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Population abundance, sexual expression, and gender ratios of *Marchantia sp.* along an elevational gradient in Monteverde, Costa Rica

Laura Garrison

Department of Biology, Northern Michigan University

ABSTRACT

Fisher's theory on sex ratios states that a 1:1 ratio of males to females typically will result when both sexes are equally expensive to produce. Many bryophytes, however, tend to express female sex biases. I took two population censuses of *Marchantia sp.* during dry season and the transition from wet to dry season along the Sendero Principal in Monteverde, Costa Rica, to determine population abundance and sex ratios. Elevation did not significantly correlate with population abundance (Spearman rank correlation census one: $\rho = -0.213$, $P = 0.372$; census two: $\rho = -0.118$, $P = 0.409$). I found local female proportions to vary at different sites in both censuses (Chi-squared test for independence census one: $\chi^2 = 175.861$, $df = 7$, $P < 0.0001$; census 2: $\chi^2 = 292.349$, $df = 7$, $P < 0.0001$) and, although non-significant, I noticed a trend towards increasing gemmae presence with elevation in census two (Spearman rank correlation $\rho = 0.405$, $P = 0.28$). Finally, I found a strong female metapopulation bias to become more pronounced as the rainy season progressed. Small dispersal ranges of *Marchantia sp.* are likely preventing higher abundance; its ability to colonize an area can be attributed more to microhabitat resource availability than elevational conditions, although trends of gemmae increase are likely due to stable moist conditions at high elevations. *Marchantia sp.* may display a higher proportion of females in the meta- and local populations due to higher male nutrient requirements, prompting local mate competition to act between males for limited resources in microhabitats.

RESUMEN

La teoría de Fisher de las proporciones sexuales indica que una proporción de 1:1 de varones a hembras resultará cuando ambos sexos son igualmente costosos producir. Sin embargo, muchos briófitos tienden a expresar sesgo hacia la expresión femenina del sexo. Hice dos censos de la población de una especie de *Marchantia* durante la estación seca y la transición de seca a la estación lluviosa, cerca del Sendero Principal en Monteverde, Costa Rica para determinar la abundancia de la población y las proporciones de los sexos. La elevación no tuvo un efecto significativo en la abundancia local de la población (Spearman rank correlación; censo primero: $\rho = -0.213$, $P = 0.372$; censo segundo: $\rho = -0.118$, $P = 0.409$). Las proporciones femeninas variaron en diversos sitios (Chi-squared examen por independencia; censo primero: $\chi^2 = 175.861$, $df = 7$, $P < 0.0001$; censo segundo: $\chi^2 = 292.349$, $df = 7$, $P < 0.0001$) y tuve un efecto no significativo, pero es una tendencia de las copas de gemmae en el segundo censo (Chi-squared test for independence census one: $\chi^2 = 82.66$, $df = 1$, $P < 0.05$; census 2: $\chi^2 = 200.8$, $df = 1$, $P > 0.05$). Finalmente, encontré en la metapoblación una mayor proporción de sexo femenino que llegó a ser más pronunciado mientras que progresó la estación de lluvias (Chi-squared examen por independencia; censo primero: $\chi^2 = 82.66$, $df = 1$, $P < 0.05$; censo segundo: $\chi^2 = 200.8$, $df = 1$, $P > 0.05$). Las limitaciones en la dispersión están limitando probablemente abundancia amueal altitudinal, aunque las tendencias con aumento de los gemmae son probablemente debido a la lluvia creciente cerca del canto al segundo censo. Los cocientes sesgados hembra de *Marchantia sp.* que fluctuaron se pueden atribuir porque los machos necesitan mas nutrientes que las hembraes, entonces la competición por cópula entre los machos por los recursos limitados en los microhábitats.

INTRODUCTION

Dioecy, a condition where an organism has separate male and female plants, is often advantageous to individuals in situations where life history and ecological conditions favor reproductive structure specialization (Lloyd 1974, Shaw 2000). This morphological specialization allows for increased egg and sperm production efficiency, and leads to greater genetic population diversity by encouraging outbreeding (Shaw 2000). Fisher's theory on sex ratios states that typically a 1:1 ratio of males to females will result if the two sexes are equally expensive to produce. If, however, the production of sons or daughters imposes different costs of production on the parent, selection will favor increased proportions of the less expensive sex when resources are limited (Charnov 1982). Different costs of production can arise from genetic mechanisms, differences in mortality rates, or differences in life histories (Meagher 1981). In extreme cases, biased reproduction costs can lead to gender specialization, where males and females of dioecious species become adapted to separate environmental conditions. Local mate competition sometimes maintains female biased sex ratios, maintaining only enough males in a given population to fertilize the area females (Charnov 1982). To enhance survival rates, sexes segregate along environmental gradients according to their differing microhabitat requirements (Stark et al. 2000).

All bryophytes depend upon water for the flagellated sperm to swim to and fertilize eggs. This means that male and female plants must be in close proximity to facilitate sexual reproduction (Schofield 2001, Shaw 2000). However, sporophyte production is rare and the plant largely relies on vegetative growth, a type of asexual reproduction. This can be disadvantageous to individuals in a dynamic environment, since asexual reproduction creates offspring of little genetic variation to adapt to changing conditions (Shaw 2000).

Approximately half of all bryophytes are dioecious, and female-biased sex ratios are typical in many species; in extreme cases, only female or sterile gametophytes may occur in a given region (Shaw 2000). Female-biased sex ratios can arise via local mate competition, where many males requiring a wider nutrient load than females grow close together and compete for valuable limited resources such as space and nutrients. Parent plants can reduce this counterproductive intraspecific competition by reducing the proportion of males produced (Charnov 1982, McLetchie 1992, Bowker et al. 2001).

Marchantia, in the order Marchantiales, is a genus of predominantly dioecious liverworts that grow successfully in a variety of conditions; as a result their distribution is worldwide. However, this genus grows best on mineral soil, rock faces, and well-lit sites. Male and female reproductive structures, called antheridiophores and archegoniophores, are unique to *Marchantia*, which often exhibits strongly female-skewed population distributions (Schofield 2001). At a given point in the organism's life cycle, these structures elongate above the reclining thallus, enhancing dispersal distances. For example, *Marchantia chenopoda* can disperse its sperm up to 65 cm from antheridiophores (Moya 1993). Rain drops splatter on the platform-shaped antheridiophores and antheridia are dispersed to fertilize the archegonia, located under the protecting umbrella of the archegoniophore. Once fertilized, archegonia develop into a diploid sporophyte, which produces haploid spores that are eventually released to colonize other areas (Figure 1). *Marchantia* also exhibits specialized means of asexual

reproduction through water-dispersed gemmae, which are asexual spores, and through vegetative adventitious branching of sterile thalli throughout its life cycle (Schofield 2001).

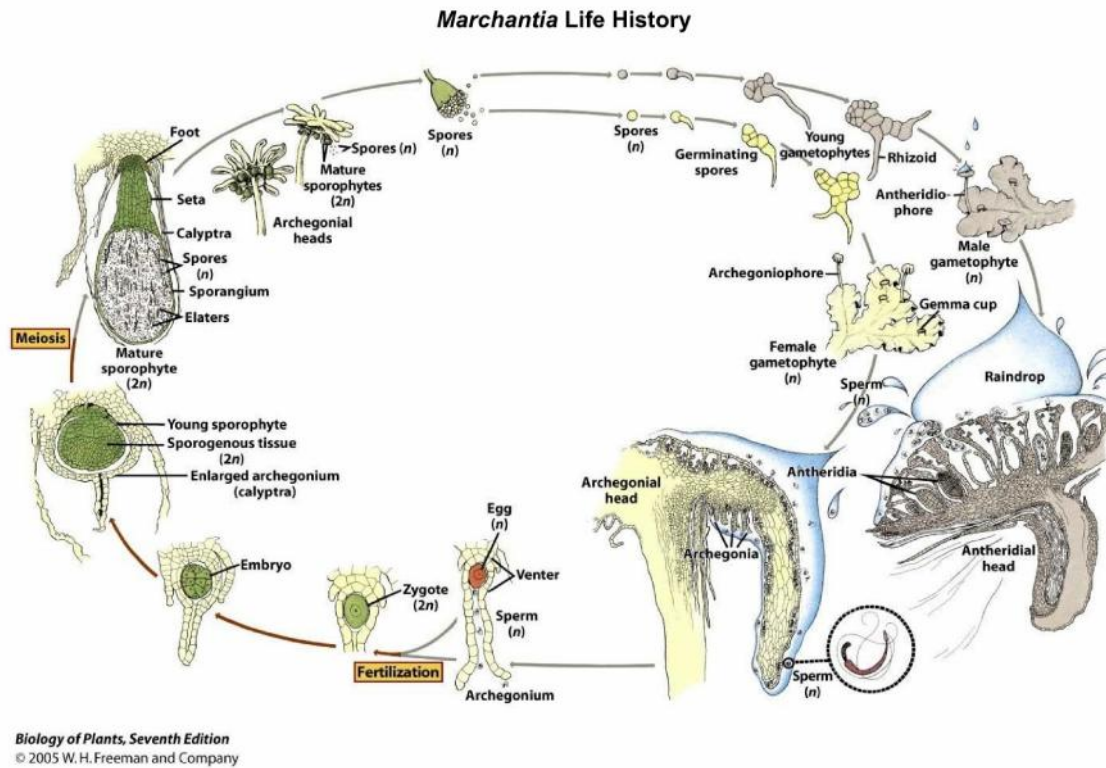


Figure 1. Description of the reproductive life cycle of *Marchantia* as it progresses from spore to gametophyte to sporophyte to spore. Raindrops disperse antheridia which fertilize archegonia that then develop into the diploid sporophyte. Spores disperse and the cycle continues.

My goal in this study was to investigate patterns of abundance and gender ratios of *Marchantia sp.* along an elevational gradient between the dry to wet season transition. Higher elevations of cloud forests tend to be wetter and thus have better growth conditions, especially for bryophytes such as *Marchantia sp.* that are heavily reliant on water for growth and reproduction (Clark 2000, Schofield 2001). Its specialized elevated reproductive structures, with more rain, should be able to disperse and fertilize other plants more often than at lower elevations where water is limited, leading to higher species abundance. Additionally, both sexes will probably be able to grow close to 1:1 ratios at higher elevations because there will be less intrasexual competition for nutrients. However, lower elevations may exhibit high female proportions due to resource limitations, where females should be produced in higher numbers because of their more relaxed nutrient requirements. Finally, temporal variation of abundance and sex expression may exist since the wet season rains may enhance dispersal and growth conditions of *Marchantia sp.*

METHODS

Study Site

My study was conducted on the property of the Monteverde Biological Station in Monteverde, Costa Rica in Lower Montane Wet Forest (Haber 2000) during a month long period from April 13th to May 7th, 2007. Two population censuses were conducted, the first from April 20th-28th, following a prolonged dry period characteristic of dry season conditions. The second census I conducted starting April 29th and ending May 7th, following a period of rainy days marking the beginning of wet season. I laid out a transect along the Sendero Principal, spanning from 1530 m to 1780 m in elevation, sampling every five meters for a total of 51 sites.

Population Sampling

At every site, I examined a one by two meter swath containing a variety of substrates directly to the left of the trail for the presence of *Marchantia sp.* If present, I recorded patch area and subsampled a 20 by 20 square cm area in the patch center, tallying the number of non-expressing thalli, gemmae cups, archegoniophores, and antheridiophores. My identification of *Marchantia sp.* was primarily based off of its antheridiophores and archegoniophores. Both structures have ruffled edges, but antheridiophores are platform-shaped while archegoniophores have an umbrella shape. Additionally, the gametophyte's strongly visible white dorsal air pores and two rows of purple scales on the thallus underside aided in identification in non-expressing gametophytes (Schofield 2001). Instead of counting individuals, I counted thalli, which are the leafy branching parts of the plant. Since *Marchantia* often reproduces via clones, it was too difficult to count individuals because one individual may be the entire patch in an area. For ease of sampling, I defined all populations of *Marchantia sp.* along the Sendero Principal to comprise the same metapopulation.

Statistical Analysis

I analyzed meta- and local populations of *Marchantia sp.* using Spearman rank correlations to test for correlations between abundance and elevation, in addition to gemmae cup proportions along an elevational gradient for both censuses. To determine whether *Marchantia sp.* meta- and local population female sex ratios were significantly different between each other I used Chi-squared tests of independence.

RESULTS

I found eight local populations of *Marchantia sp.* in differing abundances. Species abundance did not significantly increase as elevation increased in either census (Spearman rank correlation, census 1: $\rho = -0.213$, $P = 0.372$; census two: $\rho = -0.118$, $P = 0.409$, Figure 2). All populations of *Marchantia sp.* sporadically occurred between 1570 m and 1750 m.

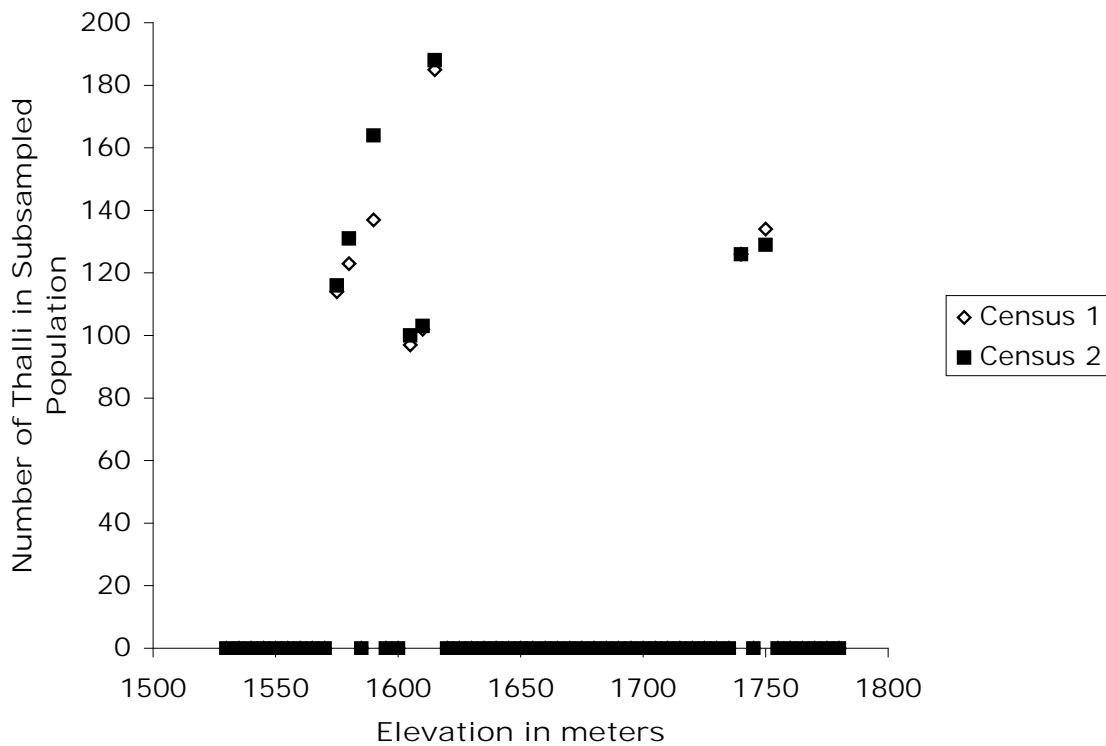
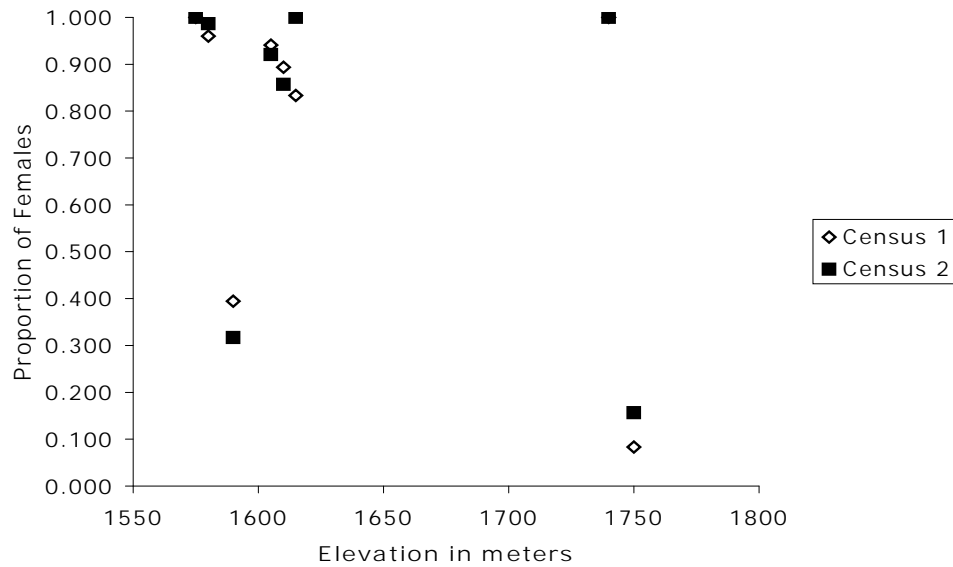


Figure 2. The number of *Marchantia* thalli observed along an elevational gradient in the Monteverde Cloud Forest. *Marchantia sp.* was found at only eight locations. Sampled areas were 20 X 20 cm located at intervals of five m in elevation along the Sendero Principal of the Monteverde Biological Station. Censuses were conducted at two separate times, the first at the end of a dry season drought, and the second following a series of rainy days.

The ratio of females and males across the eight local population sites during the first census differed significantly from each other (Chi-squared test for independence $\chi^2 = 175.861$, $df = 7$, $P < 0.0001$). Proportions of females at 1570 m, 1580 m, and 1740 m were particularly high where microhabitats seemed drier, and were very low at 1545 m and 1750 m where conditions appeared wetter (Figure 3). I found similar results in census two, where local population ratios differed significantly at each elevation, and sites with extremely high and low proportions of females were the same as those in census one (Chi-squared test for independence $\chi^2 = 292.349$, $df = 7$, $P < 0.0001$). In both censuses, females occurred at all eight sites. Males were more sparsely distributed, occurring at six of the eight locations in the first census and only at five locations in the second census (Figure 3). In all but two sites in both censuses females dominated the local populations, although no significant relationship was found between sex ratios and increasing elevation.

During the interval between the two population censuses there was an overall 9.9% reduction (50.7% to 40.8%) in the percentage of non-expressing thalli. Proportions of thalli with gemmae cups did not change along the elevational gradient for either the



first or the second census, although there may be a positive trend with elevation for census two (Spearman rank correlation census 1: $\rho = 0.905$, $P = 0.80$; census two: $\rho = 0.405$, $P = 0.28$, Figure 4).

Figure 3. Proportion of female *Marchantia sp.* thalli relative to all sex-expressing thalli in eight subsampled populations along Sendero Principal of the Monteverde Biological Station. Females were found in very high proportions at all but two sites. Censuses were conducted two separate times, the first one at the end of a dry season drought, and the second following a series of rainy days.

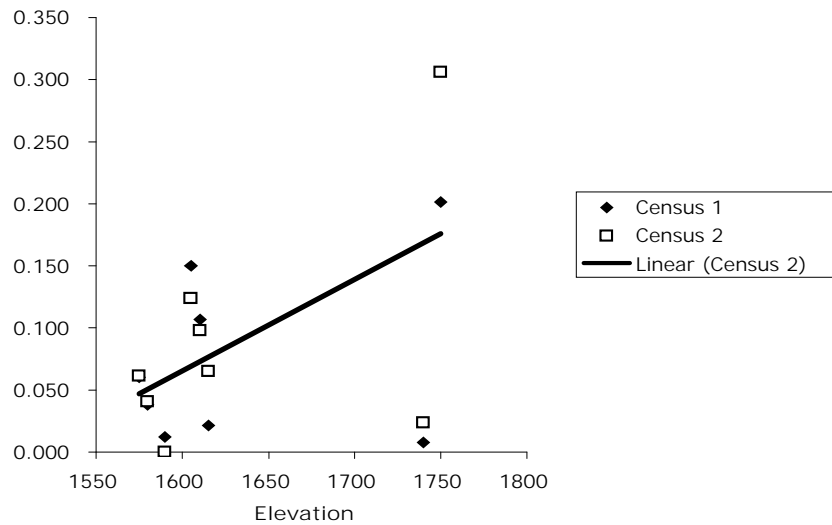


Figure 4. Proportion of *Marchantia sp.* thalli with gemmae cups in subsampled populations every five meters along the Sendero Principal of the Monteverde Biological Station. Censuses were conducted at two separate times, the first one at the end of a dry season drought, and the second following a series of rainy days. The proportion of gemmae cups in census two showed an insignificant upward trend with elevation.

Analysis of census one metapopulation sex ratios showed a skewed ratio with significantly more female than male structures in the population (Chi-squared test for independence $\chi^2 = 82.66$, $df = 1$, $P < 0.05$, Figure 5). Sex ratios from census two showed a significant female bias that was more pronounced than in census one (Chi-squared test for independence $\chi^2 = 200.8$, $df = 1$, $P > 0.05$, Figure 5).

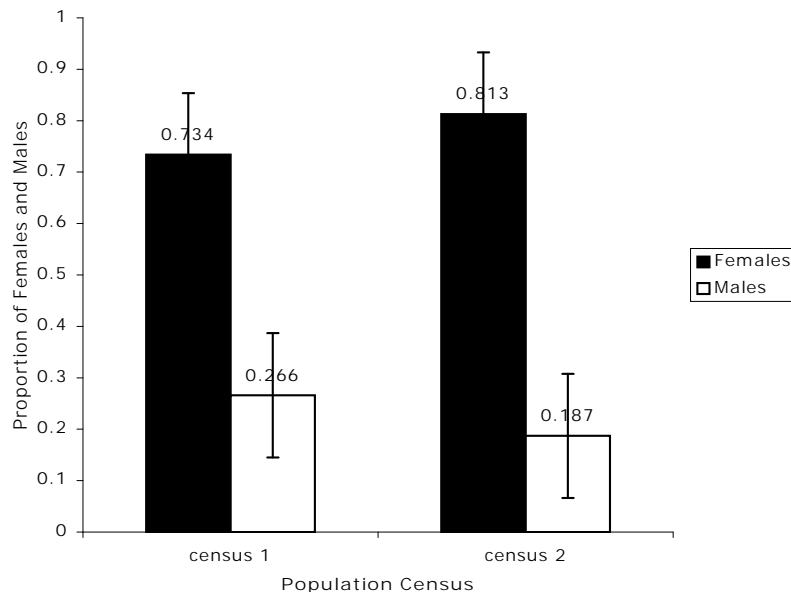


Figure 5. Proportion of male and female *Marchantia sp.* thalli in the metapopulation along Sendero Principal of the Monteverde Biological Station. During the dry stretch census females comprised 73.4 % \pm 0.120% of sex-expressing thalli and during the wet season transition census period females consisted of 81.3% \pm 0.121% of sex-expressing thalli.

DISCUSSION

The first population census was performed in a dry period while the second census followed a series of rainy days; the difference in growth displayed between the two censuses might have resulted from differing weather conditions between the two censuses. Typically, bryophytes switch from vegetative to sexually reproductive phases when microhabitat ambient temperature and moisture increase and days become slightly longer (Schofield 2001). These are characteristics of the beginning of the rainy season in Monteverde (Clark 2000). Thus, wetter conditions from the rains of the second census likely made *Marchantia sp.* sexual reproduction via sperm dispersal more optimal than vegetative branching (Bowker et al. 2000). However, the apparent lack of association between abundance and elevation suggest that resources within microhabitats play a larger role in *Marchantia sp.* growth than climatic conditions associated with elevation.

Other studies support this idea, having found that ecological differences between microsites, such as soil moisture and light availability, are likely reasons for differing population abundances (Meagher 1981, Bowker et al. 2000).

Marchantia sp., like many other bryophytes, likely cannot spread with increasing elevations because, although environmental conditions may be ripe, it is simply dispersal limited. Despite its elongated archegoniophores and antheridiophores that further spore travel distances, *Marchantia sp.* is still constrained from long-range dispersal by its small size. Patches found along the Sendero Principal might have arisen from colonization by the rare few individuals able to move long distances from their parent sporophyte. Three sporophytes were found over the entire transect in both censuses, enhancing the likelihood that most growth of *Marchantia sp.* is vegetative through either gemmae dispersal or adventitious branching. However, there could be a phenological pattern of gametophyte sexual expression not captured in this study's short time window, where non-expressing thalli do not asexually produce but await ideal conditions to express sex. Regardless, small dispersal ranges likely mean that *Marchantia sp.* may consistently colonize only at microhabitat levels.

Differing local *Marchantia sp.* sex ratios indicate that dispersal limitations are acting on proponents of the plant. Ratios were highly variable between sites – perhaps because each local patch is only comprised of those few individuals able by chance to disperse and establish a new patch, possibly causing skewed ratios. Additionally, no gradient in the sexes may indicate that neither sex particularly benefits from occupying the moister conditions found at higher elevations. This idea is assuming that the environment at higher elevations is replicated in small, moist microhabitats found everywhere, and that dispersal prevents widespread colonization. Therefore, a male or female *Marchantia* does not necessarily need to reach high elevations to flourish. It seems that, due to the rarity of long-range spore dispersal, the sexes of *Marchantia sp.* array themselves within small-scale climatic habitats instead of a broad landscape scale.

Higher gemmae abundance at higher elevations could enhance *Marchantia sp.* growth and dispersal because, unlike in microhabitat conditions, the climate near the top of the ridge is fairly stable (Clark 2000). Vegetative reproduction ensures that progeny will have the same adaptations for a given weather pattern as their parents because no new genetic information is introduced to the population (Shaw 2000). This is advantageous for *Marchantia sp.* along the ridge; climatic stability ensures that the plant can be adapted to a specific set of conditions does not need to guard against climate fluctuation by sexual reproduction. Therefore, in stable climatic conditions it may be more advantageous for the plant to asexually reproduce. Finally, the consistently wet conditions at the top of the ridge especially favor gemmae reproduction, which can only occur by raindrops splashing into the gemmae cups (Schofield 2001).

The female bias of the *Marchantia sp.* metacommunity may have arisen as a result of local mate competition, where sibling males compete over limited resources in an area. Male bryophytes have been shown to have nutrient requirements greater than those of females, which may lead to gender specialization in microhabitats (Grant 1979, Stark et al. 2000). Such high nutrient requirements tend to restrict males to protected or less-stressed microhabitats which are also more ideal for sperm dispersal (Longton 1988, Shaw & Gaughan 1993, Bowker et al. 2000). In the two study sites where males dominated the *Marchantia* patch, conditions seemed moist and ideal for liverwort

growth. Conversely, female *Marchantia sp.* were found in a variety of microclimates, including drier and more stressed areas, keeping with other studies on desert and arctic mosses asserting that females do not suffer similar nutrient limitations (Meagher 1981). The limited spore dispersal range of *Marchantia sp.* ensures that many spores will land in close proximity to the parent, leading to intrasexual competition for resources. Higher male mortality rates are a typical outcome of such competition, as nutrients become limited and thus difficult for males to obtain what they need for survival and reproduction (Charnov 1982, Stark et al. 2000). Meanwhile, low intrasexual competition between females ensures that they can remain abundant across a wide range of conditions.

This study has been the first to examine on a temporal and elevational scale the abundance, sex ratios, and sexual expression of this species in the *Marchantia* genus. Due to time constraints the sample size was small, and for a study involving sex ratios, many more samples would be needed over a longer time period to clarify sterile to sex-expressing gametophyte growth patterns, as well as species distribution. Future studies could include measuring the biomass of males and females, finding exact dispersal distance of sperm, studying success of sporophyte development, and tracking the progress of sterile thalli of *Marchantia sp.* as they express sex. The field of bryophyte sex allocation is relatively unknown, and future directions are nearly limitless.

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