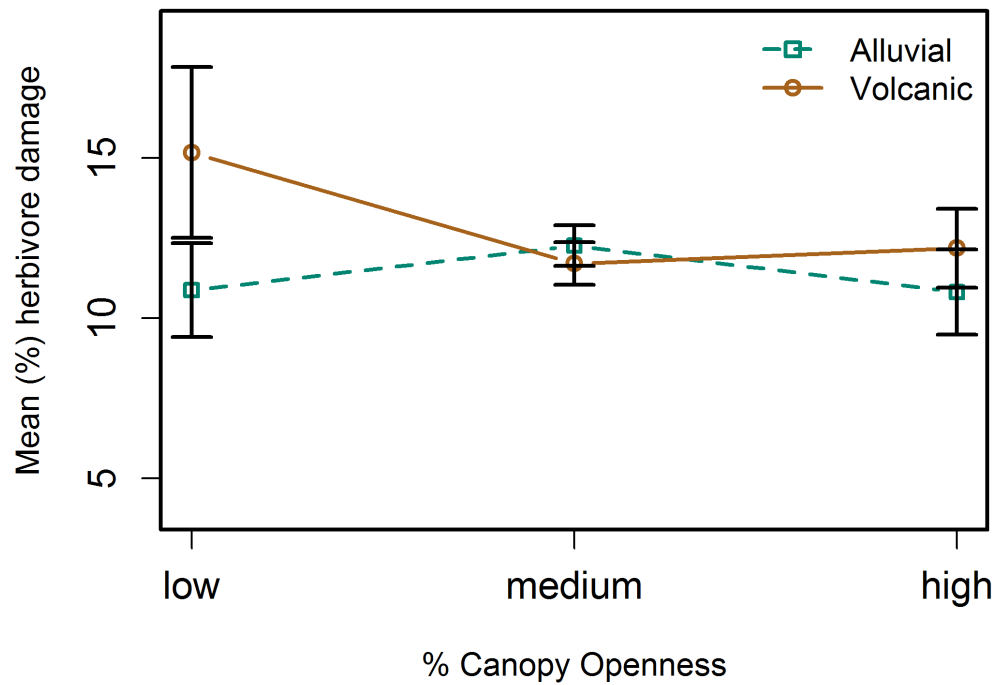
Figure 10. The interaction between soil and light shows that at low light levels, species in volcanic soils receive more herbivory than species in alluvial soils (GLMM, *p*=0.07). Canopy Openness range: low: < 3.5% , medium: ≥ 3.5 and ≤ 7%, large: > 7%. Error bars represent Standard Error.
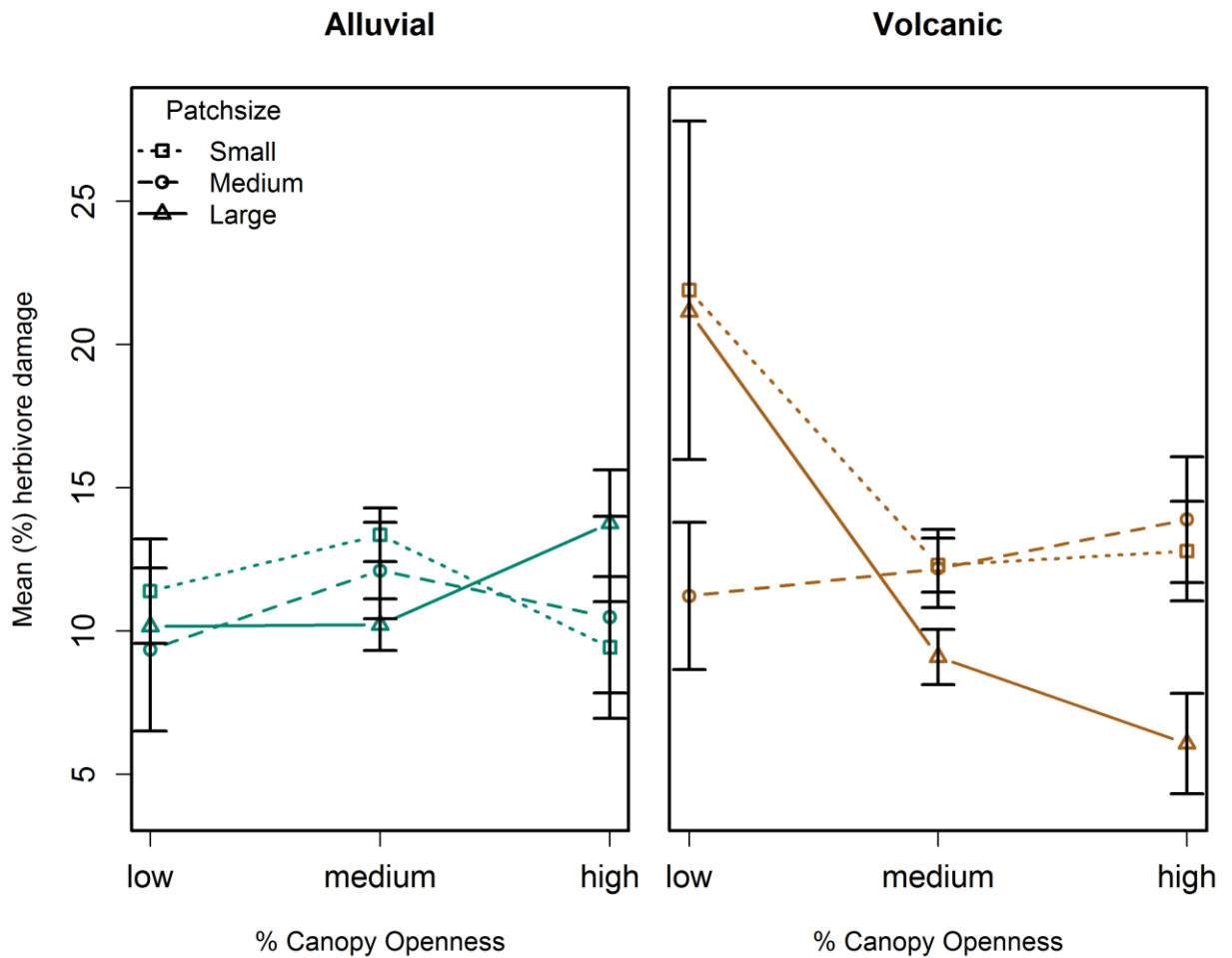
Figure 11. This graph shows the interaction between soil, light and size of the

patch. However, it seems that the only difference is between small patches at

low light levels, where plants in volcanic soils have more herbivory, and large

patches in high light levels, where plants suffer less herbivory in volcanic soils.
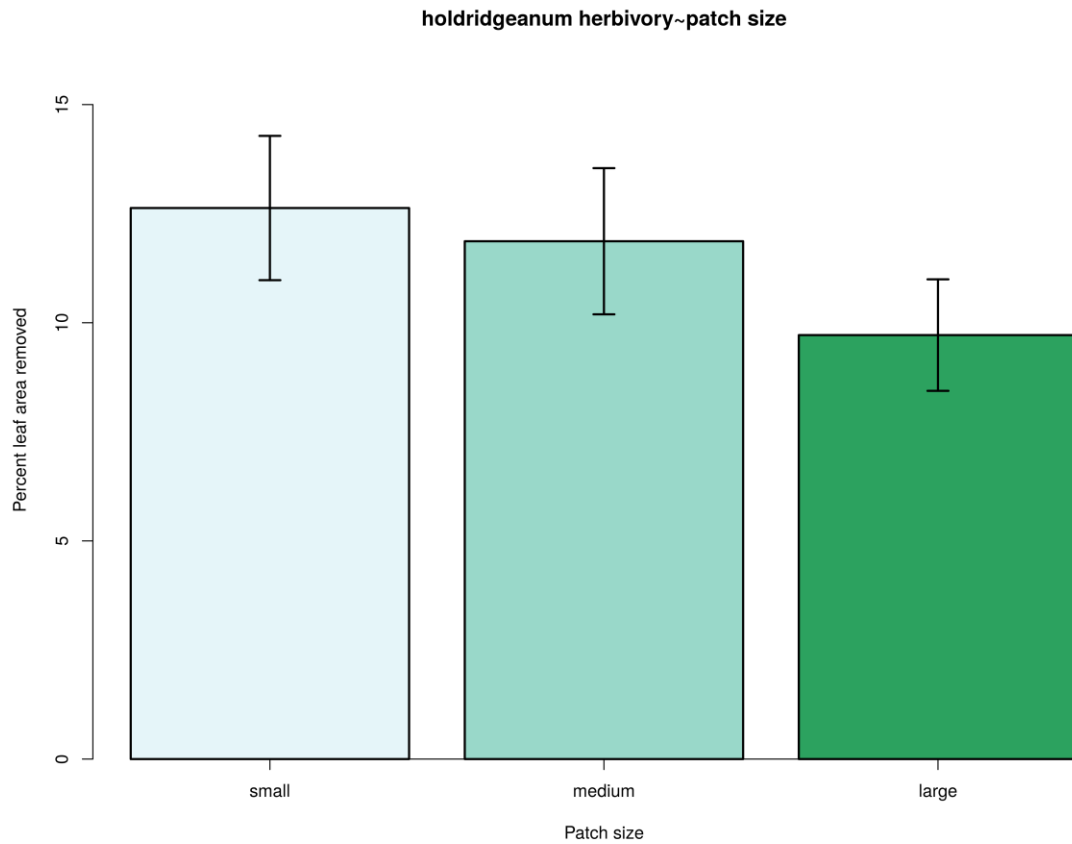
Error bars represent SE.

holdridgeanum herbivory~patch size

Figure 12. Mean leaf area (%) removed per plant for *P. holdridgeanum* at different patch sizes. Plants in larger patches suffer less herbivory than plants in smaller and medium size patches (GLMM, *p*=0.07). Error bars represent SE.
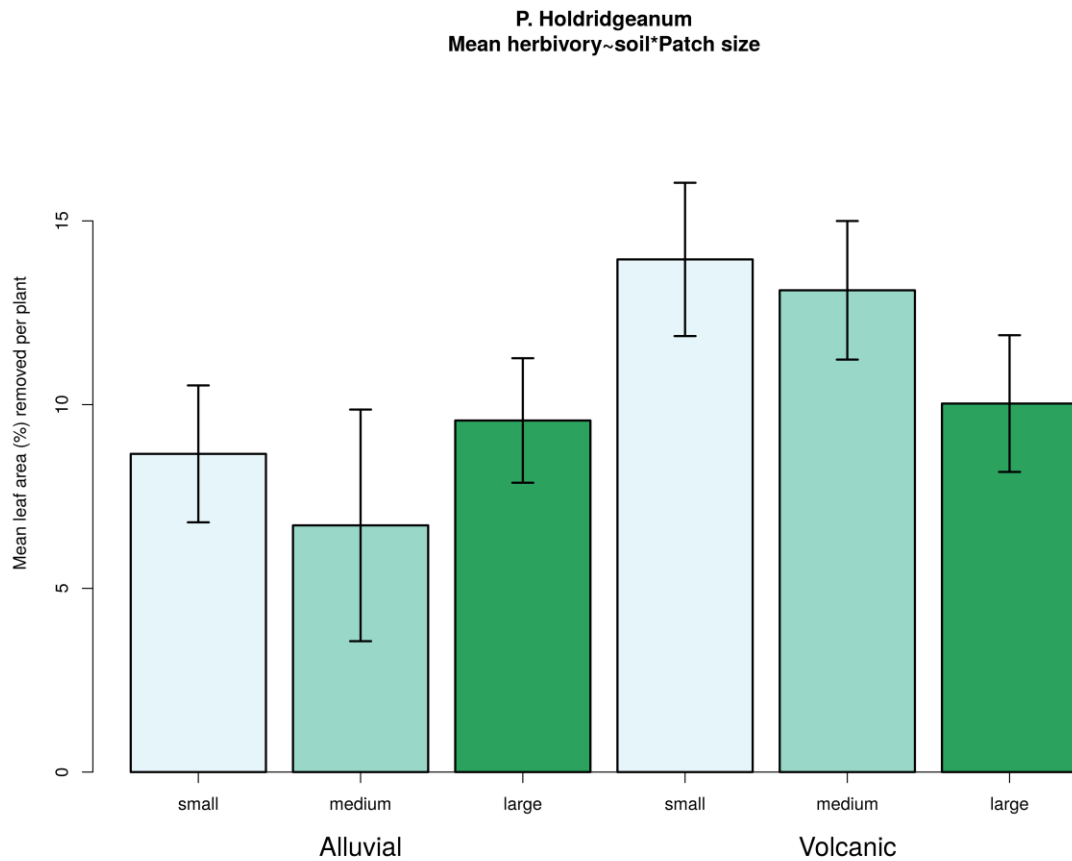
Figure 13. Difference in mean leaf area (%) removed per plant for *P. holdridgeanum*

at different patch sizes in both soil types. Plants in alluvial soils and in small to

medium size patches suffer less herbivory than plants in the same size patches in
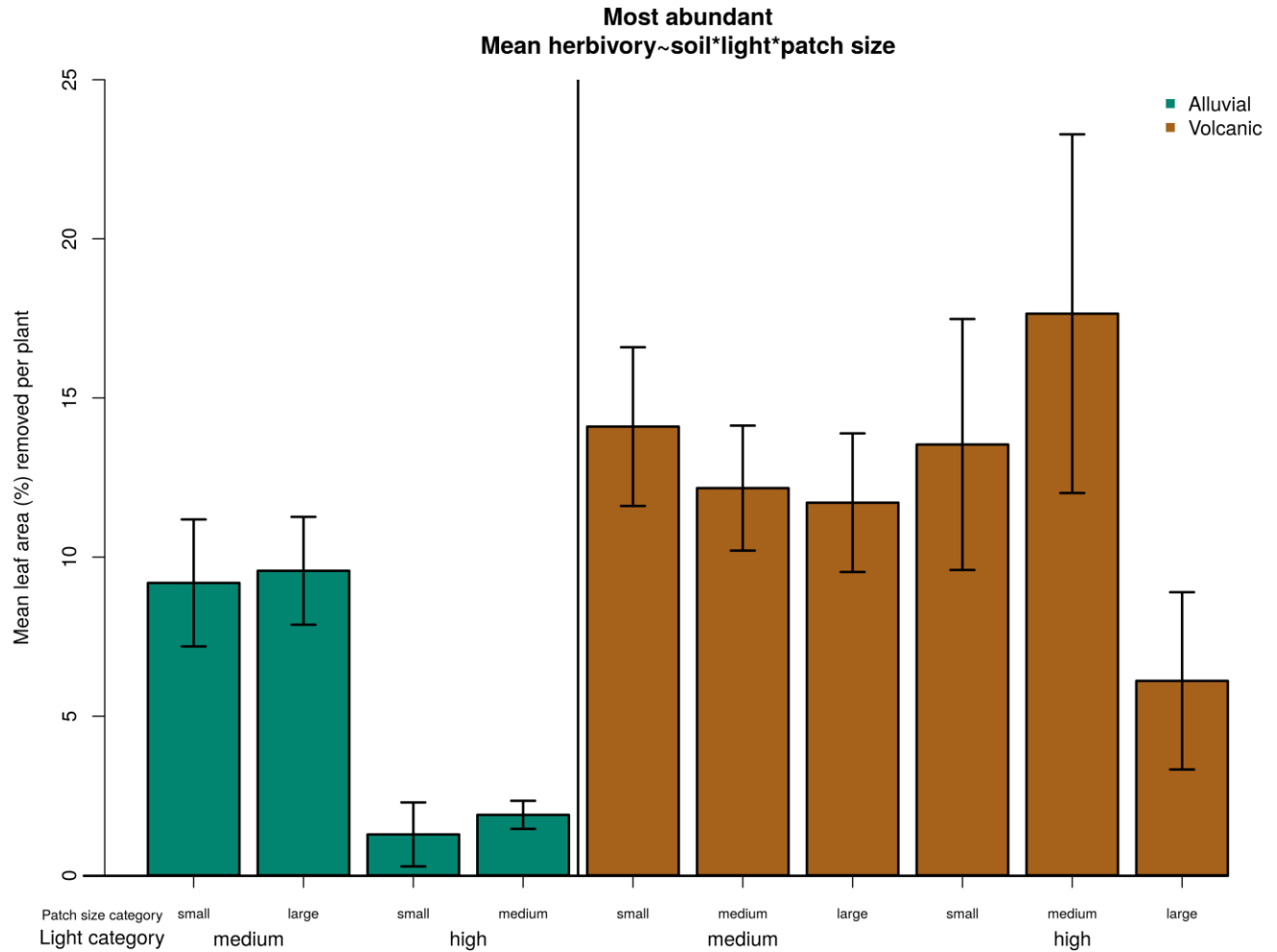
volcanic soils. Error bars represent SE.

Figure 14. Three-way interaction between soil, light and the size of the patch for *P. holdridgeanum*. Plants in alluvial soils have less herbivory than plants in volcanic soils. Error bars represent SE.
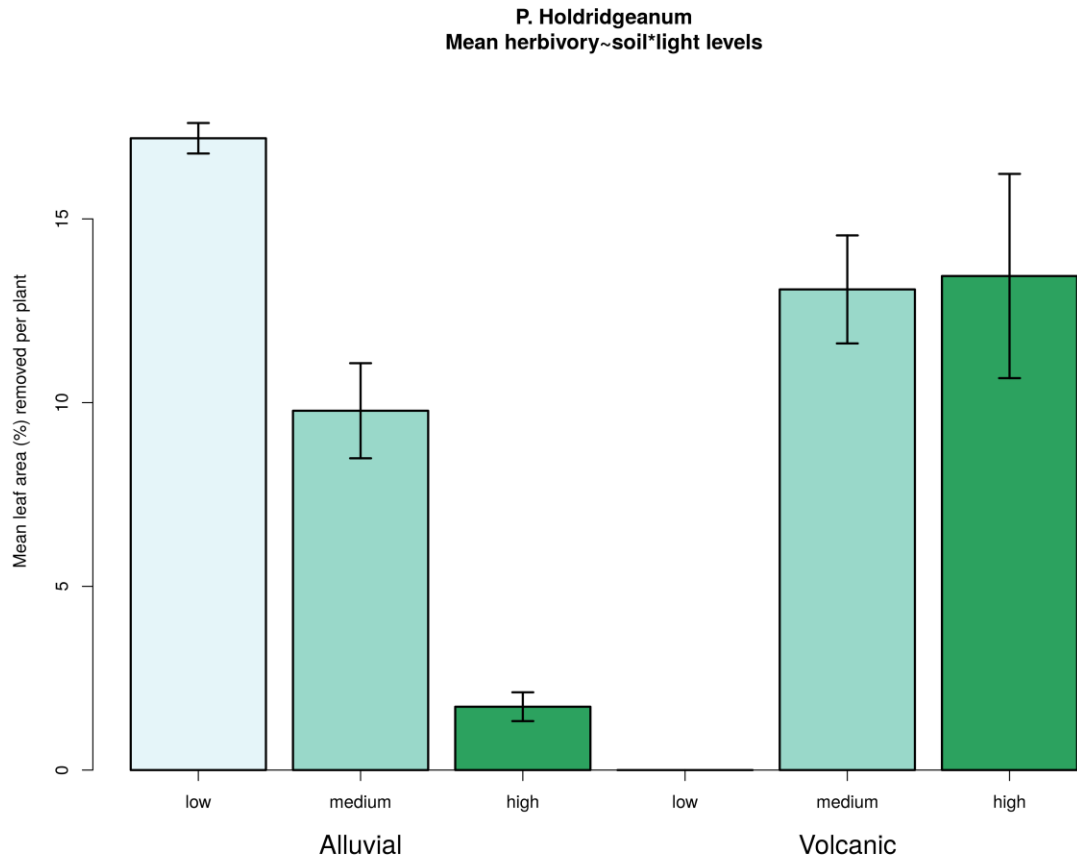
P. Holdridgeanum
Mean herbivory~soil*light levels

Figure 15. Mean leaf area (%) removed per plant for *P. holdridgeanum* at different canopy openness percentages and different soil type. In alluvial soils, light levels influence the amount of herbivory on *P. holdridgeanum* plants. Plants in high light levels suffer less herbivory than plants in lower light levels. However, volcanic soils show no differences. Error bars represent SE.
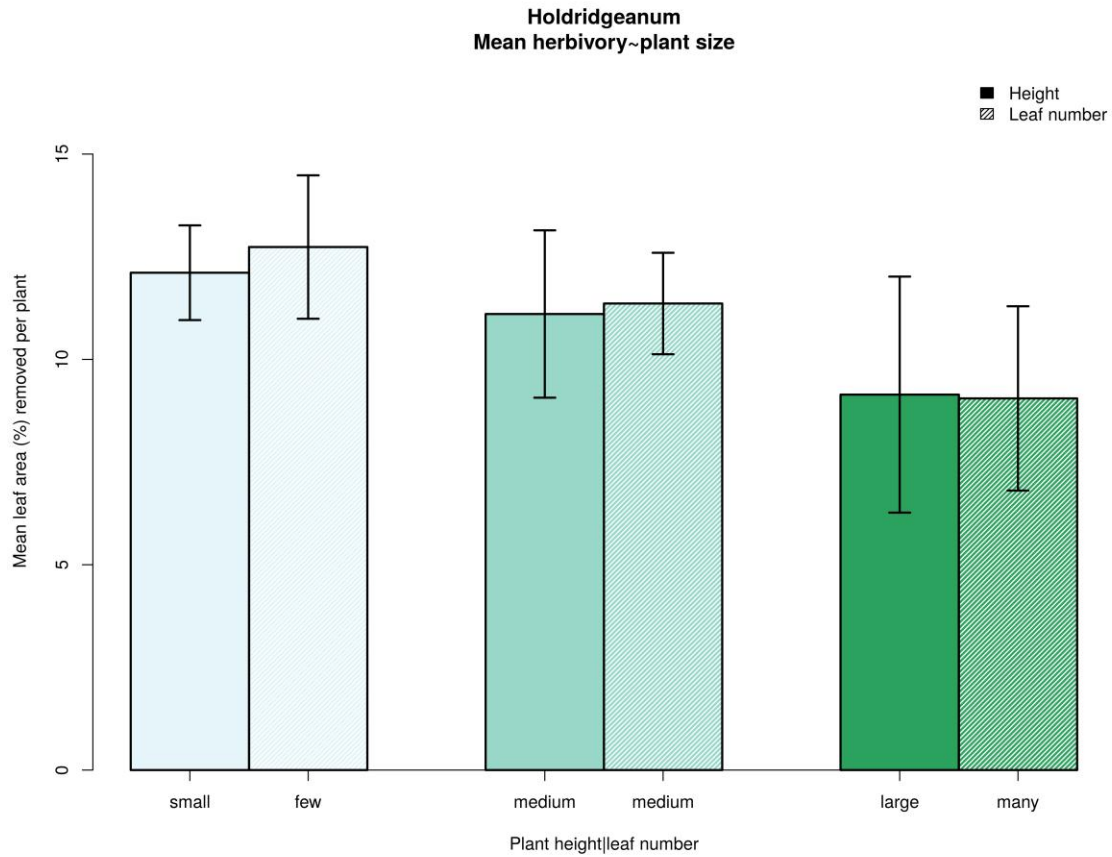
Figure 16. Mean leaf area (%) removed is affected by plant size for *P. holdridgeanum*. Larger plants and those with many leaves suffer less herbivory than smaller plants with few leaves. (GLMM, *p*=0.02). Lined bars represent leaf number and full colored bars represent plant height. Height range sizes, small: ≤ 60, medium: > 60 and ≤ 110, large: > 100 cm. Leaf range sizes, small: ≤ 4, medium: > 4 and ≤ 13, many: > 13. Error bars represent SE.