

# Sex ratios, damage and distribution of *Myrianthus holstii* Engl.: a dioecious afro-montane forest tree

## Research Article

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### Abstract

Male and female dioecious tropical trees are subjected to distinct demands that may influence their ecology. An example is *Myrianthus holstii* Engl. that produces persistent fruit eaten by elephants and other large mammals that frequently damage the trees. *Myrianthus holstii* populations were assessed with 24 2-km transects, spanning an elevation range of 1435–2495 m in the Bwindi Impenetrable National Park in Uganda. Of 1089 stems  $\geq 5$  cm diameter 449 were female, 383 were male and the rest were non-fertile. We also noted one apparently monoecious individual. Males produced flowers at smaller sizes than did females (minimum recorded diameters 5.5 cm and 6.8 cm, respectively). Both sexes had similar distributions, favouring moderately closed forest and mid-slope locations. Female trees were more frequently damaged and typically slightly shorter than males at large diameters. Seedling densities were positively associated with the presence of larger female trees. Our results are consistent with a life history where both sexes have similar requirements, but fruiting females experience a greater frequency of severe damage.

### Introduction

The prevalence and life history characteristics of dioecious plants remain incompletely understood despite considerable attention from evolutionary and ecological theorists and researchers (Bawa 1980, Charlesworth & Charlesworth 1987, Givnish 1982, Thomson & Brunet 1990). Dioecy occurs in an estimated 5–6% of angiosperm species spread over 987 genera and 175 families, with phylogenetic estimates suggesting dioecy has arisen from non-dioecious ancestors between 871 and 5000 times (Renner 2014). Dioecious tree species are especially common in tropical forests (Ohya *et al.* 2017).

Dioecious plant species exhibit male-biased (Matsushita *et al.* 2016, Ortiz *et al.* 2002, Queenborough *et al.* 2013), female-biased (Gauquelin *et al.* 2002, Ueno *et al.* 2007, Wang *et al.* 2013) and balanced populations (Morellato 2004). Our overall knowledge and understanding of the form, physiology and ecology of dioecious plants remains incomplete and in all but a few cases the causes and implications of imbalanced sex ratios remain poorly characterised (Galfrascoli & Calviño 2020, Juvany & Munné-Bosch 2015, Randriamanana *et al.* 2015, Retuerto *et al.* 2018). Nonetheless, some patterns are apparent. For example, while female-biased populations are often associated with clonal and herbaceous growth forms and with abiotic pollination and dispersal mechanisms, male-biased populations appear more common among longer-lived animal dispersed taxa (Field *et al.* 2013, Sinclair *et al.* 2012).

One area of interest is how dioecious species interact with herbivores (Ashman 2002, Avila-Sakar & Romanow 2012). Various studies, and several overviews, suggest male plants are often less well defended and tend to suffer higher levels of herbivore related damage (e.g., Cornelissen & Stiling 2005, Jing & Coley 1990, Obeso 2002, Tonnabel *et al.* 2017). Nonetheless, female plants sometimes attract greater attention leading to greater damage (Avila-Sakar & Romanow 2012, Hemborg & Bond 2007, Romero-Pérez *et al.* 2020, van Blerk *et al.* 2017). Such patterns and their implications have practical as well as theoretical implications as the need to maintain two life histories means that dioecious species may be particularly vulnerable to rapid climate change and other threats (Hultine *et al.* 2016, Petry *et al.* 2016, Tognetti 2012).

*Myrianthus holstii* Engl. is a distinctive palmate-leaved hollow-stemmed dioecious tree that can reach 20 m tall (Iversen 1991, Katende *et al.* 1995). The male staminate flowers are small green and packed together in bifurcating ‘stag horn’-like inflorescences, the clustered female

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pistillate flowers comprise more compact but still irregular inflorescences, the fruit are hard, segmented, roughly globular, variable in size, and they ripen from green to yellow to reddish brown over several months. The fruit itself is 5–10 cm diameter and long-lived: a tough yellow exo-carp ‘rind’ surrounds a pulp around each of several (typically around 10) hard seeds of 1–2 cm diameter. The pulp is sour (acidic) but sweet when sufficiently ripe (Fedrowitz *et al.* 2014). Taxonomists have moved the genus *Myrianthus* among three families: from Moraceae to Cecropiaceae and more recently to Urticaceae (Berg 1978, Wu *et al.* 2013). While mechanisms governing sex determination are unknown for *Myrianthus*, phylogenetic evidence indicates descent from a sex chromosome possessing dioecious ancestor (see e.g., Prentout *et al.* 2020, Zhang *et al.* 2019). *Myrianthus holstii* occurs in mountain forests across Central and East Africa where its fleshy fruits are sought by various wildlife (Kissa & Sheil 2012, Stanford & Nkurunungi 2003). In the Bwindi Impenetrable National Park (henceforth ‘Bwindi’), the fruits are also valued by people. While park authorities permit local people access to certain resources (Bitariho *et al.* 2016) and *M. holstii* fruits have long been requested in negotiating such access (Wild & Mutebi 1996), collection of these fruits remains illegal though not uncommon in accessible locations (pers. obs. all authors).

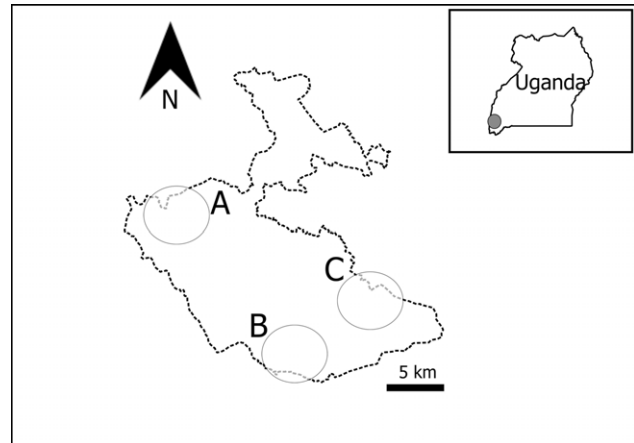
Little is known about the ecology of this species, so our study was broad and primarily exploratory. We assessed and compared the form, structure and distribution of *M. holstii* populations. We considered sex ratios, size classes, densities and environmental factors in three landscapes spanning a range of elevations. We recognised that male and female trees may be subjected to distinct pressures and requirements that might influence their distribution and form (Barrett & Hough 2013, Chen *et al.* 2010). Specifically, we knew that several large mammals, including elephants *Loxodonta africana* Blumenbach appear to break *M. holstii* stems to access the foliage and the fruits (Ssali *et al.* 2013; and pers. obs. all authors). Noting that the fruits are sought by certain large mammals we anticipated that female trees may suffer a different pattern of damage (more severe and frequent) than male trees.

### Study area

We conducted our study in the Bwindi Impenetrable National Park (‘Bwindi’), a 331-km<sup>2</sup> UNESCO World Heritage Site (0°53′–1°08′ S, 29°35′–29°50′ E, Figure 1). Terrain is generally steep with elevation ranging from 1190 m to 2607 m asl. The climate is equatorial with annual rainfall averaging between 1,130 and 2,390 mm with two rainfall peaks from March to May and September to November (Ssali *et al.* 2019).

Bwindi was managed as a production forest from 1942 and gazetted as a National Park in 1991. Past timber extraction, fires, landslides and other processes mean that areas of advanced secondary regrowth are common. Field work is challenging given the rugged and steeply sloped terrain and the often densely vegetated understorey (Sheil 2012). Land outside the forest is agricultural and densely populated (around 150 people per km<sup>2</sup> <https://www.ubos.org/explore-statistics/20/> checked December 2020). The forest fauna includes gorilla *Gorilla beringei* Matschie, chimpanzee *Pan troglodytes* Blumenbach and bush elephant *Loxodonta africana* Blumenbach—all of which feed on *M. holstii* fruit (Kissa & Sheil 2012, Stanford & Nkurunungi 2003).

In order to cover a range of contexts, we studied three landscapes with different but overlapping elevation ranges spanning over 1000 m in total (A = Buhoma, B = Rushaga and C =



**Figure 1.** Map showing the location of Bwindi Impenetrable National Park within Uganda (0°53′–1°08′ S, 29°35′–29°50′ E) and the location of the three study landscapes within the park. A, B and C represent areas near Buhoma, Rushaga and Ruhija respectively.

Ruhija; see Figure 1). Elevation ranged from 1450 m to 1850 m at landscape A, 1800 m to 2250 m at landscape B and 2100 m to 2500 m at landscape C.

### Data collection

At each of the three sampling locations, *M. holstii* were sought and assessed along eight 2-km transects, originating from the park boundary to the interior, and placed parallel to each other 700 m apart approximately perpendicular to the mean park boundary in that region. The location and direction of the first transect in each location were predetermined using random coordinates to avoid selection bias (Kissa & Sheil 2012). During field work, between October 2009 and April 2010, two sampling procedures were used: (1) a conventional belt transect approach with a fixed width of 10 m (5 m to either side of the centre line); and (2) a visual-detection-based distance approach or ‘Distance’ method (Buckland *et al.* 2001, Kissa & Sheil 2012). It is the Distance derived data that are the focus of the analyses presented here.

Along each transect, *M. holstii* trees over 1.3 m tall were searched for and recorded by one assigned observer moving along the transect centre focusing on complete coverage within 5 m either side (for the 10 m-wide belt transect). Both horizontal distance along the transect and the nearest horizontal perpendicular distance from the transect to each detected tree were recorded. Seedlings were recorded in a 4 m radius around any recognised female *M. holstii* trees found in the belt transect approach.

The relative strengths of the two approaches, the belt transect and Distance Methods, have been examined in detail elsewhere (Kissa & Sheil 2012). In brief, Distance sampling was found to be well suited to Bwindi despite the often challenging conditions posed by the dense vegetation and steep terrain (Sheil 2012). When compared by equivalent costs, effort or ‘per stem’, the visual detection approach yielded superior accuracy (narrower confidence intervals on the estimate) than the fixed-width transects. As we report in detail elsewhere, our initial assumption was that fixed-width transects provide an unbiased reference for comparison with the Distance approach. Our results indicated that some stems, particularly small stems, remained undetected in the dense understorey vegetation regardless of the approach. While both approaches have potential biases due to such omissions the

Distance Method accounts for these omissions, as perfect detection is only assumed for the central line of the transect. The Distance approach also detects many more stems than the fixed width approach, which is especially useful for larger stems that occur at low abundance (i.e., less than 10 per hectare)—important here as it is primarily these larger stems that are fertile and can contribute to our comparison of male versus female stems (Kissa & Sheil 2012).

For each tree, we recorded diameter ('dbh' measured at 1.3 m), height, presence of fruits, presence and form of flowers (male or female) and signs of damage (i.e., 'browsed' [evidence of leaves and twigs having been bitten off with flattened twig ends], 'debarked' [bark removed and showing signs of teeth or tusks and similar], 'top-broken' [missing upper portion of the stem] or 'leaning stem' [tree shows signs that it has been pushed forcefully enough to result in damage to roots and or tilted, skewed or bent growth]), distance from the transect line and location coordinates along with notes on site characteristics that include soil colour (though we lacked a systematic reference to permit objective classification). We considered multi-stemmed trees as one individual by assigning a diameter that was equivalent to a hypothetical single stem with a cross-sectional area equivalent to the combined area of individual stems assuming all stems as circular in section. The heights of trees between 1.3 m and 2.5 m tall were measured by tape, and those of taller stems estimated using a clinometer. Every 100 m along each transect, we recorded elevation (m, using a hand held Global Positioning System unit), slope (degrees°, using a clinometer), canopy closure (%), using a mirror densiometer), local basal area ( $\text{m}^2 \text{ha}^{-1}$ , using an angle gauge relascope) and slope position (visually determined). For some summaries and analyses, we categorised the trees as saplings (dbh  $\geq 0.3$  cm and  $\leq 5.0$  cm) comprising small saplings (dbh  $\geq 0.3$  cm and  $\leq 2.5$  cm) and large saplings (dbh  $> 2.5$  cm but  $\leq 5.0$  cm) and as adults (dbh  $> 5.0$  cm) comprising small adults (dbh  $> 5.0$  cm but  $\leq 10.0$  cm) and large adults (dbh  $> 10.0$  cm). We used 'non-fertile' for trees with dbh  $> 5$  cm which did not bear flowers or fruits when observed.

To summarise, our evaluations here focus on the set of individual trees detected and measured using the Distance Method. In one section, we also assess seedlings around likely-mother trees detected and measured in the 10-m wide fixed width belt transect.

### Analyses

*Myrianthus holstii* trees were designated as male, female or non-fertile, based on the presence of fruits or flowers. Using generalized linear models (GLMs) with a Gamma distribution and a log-link function, we tested whether height is related to diameter and whether the relationship differs by tree sex in each of the three landscapes. Height was included as the response variable, while diameter and tree sex were explanatory variables. We also tested for differences in the incidence of damage using negative binomial GLMs. All analyses used R (R-Core-Team 2020). Given the abundance of multi-stemmed trees, we performed analyses that involved tree size and structure both with and without multi-stemmed individuals.

The distance-based estimation of stem densities (hereafter 'Distance Method') was conducted using DISTANCE 6.1 Release 2. This software estimates density in a defined length of transect using the equation of Buckland *et al.* (2001):

$$D = \frac{n}{2WLPa}$$

where  $n$  = total number of individuals of the population of interest (trees) recorded,  $W$  and  $L$  = transect width and length, respectively, and  $Pa$  = probability of observing the population of interest. Four standard detection functions that account for the decreasing likelihood of detecting individuals at greater distance were fitted to each population of interest with 30 or more stems. After visual evaluation to check that the data are well behaved (i.e. that the likelihood of detection for any individual on the centre line is one and declines with distance), the best detection function was then selected based on possession of the lowest value 'Akaike information criterion' or AIC (Akaike 1974). This process was previously described, with results including the selected detection functions, and an assessment of various uncertainties, errors and biases in an article which uses the same populations we examine here—the curious reader should examine that article for these details (Kissa & Sheil 2012).

### Results

Using the Distance Method, we detected and measured 1643 *M. holstii* trees over our 48 km of transect (1421 stems had height  $\geq 1.3$  m while 122 stems were shorter). The total number of larger stems, dbh  $> 5$  cm  $\leq 10$  cm and dbh  $> 10$  cm, was 255 and 834, respectively.

#### Male and female trees

Flowering was prevalent throughout the study (October–March). Using the Distance Method, we recorded 832 fertile trees: 383 males and 449 females (Tables 1 and 2)—an exact binomial test indicated a significantly unbalanced secondary sex ratio,  $P = 0.024$  with the 95 per cent confidence intervals for the 'true' proportion of females lying between 0.505 and 0.574. Only 38 trees had ripe fruits at the time of recording. The smallest and largest diameters of males were 5.5 and 88.0 cm and of females were 6.4 and 84.3 cm, respectively. Multi-stemmed individuals constituted 25.8% of all individuals dbh 5 cm or greater (i.e. 281 out of 1089 individuals; 114 females, 120 males and 47 non-fertile individuals). No stems below 5 cm diameter were fertile, while 256 stems over 5 cm diameter were non-fertile and thus remained unsexed. Nonetheless, female trees appeared overrepresented among smaller size classes (Figure 2b). We chose three broad categories (diameters  $\leq 10.0$ –20.0 cm, 20.1–40.0 cm and greater than 40.0 cm) for sex ratio analyses and found a female-biased secondary sex ratio, though this tendency was insignificant for stems dbh  $> 40.0$  cm (Table 1). We noted one large tree (dbh 30 cm and outside the formal sample) bearing both male and female flowers. As the number of non-fertile stems exceeds the difference between counted males and females (i.e. 66 stems), a balanced primary sex ratio remains possible. Most non-fertile trees (86.4%) were less than 20 cm in diameter (113 of 132 at A, 76 of 90 at B and 33 of 35 at C).

#### Size and damage relationships

Visual evaluations suggested that males were typically taller than females at larger diameters (i.e. over 20 cm dbh, Figure 2a). Gamma GLMs confirmed that while height increased with diameter ( $P < 0.001$  in all cases), the inclusion of sex as a co-factor achieved significance only at landscape C, the inclusion or exclusion of damaged and/or multi-stemmed trees had little influence on these results (see also Appendices 1 and 2).

**Table 1.** *Myrianthus holstii* trees aggregated by diameter size classes before and after excluding multi-stemmed individuals (in brackets) in the three different landscapes within Bwindi (A = Buhoma, B = Rushaga and C = Ruhija)

Diameter size class (cm)	Sites	Reproductive status				Sex ratio (fraction females)	$\chi^2$	P-value
		Non-fertile	Reproductive	Female	Male			
>10 ≤ 20	A	41 (36)	139 (97)	87 (60)	52 (37)	1.67 (1.62)	8.8 (5.5)	<b>0.003 (0.020)</b>
	B	39 (30)	75 (48)	34 (24)	41 (24)	0.83 (1.0)	0.7 (0)	0.419 (1.000)
	C	7 (5)	29 (18)	16 (10)	13 (8)	1.23 (1.25)	0.3 (0.2)	0.578 (0.637)
	A+B+C	87 (71)	243 (163)	137 (94)	106 (69)	1.29 (1.36)	4.0 (3.8)	<b>0.047 (0.050)</b>
>20 ≤ 40	A	16 (14)	178 (132)	107 (84)	71 (48)	1.51 (1.75)	7.3 (9.8)	<b>0.007 (0.002)</b>
	B	10 (8)	133 (96)	74 (54)	59 (42)	1.25 (1.29)	1.7 (1.5)	0.193 (0.221)
	C	2 (2)	56 (40)	27(19)	29 (21)	0.93 (0.9)	0.1 (0.1)	0.789 (0.752)
	A+B+C	28 (24)	367 (268)	208 (157)	159 (111)	1.31 (1.41)	6.5 (7.9)	<b>0.011 (0.005)</b>
>40	A	2 (2)	32 (27)	20 (17)	12 (10)	1.67 (1.7)	2.0 (1.8)	0.157 (0.178)
	B	4 (4)	46 (41)	22 (20)	24 (21)	0.92 (0.95)	0.1 (0.02)	0.768 (0.876)
	C	0 (0)	25 (22)	10 (10)	15 (12)	0.67 (0.83)	1.0 (0.18)	0.317 (0.670)
	A+B+C	6 (6)	103 (90)	52 (47)	51 (43)	1.02 (1.09)	0.01 (0.2)	0.922 (0.673)
>10	A+B+C	121 (101)	713 (521)	397 (298)	316 (223)	1.26 (1.34)	9.2 (10.8)	<b>0.002 (0.001)</b>

Note: Significant values ( $P < 0.05$ ) are highlighted in bold.

**Table 2.** *M. holstii* tree density  $\pm$  95% confidence interval (and stem count) in each landscape (A = Buhoma, B = Rushaga, C = Ruhija). Tree density was estimated for each population of interest with 30 or more stems using the Distance Method

Population	Density ha <sup>-1</sup> (and stem count) in each landscape			Method used
	A	B	C	
1) Overall population (diameter > 0.3 cm, height $\geq$ 1.3 m)	16.34 $\pm$ 2.70 (671)	11.47 $\pm$ 1.23 (509)	4.99 $\pm$ 2.85 (241)	Distance
2) Males (diameter > 10 cm)	2.22 $\pm$ 1.53 (135)	1.96 $\pm$ 0.93 (124)	0.88 $\pm$ 0.32 (57)	Distance
3) Females (diameter > 10 cm)	3.61 $\pm$ 2.22 (214)	2.01 $\pm$ 1.21 (130)	0.67 $\pm$ 0.48 (53)	Distance
4) Non-fertile (diameter > 10 cm)	1.96 $\pm$ 1.53 (59)	1.18 $\pm$ 0.95 (53)	0.41 $\pm$ 0.28 (9)	Distance
5) Males (diameter > 5 cm $\leq$ 10 cm)	1.47 $\pm$ 0.51 (33)	1.08 $\pm$ 0.44 (26)	0.32 $\pm$ 0.14 (8)	Distance
6) Females (diameter > 5 cm $\leq$ 10 cm)	1.25 $\pm$ 0.32 (29)	0.79 $\pm$ 0.27 (16)	0.29 $\pm$ 0.21 (7)	Distance
7) Non-fertile (diameter > 5 cm $\leq$ 10 cm)	2.17 $\pm$ 1.52 (73)	1.03 $\pm$ 0.97 (37)	1.13 $\pm$ 0.22 (26)	Distance
8) Large saplings (diameter > 2.5 cm $\leq$ 5 cm)	3.17 $\pm$ 1.24 (60)	2.81 $\pm$ 1.67 (59)	1.34 $\pm$ 0.82 (38)	Distance
9) Small saplings (diameter $\geq$ 0.3 cm $\leq$ 2.5 cm)	3.91 $\pm$ 2.28 (68)	3.08 $\pm$ 4.2 (64)	2.23 $\pm$ 0.75 (43)	Distance
10) Seedlings (height < 1.3 m)	1.56 $\pm$ 0.15 (25)	0.69 $\pm$ 0.16 (11)	0.38 $\pm$ 0.18 (6)	Fixed width
11) Top-broken trees (height < 1.3 m)	2.63 $\pm$ 0.17 (42)	1.69 $\pm$ 0.31 (27)	0.69 $\pm$ 0.24 (11)	Fixed width

Six-hundred and ninety-eight trees (64.1%) showed significant damage, with the form and nature of this damage varying with size. GLM models estimated that at 10 cm dbh the probability of overall damage sums to 90% but decreases at larger sizes (e.g., 39% at 40 cm dbh). Female trees exhibited browsing damage more frequently than males (80% versus 63%, and 31% versus 24%, at 10 and 40 cm dbh, respectively, see also Table 3; Figure 3).

### Densities

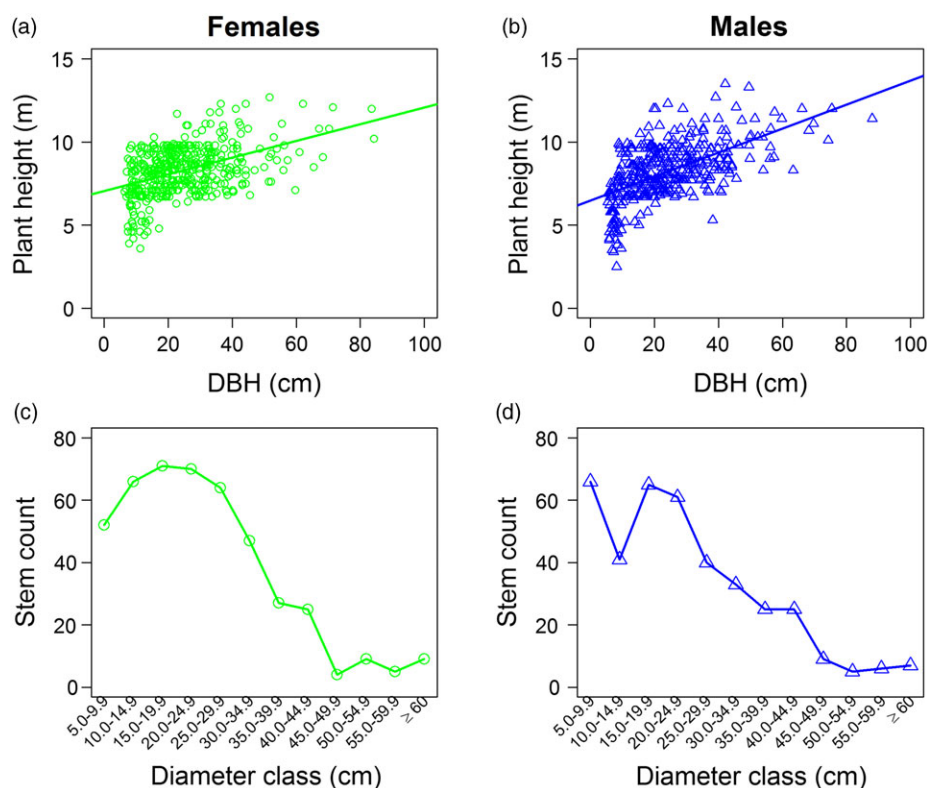
Based on the Distance Method estimates, the density of *M. holstii*  $\geq$  1.3 m tall ( $\pm$  95% confidence) averaged 8.65  $\pm$  2.13 ha<sup>-1</sup>, with differences among landscapes (Kruskal-Wallis test:  $H = 15.7$ ,  $P < 0.001$ , Table 2). Local (plot-based) variation in the frequency of females was positively associated with that of males and other sub-populations (Figure 4). Our survey of seedlings around

likely-mother trees revealed that 73 of the 449 females had one or more seedlings (stems < 1.3 m tall) within 4 m. The highest number of seedlings recorded beneath a single female was 7 at A, 13 at B and 4 at C, while the average in each case was less than 1. The number of seedlings increased with female diameter in all three landscapes (Spearman's rank correlation:  $\rho = 0.34$ ,  $P < 0.001$  at A;  $\rho = 0.40$ ,  $P < 0.001$  at B;  $\rho = 0.33$ ,  $P < 0.001$  at C and  $\rho = 0.37$ ,  $P < 0.001$  for all landscapes combined).

### Environmental relationships

**Elevation and soils:** *Myrianthus holstii* (diameter > 5.0 cm) were detected over nearly the entire elevation range examined (1451–2342 m of 1435–2495 m). Detection declined significantly with elevation for all subpopulations except saplings (Figure 5a). GLM analysis revealed that stem damage was significantly greater





**Figure 2.** (a-b) Plant height (m) versus stem diameter (cm) for female and male *M. holstii* stems (all data combined); (c-d) Size-class distribution of detected and measured male and female *M. holstii* trees.

at higher elevations, with a distinct rise in the likelihood of damage of female trees in locations above 2000 m asl (see Appendices 3 and 4). We noted that *M. holstii* appeared to favour darker soils being scarce in valleys with pale-grey soils (DK pers. obs.).

#### Canopy closure and basal area

Number of detections by distance travelled increased with broad categories of canopy cover (Figure 6a). This increase was most obvious at the transition between the 51–75% and the 76–100% cover categories, and significant differences were exhibited by all subpopulations in the three landscapes. Nonetheless, these detections declined where basal area was above average (Figure 6b).

#### Slope position

Both male and female trees were detected more on mid-slopes than in other topographic areas, though non-fertile individuals and saplings were most frequently detected in hilltop locations (Figure 6c).

#### Discussion

Previous work explored the value of Distance Methods in surveying *M. holstii* populations in Bwindi's rugged and sometimes densely vegetated environment—that work also highlighted the poor results and inefficiency of standard (fixed width) transects in detecting stems and determining local stem densities in this environment (Kissa and Sheil 2012). The work presented here examines the ecological value of these data while also noting their limitations. In due time, further improvements in how the Distance Method and analyses are being applied should permit a more locally nuanced examination that better distinguishes the factors that influence local density from those that determine the probability of detections (Marques *et al.* 2007, Miller *et al.* 2013, Schmidt & Deacy

2021). These methods and related developments deserve greater application and evaluation in vegetation sciences where their use remains scarce (e.g., Dias *et al.* 2016, Flesch *et al.* 2019). Our study shows these methods are efficient and useful.

While we recorded a significantly female-biased secondary sex ratio, males and females were detected to a similar degree in similar environments. Both sexes suffered frequent damage, though larger females appeared more frequently browsed than males and were also shorter. While the trees spanned the full range of elevations surveyed, they appeared moderately more abundant at lower elevations—an effect slightly more marked for females than males. Detection data suggest that the species favoured relatively closed forest but avoided (or were less noted in) the densest areas. They also were more often detected in mid-slope positions compared to valley bottoms or ridge tops. While our detection method may confound local factors that influence abundance and detectability, it does permit us to ask if the resulting detection patterns differ—for example, among male and female trees. Taken together, these results indicate that while both sexes have similar requirements (exhibit similar patterns of detection) female trees exhibit more damage than do males.

We observed one apparently monoecious tree. One of us has subsequently observed another monoecious individual elsewhere (in Uganda's Buvuma Islands, DK pers. obs.). Taxonomic accounts describe the genus *Myrianthus* as dioecious (De Ruiter 1976). One monograph that considered *Myrianthus* as Cecropiaceae noted that 'all species of the Cecropiaceae family have unisexual inflorescences and are strictly dioecious' (see page 43 of Berg 1978). Our observations of *M. holstii* bearing both male and female inflorescences are thus surprising for indicating occasional monoecy. Further work would be required to clarify if these observations are anomalous, perhaps due to pathology or mutation, or are characteristic.

**Table 3.** Influence of diameter and sex on stem damage based on negative binomial GLMs. Only female and male trees with diameter > 10 cm were considered

	$\chi^2$	df	<i>P</i>
<b>Debarking</b>			
DBH	7.4	1	<b>0.007</b>
Tree sex	0.003	1	0.958
DBH × tree sex	1.2	1	0.283
<b>Top-breaking</b>			
DBH	49.7	1	<b>&lt;0.001</b>
Tree sex	0.1	1	0.750
DBH × tree sex	0.1	1	0.808
<b>Browsing</b>			
DBH	36.6	1	<b>&lt;0.001</b>
Tree sex	5.2	1	<b>0.022</b>
DBH × Tree sex	0.003	1	0.955
<b>Leaning</b>			
DBH	1.0	1	0.321
Tree sex	0.2	1	0.692
DBH × tree sex	0.9	1	0.332
<b>Any sign of stem damage</b>			
DBH	36.1	1	<b>&lt;0.001</b>
Tree sex	1.4	1	0.232
DBH × tree sex	<0.001	1	0.996

Note: Significant values ( $P < 0.05$ ) are highlighted in bold.

Though Bwindi includes substantial areas of open forest (canopy cover < 50%), *M. holstii* is associated with more closed locations (c.f. Hawthorne's Shade-bearers, Hawthorne 1996, Sheil *et al.* 2006) but avoids (or is less readily detected in) forest with the highest basal area (Figure 6). Furthermore, young trees tend to be aggregated near mother plants (see Table 2). Despite the higher abundance of adult trees at lower elevations, saplings around mother trees appeared more abundant at higher elevations (Figure 5a)—we speculate that this pattern may result from more effective seedling establishment at higher elevations due to greater densities of suitable seed dispersers (Mugerwa *et al.* 2013).

### Sex ratios

We found a female-biased secondary sex ratio for *M. holstii*. Such unbalanced sex ratios may reflect the adaptive consequences of differences in male and female life histories (Tonnabel *et al.* 2017) or may reflect relative differences in detection. In many plot-based studies of dioecious trees, small-sized non-fertile stems have dominated, making assessments of sex ratios dependent on a minority of fertile stems (but see, Queenborough *et al.* 2007, Gao *et al.* 2012, Thomas & Lafrankie 1993). Our approach, using the Distance Method, focuses greater attention on larger stems with the majority being fertile (~ 76%). The earlier maturation observed for males versus females in our study (see Figure 2b) is common in dioecious species and is normally explained by lower reproductive costs (Opler & Bawa 1978). Though a male biased ratio only arises for stems smaller than 10 cm dbh in our study, such maturation differences may generate overall male-biased secondary sex ratios

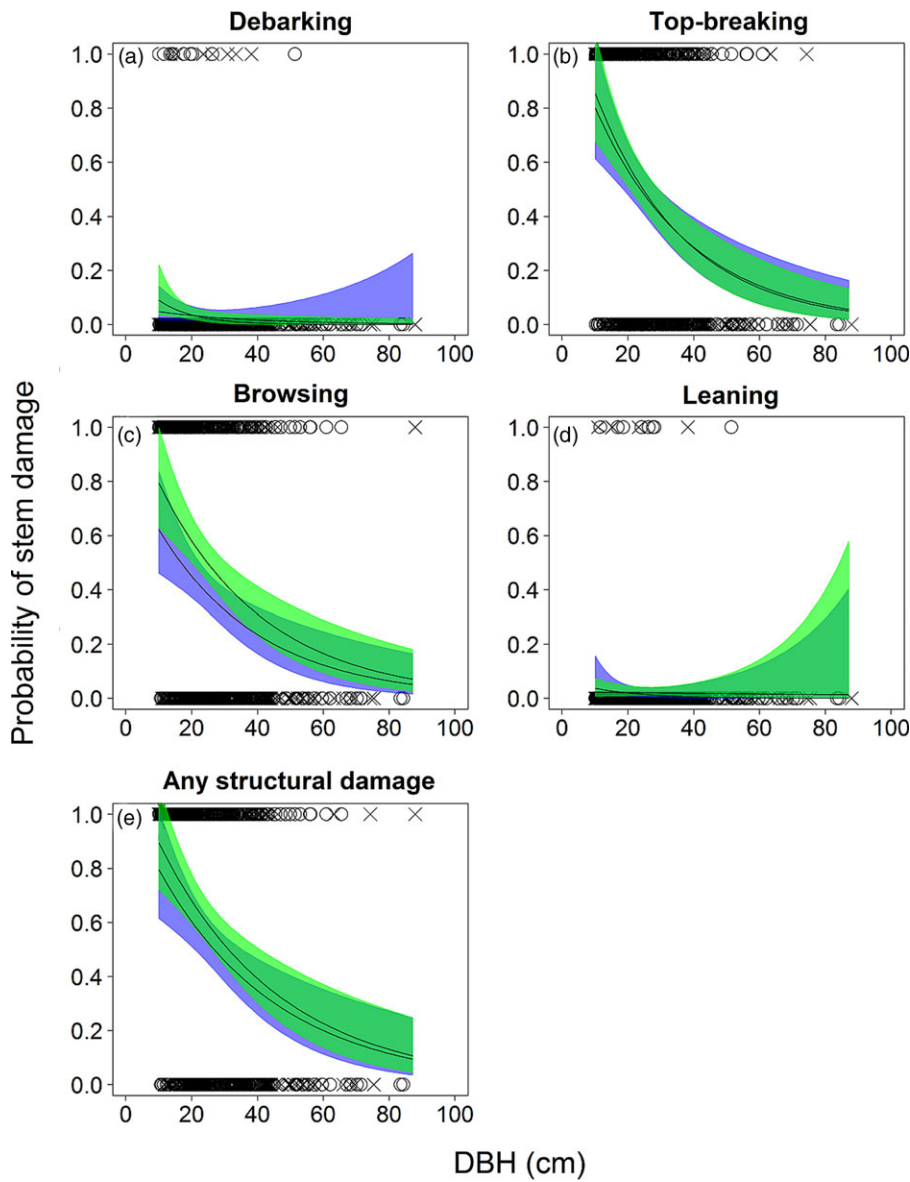
in some species when larger adult stems are poorly represented (Gao *et al.* 2012, Queenborough *et al.* 2007, Ueno *et al.* 2007).

In our study, non-fertile stems predominate at small sizes and remain sufficiently common at larger sizes that a balanced primary ratio remains plausible. The greater representation of females at larger sizes (> 10 cm dbh) likely reflects phenology with female trees typically bearing recognisable flowers or fruits for a greater period than male trees bear flowers. Drawing on observations made in the same forest, we note that the fruiting and flowering phenology of 12 female (20.1 to 61.0 cm dbh) and 3 male *M. holstii* (16.3 to 35.6 cm dbh) trees were assessed with monthly (but incomplete) observations spanning 8 years (September 2004–September 2012, see, Adamescu *et al.* 2018). These observations indicated that females typically lack fertile structures, revealing their sex, less frequently than males (11% versus 27% of observations, respectively, while mean values for October–March, when our survey was conducted, are 13% versus 36%, and the ratios for these same months in the specific year of the study were 7% versus 14%). These limited observations suggest that larger infertile trees are approximately twice as likely to be male as female, which is consistent with a balanced primary sex ratio underlying our survey data (i.e., assuming two out of three non-fertile trees are male gives a similar count for each sex, 480–490 individuals > 5 cm dbh).

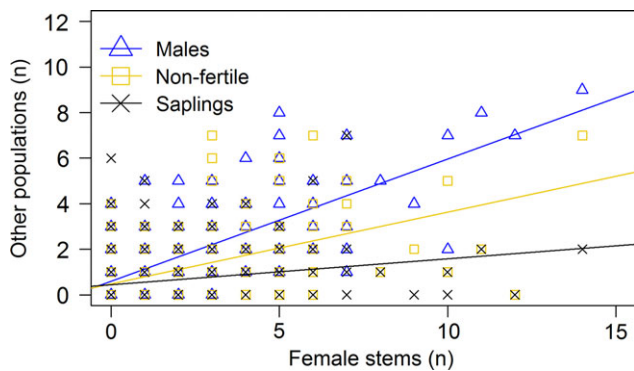
Greater female representation at lower elevations, as seen in our data, has been observed for other dioecious species in various contexts (e.g., Garbarino *et al.* 2015, Grant & Mitton 1979, Ortiz *et al.* 2002, Petry *et al.* 2016). Interestingly, this tendency for female versus male function to increase at lower versus higher elevations has been seen for flower ratios on monoecious taxa too (Vélez-Mora *et al.* 2020). This pattern is generally attributed to less favourable conditions constraining female functions more severely than male (Cox 1981). In our study, both the frequency of fruit removal and tree damage may also play a role: complete fruit removal prevents a tree being allocated a sex, while any associated increase in canopy breakage reduces the resources that a tree can invest in producing fruit. Thus, female trees may fruit over a more extended period—and thus be more likely to be recorded as female versus infertile—at lower elevations in Bwindi in part because of greater investment in fruiting and in part due to a lower intensity of large herbivore activity and associated fruit removal and damage at these locations (e.g., for elephants, see, Mugerwa *et al.* 2013, Ssali *et al.* 2013).

### Size and damage

Damage was common on both sexes but more frequent and severe on females. This is unlikely to be an artefact of our method as we would expect more damaged trees (being incomplete and thus less visible) to be less detected than less damaged stems. Studies of 'artificial seedlings' in Bwindi (an area near Ruhija and overlapping our Landscape C) show that mean yearly damage per 'seedling' was  $59.5 \pm \text{SE } 2.3\%$  with most,  $45.8 \pm 2.1\%$ , due to vertebrates (Ssali *et al.* 2019). While we cannot identify the various sources of damage to larger trees with certainty, our observations suggest that large mammals are a major cause, unlike the case with 'artificial seedlings', the animals may be attracted by these palatable food plants for both their foliage and their fruits. We know that elephants push down *M. holstii* stems while browsing (Ssali *et al.* 2013), while ripe fruits attract attention from elephants and other large mammals such as gorillas and chimpanzees (Stanford & Nkurunungi 2003) that sometimes break stems and branches while feeding (Neufuss *et al.* 2019). *M. holstii* fruit draw particular attention from various larger mammals that can and do



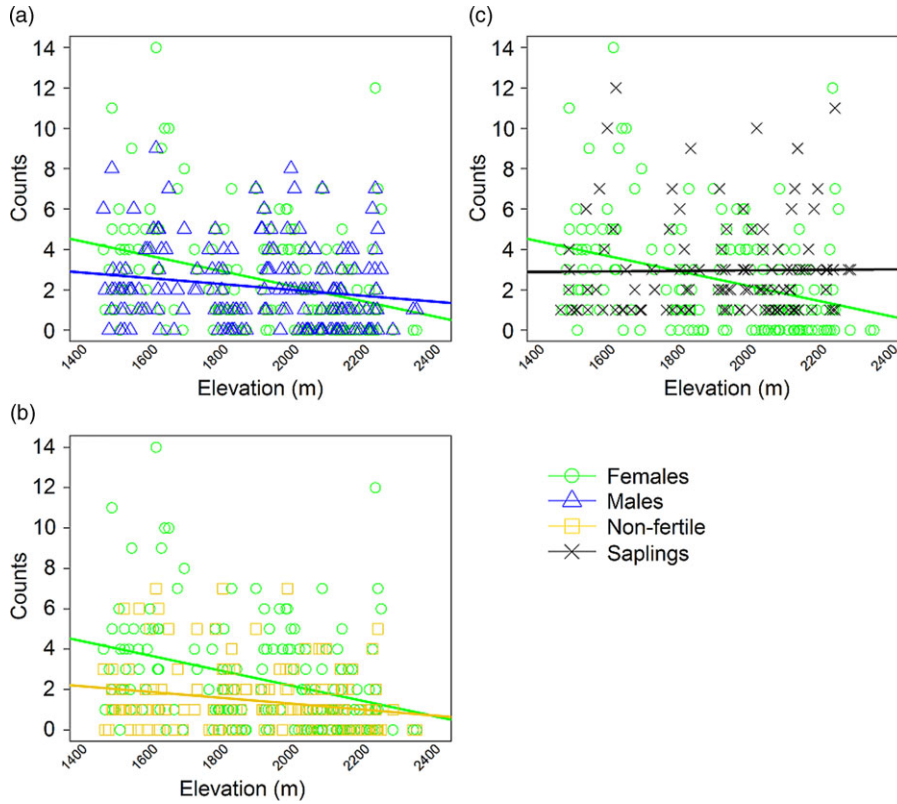
**Figure 3.** Per-stem likelihood of a *M. holstii* tree being damaged versus diameter (dbh) for each tree sex. Females are denoted by open circles (and green shading) and males by crosses (and blue shading). Prediction lines and 95% confidence intervals are based on coefficients of negative binomial GLMs (see Table 2).



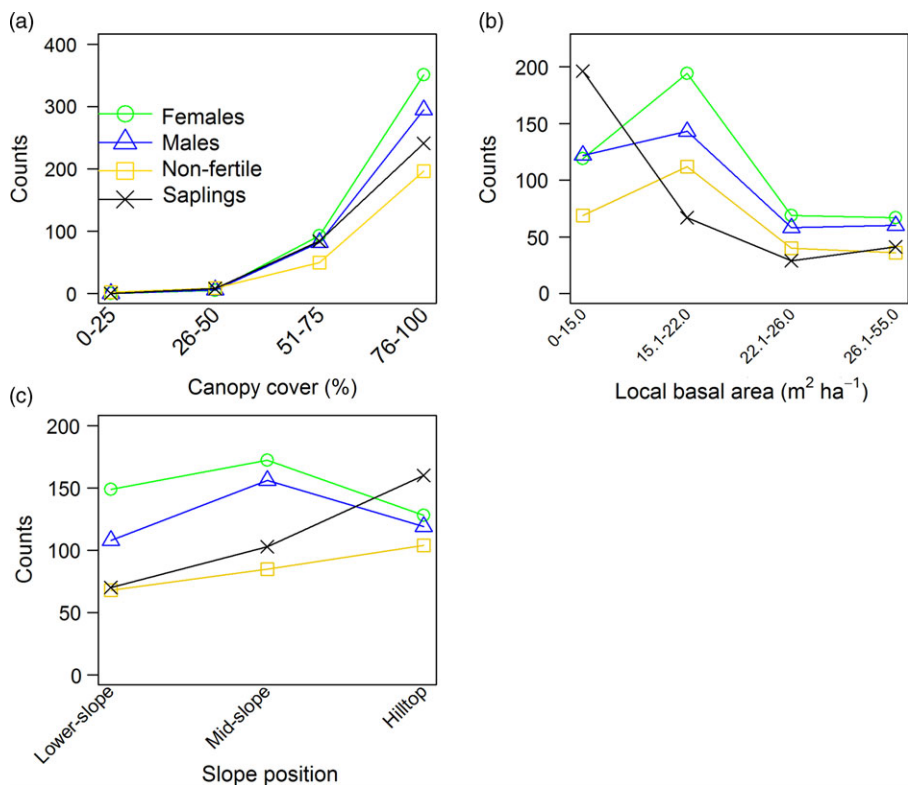
**Figure 4.** Association between females and other populations of *M. holstii* (detected males dbh > 5 cm, non-fertile individuals dbh > 5 cm and saplings dbh ≥ 0.3 cm ≤ 5 cm) for all three landscapes combined. Each point is the sum of detected stems within a 200 m-transect segment. The tested relationships were positive and highly significant (females versus males: Spearman rank correlation,  $\rho = 0.68$ ,  $n = 240$ ,  $P < 0.001$ ; females versus saplings:  $\rho = 0.35$ ,  $n = 240$ ,  $P < 0.001$ ).

cause damage to these trees—thus impacting females in particular. We note that *M. holstii* stems are hollow and weak for their size when compared to other species of trees in the same region. As seen in other forests where elephant damage is observed, severe damage becomes less frequent as stems reach larger sizes, crown accessibility declines and stem strength increases (Sheil & Salim 2004).

Our observations for *M. holstii* thus contrast with generalisations from other biomes suggesting that female dioecious plants experience less damage from herbivores than do males—a pattern typically explained in terms of differences in defence and palatability (Jing & Coley 1990, Obeso 2002, Tonnabel *et al.* 2017). We note that while the foliage of both sexes of *M. holstii* attracts large herbivores, we remain unsure about differences in palatability. We could envisage female trees being worse or better defended than males due to the differing investments made in reproduction. For example, females may plausibly have fewer resources available to invest in defence or may have evolved to grow slower and be better-defended compared to males. In any case, we are confident



**Figure 5.** Number of detected females (a), males (b), non-fertile trees (c) and saplings of *M. holstii* versus (a-c) mean elevation for each 200 m-transect segment.



**Figure 6.** Number of detected females, males, non-fertile trees and saplings of *M. holstii* in each 200 m-transect-segments versus canopy cover (a), local basal-area (b) and slope position (c). Tested relationships are as follows: canopy cover (a) for females  $\chi^2 = 471.3, P < 0.001$  at A;  $\chi^2 = 192.3, P < 0.001$  at B;  $\chi^2 = 76.9, P < 0.001$  at C;  $\chi^2 = 725.8, P < 0.001$  in all landscapes; males:  $\chi^2 = 332.6, P < 0.001$  at A;  $\chi^2 = 198.2, P < 0.001$  at B;  $\chi^2 = 79.8, P < 0.001$  at C;  $\chi^2 = 596.5, P < 0.001$  in all landscapes; non-fertile trees:  $\chi^2 = 253.5, P < 0.001$  at A;  $\chi^2 = 128.9, P < 0.001$  at B;  $\chi^2 = 20.2, P < 0.001$  at C;  $\chi^2 = 381.2, P < 0.001$  in all landscapes; saplings:  $\chi^2 = 235.8, P < 0.001$  at A;  $\chi^2 = 158.9, P < 0.001$  at B;  $\chi^2 = 72.7, P < 0.001$  at C;  $\chi^2 = 450.2, P < 0.001$  in all landscapes, local basal area (b) for 37.4,  $P < 0.001$  across all landscapes.



that the role of the large fleshy fruit is to attract animals that can disperse the seeds and some of the difference in damage seen among trees results from this fruit-related attention.

The situation with *M. holstii* has similarities to that of the African dioecious savanna trees *Sclerocarya birrea* (A. Rich.) Hochst (Anacardiaceae). Fruiting females of this species attract damage from elephants and tend to possess shorter, stockier stems and less ramified branches than males suggesting adaptations to resist such injuries (Hemborg & Bond 2007). From our data on *M. holstii*, we are unable to distinguish with confidence if females being typically shorter than males at larger diameters was an inherent character, or a consequence of repeated damage, or might reflect both. As a suggestion for future work, we note this might be more easily clarified by also considering locations where large frugivores are scarce or absent thus reducing associated damage. In any case, both tree species, *M. holstii* and *S. birrea*, represent cases where fruit or seed eating animals cause greater damage to female plants (see also, e.g., Avila-Sakar & Romanow 2012, Romero-Pérez *et al.* 2020, van Blerk *et al.* 2017).

The evolutionary context for these trees in terms of the nature, intensity and variation in herbivore-related damage may not be well represented by current conditions. The rates of animal damage seen in Bwindi may differ from those under which *M. holstii* evolved. We suspect that while some variation will always arise, much larger differences have likely arisen in recent centuries as densities of larger fauna, such as elephants, have fluctuated far outside prehistoric norms as populations have been eliminated from some forests and restricted to others (Sheil 2020). The consequences of variable conditions on dioecious populations remain an important subject of research (Bialic-Murphy *et al.* 2020, Tonnabel *et al.* 2017).

### Stem densities and distributions

Our observations show that male and female *M. holstii* favour similar environments (Figure 4). Mature stems (male and female) decreased significantly with elevation across all landscapes (Figure 5a).

### Conclusions

Male and female *M. holstii* trees are similarly distributed within the landscape. The populations indicate a female-biased secondary sex ratio, while a close to balanced primary ratio appears likely. Among larger stems, female trees tend to be shorter and more frequently damaged than males of similar diameters. Our observations of *M. holstii* add to a handful of studies of dioecious plants in which female plants suffer greater damage than males.

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**Competing interests.** The authors have no competing interests to declare.

### References

- Adamescu GS, Plumptre AJ, Abernethy KA, Polansky L, Bush ER, Chapman CA, Shoo LP, Fayolle A, Janmaat KRL, Robbins MM, Ndangalasi HJ, Cordeiro NJ, Gilby IC, Wittig RM, Breuer T, Hockemba MB-N, Sanz CM, Morgan DB, Pusey AE, Mugerwa B, Gilagiza B, Tutin C, Ewango CEN, Sheil D, Dimoto E, Baya F, Bujo F, Ssali F, Dikangadissi J-T, Jeffery K, Valenta K, White L, Masozera M, Wilson ML, Bitariho R, Ndolo Ebika ST, Gourlet-Fleury S, Mulindahabi F and Beale CM (2018) Annual cycles are the most common reproductive strategy in African tropical tree communities. *Biotropica* **50**, 418–430.
- Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control* **19**, 716–723.
- Ashman T-L (2002) The role of herbivores in the evolution of separate sexes from hermaphroditism. *Ecology* **83**, 1175–1184.
- Avila-Sakar G and Romanow CA (2012) Divergence in defence against herbivores between males and females of dioecious plant species. *International Journal of Evolutionary Biology* **2012**, 897157.
- Barrett SC and Hough J (2013) Sexual dimorphism in flowering plants. *Journal of Experimental Botany* **64**, 67–82.
- Bawa KS (1980) Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* **11**, 15–39.
- Berg CC (1978) Cecropiaceae a new family of the Urticales. *Taxon* **27**, 39–44.
- Bialic-Murphy L, Heckel CD, McElderry RM and Kalisz S (2020) Deer indirectly alter the reproductive strategy and operational sex ratio of an unpalatable forest perennial. *The American Naturalist* **195**, 56–69.
- Bitariho R, Sheil D and Eilu G (2016) Tangible benefits or token gestures: does Bwindi impenetrable National Park's long established multiple use programme benefit the poor? *Forests, Trees and Livelihoods* **25**, 16–32.
- Buckland ST, Anderson DR, Burnham KP, Laake JL, Borchers DL and Thomas L (2001) *Introduction to Distance Sampling: Estimating Abundance of Biological Populations*. Oxford: Oxford University Press.
- Charlesworth D and Charlesworth B (1987) The Effect of investment in attractive structures on allocation to male and female functions in plants. *Evolution* **41**, 948–968.
- Chen L, Zhang S, Zhao H, Korpelainen H and Li C (2010) Sex-related adaptive responses to interaction of drought and salinity in *Populus yunnanensis*. *Plant, Cell & Environment* **33**, 1767–1778.
- Cornelissen T and Stiling P (2005) Sex-biased herbivory: a meta-analysis of the effects of gender on plant-herbivore interactions. *Oikos* **111**, 488–500.
- Cox PA (1981) Niche partitioning between sexes of dioecious plants. *The American Naturalist* **117**, 295–307.
- De Ruiter G (1976) Revision of the genera *Myrianthus* and *Musanga* (Moraceae). *Bulletin du Jardin Botanique National de Belgique* **46**, 471–510.
- Dias FS, Miller DL, Marques TA, Marcelino J, Caldeira MC, Orestes Cerdeira J and Bugalho MN (2016) Conservation zones promote oak regeneration and shrub diversity in certified Mediterranean oak woodlands. *Biological Conservation* **195**, 226–234.
- Fedorowicz K, Koricheva J, Baker SC, Lindenmayer DB, Palik B, Rosenvald R, Beese W, Franklin JF, Kouki J and Macdonald E (2014) Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology* **51**, 1669–1679.
- Field DL, Pickup M and Barrett SC (2013) Comparative analyses of sex-ratio variation in dioecious flowering plants. *Evolution* **67**, 661–672.
- Flesch AD, Murray IW, Gickhorn JM and Powell BF (2019) Application of distance sampling for assessing abundance and habitat relationships of a rare Sonoran Desert cactus. *Plant Ecology* **220**, 1029–1042.
- Galfrascoli GM and Calviño A (2020) Secondary sexual dimorphism in a dioecious tree: a matter of inter-plant variability? *Flora* **266**, 151595.
- Gao J, Queenborough S and Chai J (2012) Flowering sex ratios and spatial distribution of dioecious trees in a South-East Asian seasonal tropical forest. *Journal of Tropical Forest Science* **24**, 517–527.
- Garbarino M, Weisberg PJ, Bagnara L and Urbinati C (2015) Sex-related spatial segregation along environmental gradients in the dioecious conifer, *Taxus baccata*. *Forest Ecology and Management* **358**, 122–129.

- Gauquelin T, Bertaudière-Montès A, Badri W and Montès N** (2002) Sex ratio and sexual dimorphism in mountain dioecious thuriferous juniper (*Juniperus thurifera* L., Cupressaceae). *Botanical Journal of the Linnean Society* **138**, 237–244.
- Givnish TJ** (1982) Outcrossing versus ecological constraints in the evolution of dioecy. *American Naturalist* **119**, 849–865.
- Grant MC and Mitton JB** (1979) Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. *Evolutionary Anthropology* **33**, 914–918.
- Hawthorne WD** (1996) Holes and the sums of parts in Ghanaian forest: regeneration, scale and sustainable use. *Proceedings of the Royal Society of Edinburgh* **104B**, 75–176.
- Hemborg ÅM and Bond WJ** (2007) Do browsing elephants damage female trees more? *African Journal of Ecology* **45**, 41–48.
- Hultine KR, Grady KC, Wood TE, Shuster SM, Stella JC and Whitham TG** (2016) Climate change perils for dioecious plant species. *Nature Plants* **2**, 1–8.
- Iverson S** (1991) The Usambara Mountains, ne Tanzania: phytogeography of the vascular plant flora. *Acta Universitatis Upsaliensis- Symbolae Botnicae Upsaliensis* **29**, 1–234.
- Jing SW and Coley PD** (1990) Dioecy and herbivory: the effect of growth rate on plant defense in *Acer negundo*. *Oikos* **58**, 369–377.
- Juvany M and Munné-Bosch S** (2015) Sex-related differences in stress tolerance in dioecious plants: a critical appraisal in a physiological context. *Journal of Experimental Botany* **66**, 6083–6092.
- Katende A, Birnie A and Tengnäs B** (1995) *Useful Trees and Shrubs for Uganda*. Nairobi: Regional Soil Conservation Unit, Swedish International Development Cooperation Agency.
- Kissa DO and Sheil D** (2012) Visual detection based distance sampling offers efficient density estimation for distinctive low abundance tropical forest tree species in complex terrain. *Forest Ecology and Management* **263**, 114–121.
- Marques TA, Thomas L, Fancy SG and Buckland ST** (2007) Improving estimates of bird density using multiple- covariate distance sampling. *The Auk* **124**, 1229–1243.
- Matsushita M, Takao M and Makita A** (2016) Sex-different response in growth traits to resource heterogeneity explains male-biased sex ratio. *Acta Oecologica* **75**, 8–14.
- Miller DL, Burt ML, Rextad EA and Thomas L** (2013) Spatial models for distance sampling data: recent developments and future directions. *Methods in Ecology and Evolution* **4**, 1001–1010.
- Morelato L** (2004) Phenology, sex ratio, and spatial distribution among dioecious species of *Trichilia* (Meliaceae). *Plant Biology* **6**, 491–497.
- Mugerwa B, Sheil D, Ssekiranda P, Heist M and Ezuma P** (2013) A camera trap assessment of terrestrial vertebrates in Bwindi Impenetrable National Park, Uganda. *African Journal of Ecology* **51**, 21–31.
- Neufuss J, Robbins M. M, Baeumer J, Humle T and Kivell TL** (2019) Manual skills for food processing by mountain gorillas (*Gorilla beringei beringei*) in Bwindi Impenetrable National Park, Uganda. *Biological Journal of the Linnean Society* **127**, 543–562.
- Obeso JR** (2002) The costs of reproduction in plants. *New Phytologist* **155**, 321–348.
- Ohya I, Nanami S and Itoh A** (2017) Dioecious plants are more precocious than cosexual plants: a comparative study of relative sizes at the onset of sexual reproduction in woody species. *Ecology and Evolution* **7**, 5660–5668.
- Opler PA and Bawa KS** (1978) Sex ratios in tropical forest trees. *Evolution* **32**, 812–821.
- Ortiz PL, Arista M and Talavera S** (2002) Sex ratio and reproductive effort in the dioecious *Juniperus communis* subsp. *alpina* (suter) čelak. (cupressaceae) along an altitudinal gradient. *Annals of Botany* **89**, 205–211.
- Petry WK, Soule JD, Iler AM, Chicas-Mosier A, Inouye DW, Miller TE and Mooney KA** (2016) Sex-specific responses to climate change in plants alter population sex ratio and performance. *Science* **353**, 69–71.
- Prentout D, Razumova O, Rhoné B, Badouin H, Henri H, Feng C, Käfer J, Karlov G and Marais G** (2020) An efficient RNA-seq-based segregation analysis identifies the sex chromosomes of *Cannabis sativa*. *Genome Research* **30**, 164–172.
- Queenborough SA, Burslem DF, Garwood NC and Valencia R** (2007) Determinants of biased sex ratios and inter-sex costs of reproduction in dioecious tropical forest trees. *American Journal of Botany* **94**, 67–78.
- Queenborough SA, Humphreys AM and Valencia R** (2013) Sex-specific flowering patterns and demography of the understorey rain forest tree *Iryanthera hostmannii* (myristicaceae). *Tropical Conservation Science* **6**, 637–652.
- R-Core-Team** (2020) R: A Language and Environment for Statistical Computing (online).
- Randriamanana TR, Nissinen K, Moilanen J, Nybakken L and Julkunen-Tiitto R** (2015) Long-term UV-B and temperature enhancements suggest that females of *Salix myrsinifolia* plants are more tolerant to UV-B than males. *Environmental and Experimental Botany* **109**, 296–305.
- Renner SS** (2014) The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany* **101**, 1588–1596.
- Retuerto R, Sánchez Vilas J and Varga S** (2018) Sexual dimorphism in response to stress. *Environmental and Experimental Botany* **146**, 1–4.
- Romero-Pérez A, Gómez-Acevedo S, Cano-Santana Z and Hernández-Cumplido J** (2020) *Sex-biased herbivory and its effects on tritrophic interactions*. In Núñez-Farfán J and Valverde PL (eds), *Evolutionary Ecology of Plant-Herbivore Interaction*. Cham: Springer International Publishing, pp. 173–189.
- Schmidt JH and Deacy WW** (2021) Using spatial distance sampling models to optimize survey effort and address violations of the design assumption. *Ecological Solutions and Evidence* **2**, e12091.
- Sheil D** (2012) The impenetrable challenge of an overwhelming understorey. *Bulletin of the British Ecological Society* **43**, 45–47.
- Sheil D** (2020). Dangerous giants?—Large herbivores, forest feedbacks and climate tipping points. *Russian Journal of Ecosystem Ecology* **5**, 1–33.
- Sheil D and Salim A** (2004) Forest tree persistence, elephants, and stem scars. *Biotropica* **36**, 505–521.
- Sheil D, Salim A, Chave JR, Vanclay J and Hawthorne WD** (2006) Illumination-size relationships of 109 coexisting tropical forest tree species. *Journal of Ecology* **94**, 494–507.
- Sinclair J. P, Emlen J and Freeman D** (2012) Biased sex ratios in plants: theory and trends. *The Botanical Review* **78**, 63–86.
- Ssali F, Moe SR and Sheil D** (2019) Damage to artificial seedlings across a disturbed Afromontane forest landscape. *Biotropica* **2019**, 652–663.
- Ssali F, Sheil D and Nkurunungi JB** (2013) How selective are elephants as agents of forest tree damage in Bwindi Impenetrable National Park, Uganda? *African Journal of Ecology* **51**, 55–65.
- Stanford CB and Nkurunungi JB** (2003) Behavioral ecology of sympatric chimpanzees and gorillas in Bwindi impenetrable National Park, Uganda: diet. *International Journal of Primatology* **24**, 901–918.
- Thomas SC and Lafrankie JV** (1993) Sex, size, and interyear variation in flowering among dioecious trees of the Malayan rain-forest. *Ecology* **74**, 1529–1537.
- Thomson JD and Brunet J** (1990) Hypotheses for the evolution of dioecy in seed plants. *Trends in Ecology & Evolution* **5**, 11–16.
- Tognetti R** (2012) Adaptation to climate change of dioecious plants: does gender balance matter? *Tree Physiology* **32**, 1321–1324.
- Tonnabel J, David P and Pannell JR** (2017) Sex-specific strategies of resource allocation in response to competition for light in a dioecious plant. *Oecologia* **185**, 675–686.
- Ueno N, Suyama Y and Seiwa K** (2007) What makes the sex ratio female-biased in the dioecious tree *Salix sachalinensis*? *Journal of Ecology* **95**, 951–959.
- van Blerk JJ, West AG and Midgley JJ** (2017) Restio culm felling is a consequence of pre-dispersal seed predation by the rodent *Rhabdomys pumilio* in the Fynbos. *South African Journal of Botany* **112**, 123–127.
- Vélez-Mora D, Ramón P, Vallejo C, Romero A, Duncan D and Quintana-Ascencio PF** (2020) Environmental drivers of femaleness of an inter-Andean monoecious shrub. *Biotropica* **53**, 17–27.

Wang J, Zhang C, Zhao X and Gadow KV (2013) Limitations to reproductive success in the dioecious tree *Rhamnus davurica*. *PLOS One* **8**, e81140.

Wild RG and Mutebi J (1996) *Conservation through Community Use of Plant Resources. People and Plants Working Paper*. Paris: UNESCO.

Wu Z-Y, Monro AK, Milne RI, Wang H, Yi T-S, Liu J and Li D-Z (2013) Molecular phylogeny of the nettle family (Urticaceae) inferred from

multiple loci of three genomes and extensive generic sampling. *Molecular Phylogenetics and Evolution* **69**, 814–827.

Zhang Q, Onstein RE, Little SA and Sauquet H (2019) Estimating divergence times and ancestral breeding systems in *Ficus* and Moraceae. *Annals of Botany* **123**, 191–204.

### Appendix 1:

Height and diameter (dbh) relationship for male and female *M. holstii* trees in each of the sampled landscapes based on Gamma GLMs with log link. Significant values ( $P < 0.05$ ) are highlighted in bold. Height was included as a response variable. Details of the GLMs are provided in Appendix 2.

	All trees included			Damaged trees excluded			Multi-stemmed trees excluded		
	$\chi^2$	Df	<i>P</i>	$\chi^2$	Df	<i>P</i>	$\chi^2$	Df	<i>P</i>
a) Without sex									
Landscape A									
dbh	66.4	1	<0.001	13.2	1	<0.001	42.4	1	<0.001
Landscape B									
dbh	53.0	1	<0.001	22.2	1	<0.001	47.4	1	<0.001
Landscape C									
dbh	23.9	1	<0.001	0.26	1	0.612	18.4	1	<0.001
All landscapes combined									
dbh	147.3	1	<0.001	26.2	1	<0.001	113.1	1	<0.001
b) With sex									
Landscape A									
dbh	66.2	1	<0.001	13.2	1	<0.001	42.9	1	<0.001
Tree sex	0.1	1	0.819	0.5	1	0.485	0.8	1	0.388
Landscape B									
dbh	52.2	1	<0.001	22.0	1	<0.001	46.3	1	<0.001
Tree sex	1.1	1	0.304	0.01	1	0.927	0.6	1	0.459
Landscape C									
dbh	23.2	1	<0.001	0.4	1	0.512	18.8	1	<0.001
Tree sex	5.0	1	0.026	1.0	1	0.312	2.4	1	0.119
All landscapes combined									
dbh	146.2	1	<0.001	26.0	1	<0.001	112.4	1	<0.001
Tree sex	1.8	1	0.177	0.6	1	0.440	3.1	1	0.077

**Appendix 2:**

Outputs from Gamma GLMs (log link) on height and diameter (dbh) relationship between male and female *M. holstii* trees in each of the sampled landscapes. Height was included as a response variable. Significant values ( $P < 0.05$ ) are highlighted in bold.

	All trees included			Damaged trees excluded			Multi-stemmed trees excluded		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
Without sex									
<i>Landscape A</i>									
Intercept	0.14	0.002	<0.001	0.13	0.003	<0.001	0.13	0.003	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
<i>Landscape B</i>									
Intercept	0.14	0.002	<0.001	0.13	0.01	<0.001	0.14	0.003	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
<i>Landscape C</i>									
Intercept	0.13	0.004	<0.001	0.12	0.004	<0.001	0.13	0.005	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
All landscapes combined									
Intercept	0.13	0.002	<0.001	0.13	0.002	<0.001	0.13	0.002	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
With sex									
<i>Landscape A</i>									
Intercept (male)	0.14	0.003	<0.001	0.13	0.003	<0.001	0.13	0.003	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
Tree sex (female)	0.001	0.002	0.819	-0.004	0.002	0.088	0.002	0.002	0.388
<i>Landscape B</i>									
Intercept (male)	0.13	0.003	<0.001	0.13	0.01	<0.001	0.14	0.003	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
Tree sex (female)	0.002	0.002	0.305	0.01	0.004	0.191	0.002	0.002	0.460
<i>Landscape C</i>									
Intercept (male)	0.12	0.004	<0.001	0.12	0.004	<0.001	0.12	0.01	<0.001
dbh	0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
Tree sex (female)	0.01	0.003	0.028	0.01	0.003	0.013	0.01	0.004	0.123
All landscapes combined									
Intercept (male)	0.13	0.002	<0.001	0.13	0.002	<0.001	0.13	0.002	<0.001
dbh	-0.001	0.001	<0.001	-0.001	0.0001	<0.001	-0.001	0.0001	<0.001
Tree sex (female)	0.002	0.001	0.177	0.001	0.002	0.515	0.003	0.002	0.077

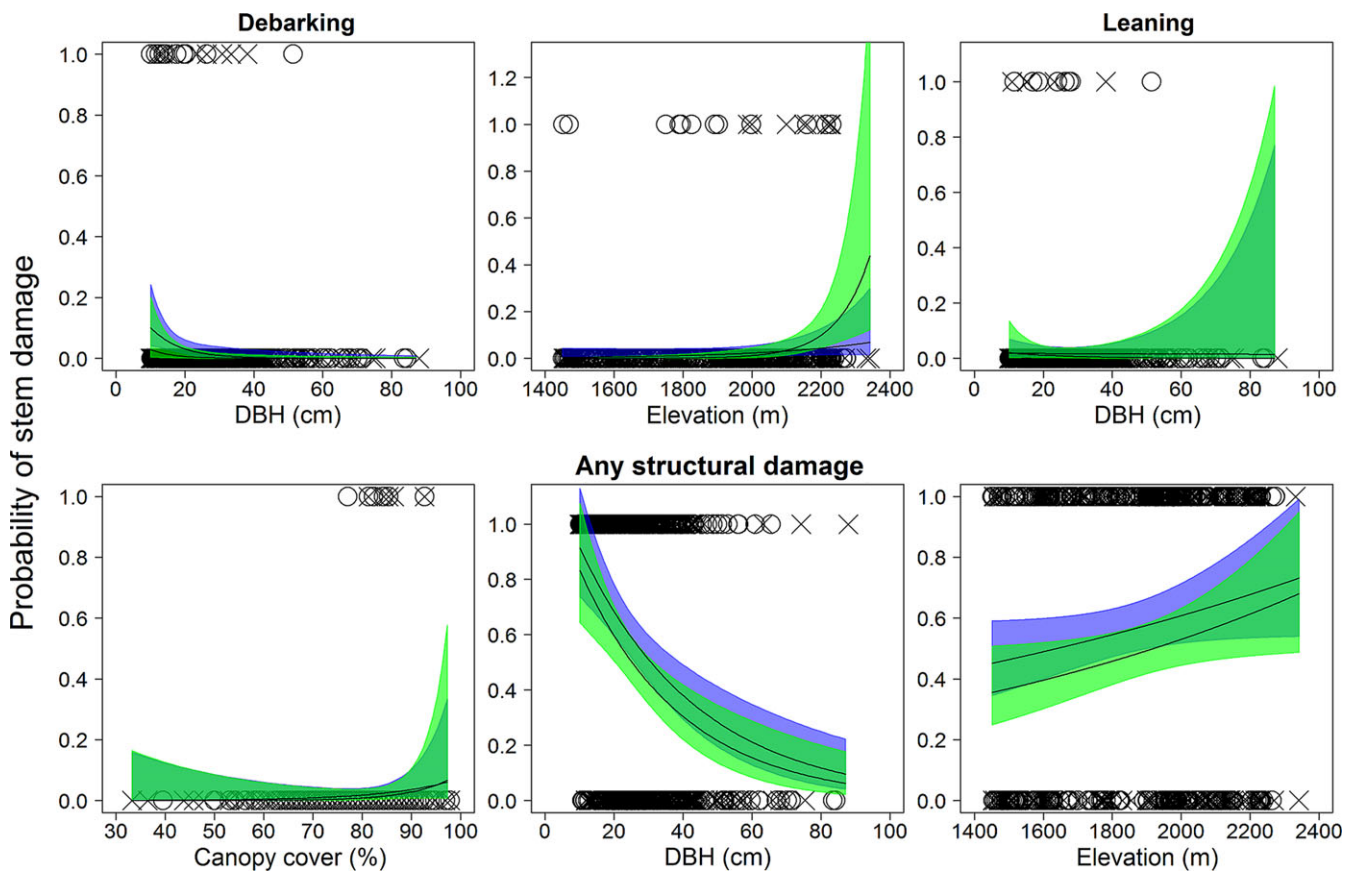


**Appendix 3:**

Influence of location on the occurrence (with shaded 95% confidence intervals) of stem damage based on negative binomial GLMs. Each of these five models included seven single factor variables. Significant values ( $P < 0.05$ ) are highlighted in bold. Predicted effects of the significant variables are presented graphically in Appendix 4.

	df	Debarking		Top-breaking		Browsing		Leaning		Any sign of stem damage	
		$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
dbh	1	9.6	<b>0.002</b>	46.1	<b>&lt;0.001</b>	32.5	<b>&lt;0.001</b>	1.1	0.286	34.2	<b>&lt;0.001</b>
Tree sex	1	0.1	0.784	0.4	0.523	7.0	<b>0.008</b>	0.3	0.611	2.6	0.107
Elevation	1	10.0	<b>0.002</b>	2.2	0.134	1.7	0.189	0.2	0.677	5.8	<b>0.016</b>
Edge distance	1	0.01	0.918	3.2	0.076	3.6	0.057	0.9	0.353	2.9	0.088
Canopy cover	1	0.003	0.959	0.01	0.909	0.3	0.571	5.0	<b>0.025</b>	0.4	0.508
Local basal area	1	0.6	0.456	1.4	0.242	2.1	0.147	1.0	0.327	0.6	0.437
Slope position	2	0.5	0.793	0.3	0.847	1.9	0.390	0.1	0.947	1.2	0.547

**Appendix 4:**



Per-stem likelihood (with shaded 95% confidence intervals) of stem damage based on negative binomial GLMs of the significant predictor variables (see Appendix 3). Females are denoted by open circles (and green shading) and males by crosses (and blue shading).