Twelve-year changes in palm populations from a tropical lowland forest in the Philippines

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Abstract
Arecaceae (Palmae) is an ecologically and economically important family characteristic of the vegetation in tropical and subtropical regions, with at least 125 species occurring in the Philippines, most of them endemics. We monitored changes in stem density, mortality and recruitment of palm populations for 12 years within a 16-ha Forest Dynamic Plot located in northern Luzon, the Philippines. We recorded a total of 4060 stems, dominated by Pinanga insignis (46%) and P. maculata (34%), followed by Caryota cumingii (19%), and a few stems (< 1%) of Orania decipiens and Areca whitfordii. Half (51%) of the initially recorded stems in the 2004 census died by the time of the 2016 census, while 1086 (36%) additional stems were recorded in the same period. Overall palm population declined with the decreasing populations of P. insignis and P. maculata due to higher mortality than recruitment during the 2004–2010 and 2010–2016 census intervals while C. cumingii population increased in the same period. Regarding topographic position, the stem density of P. maculata is higher in valleys > midslopes > ridges across censuses, higher in valleys and midslopes than ridges for C. cumingii across censuses, and higher in midslopes than valleys for P. insignis during the 2016 census only. Mortality and recruitment were weakly observed along topographic positions between species and across censuses. Our result presents how palm population may change within 12 years with population trends differing between species, indicating the importance of palms in understanding the population dynamics of plant communities in a fast-changing environment.

Keywords Plant demography · Endemic species · Mortality · Population dynamics · Permanent plot · Recruitment

Introduction
Palms are a diverse plant group constituting the family Arecaceae (Palmae) and one of the most ecologically and economically important species (Eiserhardt et al., 2011; Johnson, 2011). They are characteristic components of the vegetation of tropical and subtropical regions with various growth forms, ranging from understory layer species to sub-canopy and canopy layer species including climbers (Kissling et al., 2019). Palms are also one of the most speciose families in the tropics; hence, they can be considered as model species to understand patterns of plant biodiversity and distribution (Couvreur & Baker, 2013). However, the documented number of palm species (~80%) and studies are from the Neotropics and are less understood in the Afrotropics and the Asian tropics (Muscarella et al., 2020), especially in the Philippines.

The current checklist of known palms in the Philippines listed at least 125 species of mostly endemic palm species or species found only in the Philippines (Pelser et al.,
Palms are also species-rich plant groups present in various habitat types in the country (Adorador & Fernando, 2017; Fernando, 1990). Despite discoveries and addition to palm species recorded in the Philippines, there is generally a lack of studies related to their ecology, distribution, and responses to different environmental gradients, which will significantly contribute to our understanding of community assembly and population dynamics.

Studies of population dynamics help us understand how a population changes across time, as such, by monitoring mortality, recruitment, growth rates, and phenological sequences (Treurnicht et al., 2016). Results can be useful in predicting population trajectory concerning changes in climate extremes (Montúfar et al., 2011), habitat variables (Emilio et al., 2014; Queenborough et al., 2012), and anthropogenic disturbance (Galetti et al., 2006). While related population dynamics have been well studied, few studies have been presented from the Philippines, with no demographic studies conducted on palms.

Furthermore, topography is an important predictor which may represent environmental resource availability, confounding the effects of soil conditions, hydrology, wind exposure, and light availability (Eiserhardt et al., 2011; Svenning, 2001). Certain palm species are light tolerant, preferring more exposed ridges, shade-tolerant species preferring darker valleys, and generalist species appearing in all topographic positions (Salm et al., 2007; Vormisto et al., 2004). The topographic variable is, therefore, necessary to elucidate the factors determining the population dynamics of palms.

Considering the limited understanding of population dynamics in plant communities in the Philippines, especially on palms, we monitored 12-year changes in palm population within a permanent forest dynamic plot located in a tropical lowland forest in northern Luzon, the Philippines. We asked the following specific questions: (1) Do stem density, mortality, recruitment, and population growth of palms differ across the census period? (2) Do stem density, mortality and recruitment differ along topographic position? and (3) Are patterns consistent between palm species?

Methods

Study area

We conducted this study within a 16-ha (400x400 m) Palanan Forest Dynamic Plot (FDP), located in the northeastern part of Luzon Island, in the coastal town of Palanan, Isabela, Philippines (Fig. 1). The location of the plot lies under a Type IV climate classification, with an evenly distributed rainfall occurring throughout the year (Corporal-Lodangco & Leslie, 2017) and the Palanan FDP within the path of cyclones (Monoy et al., 2016). The plot is in a lowland dipterocarp forest at an
elevation between 77 and 118 m a.s.l. There have been around 340 tree species recorded within the FDP, where 40% of the species are endemic to the Philippines (Co et al., 2004).

The Palanan FDP is a member of the CTFS-ForestGEO global network of permanent forest plots (Anderson-Teixeira et al., 2015, Davies et al., 2021), where all free-standing trees with ≥ 1 cm diameter-at-breast-height (DBH) were measured, tagged, and identified. It was established in 1994 and has been re-censused in 1998, 2004, 2010, and 2016. The inclusions of palms in the Palanan FDP inventory started in the 2004 census and have been re-censused in 2010 and 2016. Planting, fencing, harvesting, and other silvicultural activities are prohibited within the FDP.

**Data analysis**

We first determined the differences in the number of stems (ha\(^{-1}\)) between each census (2004, 2010, and 2016) using a paired \(t\) test with Bonferroni adjustment for all palm stands and for each palm species. Second, we conducted another paired \(t\) test to compare annual demographic patterns (i.e. mortality, recruitment, and population growth) between 2010 data (2004–2010 census interval) and 2016 data (census interval) (2004–2010 vs. 2004–2016). Annual rates in mortality, recruitment and population growth were calculated for each census interval, for all palm stands and for each species using the demographic formulae of Condit et al., (1999) as shown in Eqs. 1–3 as follows:

\[
\text{Mortality rate} = \frac{\log(N_1) - \log(S_2)}{t} \times 100
\]

\[
\text{Recruitment rate} = \frac{\log(N_2) - \log(S_2)}{t} \times 100
\]

\[
\text{Population growth rate} = \frac{\log(N_2) - \log(N_1)}{t} \times 100
\]

where \(N_1\) and \(N_2\) represent the number of stems in time1 and time2, respectively; \(S_2\) represents the number of stems from time1 that survived until time2; and \(t\) represents the time interval between time2 and time1 (days between census midpoints to each quadrat divided by 365.25).

We then predicted the number of stems (quadrat\(^{-1}\)) and the probability of mortality and recruitment along topographic positions (valleys, midslopes, and ridges) using a general linear model (GLM) following Poisson error distribution for stem count data and binomial error distribution for binary data on mortality (1 = dead, 0 = survived) and recruitment (1 = recruit, 0 = survived). Separate GLMs were performed for each palm species in each sampling census (2004, 2010, and 2016 count data) and for each census interval (2004–2010 and 2010–2016 binary data). We tested the significance of each GLMs using a chi-square test with ANOVA type III sum of squares.

We performed all our analyses using the R statistical software v3 (R Core Team, 2019). We conducted a paired \(t\) test using the function `compare_means()` in the R package “ggpubr” (Kassambara & Kassambara, 2020). We then modelled all GLMs using the function `glm()` with a logit link function for Poisson or binomial error distribution in the R “stats” package and plotted the GLMs fitted coefficients using the R package “visreg” (Breheny & Burchett, 2017).

**Results**

A total of 4060 palm stems have been tagged and measured over the twelve-year monitoring of palms in the 16-ha Palanan FDP (Table 1). There were five species identified: *A. whitfordii* Becc., *C. cumingii* Lodd. ex Mart., *O. decipiens* Becc., *P. insignis* Becc. and *Pinanga maculata* Porte ex Lem. The most abundant palm species is *P. maculata* with 1863 (46%) stems, followed by *P. insignis* with 1397 (34%) stems and *C. cumingii* with 763 (19%) stems (Table 1). Half (51%) of the stems initially recorded in the 2004 census were dead by the 2016 census, with mortality recorded mostly

| Species                  | Census year |      |      |      |      |      |      |      |
|-------------------------|-------------|------|------|------|------|------|------|------|
|                         | 2004        | 2010 | 2016 | 2004 | 2016 | 2004 | 2016 |      |
|                         | Alive       | Alive| Recruit| Dead| Alive| Recruit| Dead| Total |
| Areca whitfordii Becc   | 2           | 2    | 0     | 0   | 0    | 0     | 0   | 2    |
| Caryota cumingii Lodd. ex Mart | 395     | 472  | 172   | 95  | 483  | 196   | 185 | 368  |
| Oramia decipiens Becc   | 29          | 32   | 5     | 2   | 26   | 1     | 7   | 8    |
| Pinanga insignis Becc    | 1100        | 1079 | 172   | 193 | 860  | 125   | 344 | 297  |
| Pinanga maculata Porte ex Lem | 1448     | 1290 | 178   | 336 | 1024 | 237   | 503 | 415  |
| **TOTAL**               | **2974**    | **2875** | **527** | **626** | **2393** | **559** | **1041** | **1086** | **1517** | **4060** |
between the 2010–2016 census interval. There are 1086 (36%) new stems recorded in the 2010 and 2016 censuses. *O. decipiens* comprised < 1% of all stems across the study and the two *A. whitfordii* stems measured in the 2004 census and still alive during the 2010 census were dead by the 2016 census. With this, we excluded *A. whitfordii* and *O. decipiens* in our preceding analysis; hence, “all stands” hereby represent *P. insignis*, *P. maculata*, and *C. cumingii*.

Stem density declined significantly throughout each census period for the *P. maculata* population, declined for all stands (all palms) and *P. insignis* populations between the 2010 and 2016 censuses, and increased for *C. cumingii* population between the 2004 and 2010 censuses (Fig. 2). The annual mortality rate for all palms increased twice as much from 2004 to 2010 compared to the 2010–2016 census intervals (Fig. 3a), while the annual recruitment rate was higher only for all stands and *P. maculata* during the same census intervals (Fig. 3b). Negative growth rates were observed for all palm species except for *C. cumingii* across censuses, which differed significantly between census intervals (Fig. 3c).

Along topographic gradients, stem density decreased from valleys–midslopes–ridges for *P. maculata* across censuses and for all stands during the 2004 census; lowest in ridges compared to valleys and midslopes for all stands and *C. cumingii* in 2010 and 2016 censuses; and lower along valleys than midslopes for *P. insignis* in the 2010 census (Fig. 4). The mortality pattern along topographic position differed only during the 2004–2010 census intervals, with increasing mortality from ridges–midslopes–valleys for all stands, higher along valleys than midslopes for *C. cumingii*, and higher along valleys than in midslopes and ridges for *P. insignis* (Fig. 5). Recruitment pattern along topographic position was observed only for *P. insignis* during the 2004–2010 census interval with higher mortality along valleys than midslopes and ridges (Fig. 5).

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Fig. 2 The number of stems (mean ± se stems ha⁻¹) for all palm species combined and for each palm species (*Caryota cumingii*, *Pinanga insignis*, *Pinanga maculata*) between census years. For all stems and for each species, a paired t test was used to compare the number of stems between 2004 (red bars), 2010 (green bars), and 2016 (blue bars) censuses. The different letter inside bars indicates significant differences between census year for each species group.

Fig. 3 Annualized demographic change (mean ± se of stems ha⁻¹) for mortality (a), recruitment (b), and population change (c) for each palm species between census intervals. A paired t test was used to compare the demographic patterns between 2004 and 2010 (red bars) and 2010–2016 (blue bars). Codes indicate statistical significance: ns is not significant; *, **, *** are significant p values at 0.05, 0.01, and > 0.001.
Fig. 4 Predicted stem density (stem quadrat$^{-1}$) of all stands and each palm species (Caryota cumingii, Pinanga insignis, and Pinanga maculata) as a function of topographic position (valley, midslope, and ridge) in Palanan FDP for each census year (2004, 2010, and 2016). The horizontal blue line with grey shades represents the model coefficient fitted with the 95% confidence intervals. Letters within each plotted coefficient indicate significant differences using the chi-square test following a Poisson error distribution for stem count in each quadrat in each census year.
Discussion

Palms of Palanan forest dynamic plot

The five species of erect palms recorded within the Palanan FDP were all native to the Philippines. *P. insignis* and *C. cumingii* are widely distributed throughout the Philippines; *P. maculata* and *A. whitfordii* occur in the eastern Luzon-Mindoro islands; and *O. decipiens* in the eastern Luzon-Mindoro-Samar-Mindanao islands (Fernando, 1990; Pelser et al., 2011). *P. insignis* is an indigenous species as it can also be found in the Sulawesi and Caroline Islands, and the
remaining four species can only be found in the Philippines (Pelser et al., 2011), highlighting the importance of Palanan FDP as home of endemic palms in the country. However, the two stems recorded for A. whitfordii during the 2004 census and still present during the 2010 census have died by the 2016 census. Considering that Palanan FDP is only a 16-ha plot, A. whitfordii might still be present as well as the likelihood of more palm species present in the study landscape, as observed in a larger study landscape in Samar island in the central Philippines, recording 50 species of mostly endemics and some species new to science (Adorador & Fernando, 2017).

With more than 4000 stems recorded across the 12-year monitoring period, palms are considered a dominant family within the Palanan FDP following families such as Dipterocarpaceae, Sapindaceae, Meliaceae, Lauraceae, and Leaceae (Co et al., 2004). There could be more palm stems with the climbing palms that were also abundant in the plot (Yap, 2010). Also, unlike trees, palm stems are measured only when their leaf sheaths are at least 1.3 m above ground though they have > 1 cm diameter under their leaf sheaths. With this, the number of palm stems in the 16-ha FDP may have been overlooked, where tree species are most abundant within the 1–5 cm diameter classes (Monoy et al., 2016), emphasizing the remarkable presence of palms in the lowland dipterocarp forest of Sierra Madre Mountain range.

These findings highlight the dominance of palms observed in other tropical regions (Couvreur & Baker, 2013; Muscarella et al., 2020).

**Temporal dynamics of palms in Palanan FDP**

Our results revealed that the overall palm population declined within the 12-year monitoring from 180 palm stems per ha in 2004 to 150 palm stems per ha in 2016. In neotropical studies, the decline in palm population is attributed to deforestation and forest fragmentation (Galetti et al., 2006), but in Palanan FDP, forest disturbance is mainly due to cyclonic events rather than anthropogenic (Yap et al., 2016). Records from Japan Meteorological Agency (JMA) Digital Typhoon website (http://www.digital-typhoon.org/) showed an increase in the number of intense cyclones (> 145 kph) that hit Palanan FDP between 2004 and 2016 that became frequent between 2010 and 2016 census interval. Although we did not directly test cyclone effects on palm demographic patterns, previous results indicated how cyclones impacted the population dynamics of trees in Palanan FDP (Monoy et al., 2016; Yap et al., 2016), in agreement with results from other cyclone impacted tropical forests (Ibanez et al., 2019).

Cyclones may have a differential effect between Pinanga spp. and C. cumingii in Palanan FDP, as census-year trends differed between species. Specifically, we found population decline for both P. maculata and P. insignis due to mortality of at least twice as much as the recruitment rate while C. cumingii showed a positive population growth rate with a high recruitment rate observed between 2010 and 2016 censuses. Cyclones caused large canopy openings in the Palanan FDP (Yap et al., 2016), which favours light-responsive species and affects shade-tolerant species. In the case of the palms in our study, Pinanga spp., being understory species, would tend to prefer shaded areas of the forest while Caryota spp., being a larger and taller species, are generally in forest gaps and forest edges; therefore, cyclones may perhaps favour C. cumingii but negatively affect P. maculata and P. insignis since forest canopy are becomingly more open due to defoliation brought by frequent cyclones in the Palanan permanent monitoring plot. This finding has been observed in previous studies, where the distribution of species, such as taller and more light tolerant palms, is found to be more abundant in forests with a more open canopy and more signs of disturbance regime (Latifah et al., 2017; Salm et al., 2007; Svenning, 2001), which agrees with the trend observed for C. cumingii from Palanan FDP.

Although there seems to be an increasing C. cumingii population across the census period, we detected a lower population growth rate during the 2016 census compared with the 2010 census. C. cumingii can be even more vulnerable if intense cyclones become more frequent in the future. Unlike Pinanga spp., which flowers/fruits (in small quantities) continuously during their lifetime, Caryota spp. take longer years before they flower/fruit producing huge male and female inflorescences from the stem apex towards the base of the trunk and die after they reach their reproductive stage. This means that the reproductive stage of C. cumingii requires them to overcome intense cyclones. However, the cyclone trend in the Philippines might significantly reduce the population of palms in Palanan FDP, given that climate predictions in the region indicated that intense cyclones be more frequent in the future (Cinco et al., 2016).

**Topographic pattern in stem density, mortality and recruitment of palms in Palanan FDP**

Palm species distribution patterns along topographic position within the Palanan FDP were generally higher along valleys and lowest along ridges, but topographic partitioning was weakly observed on P. insignis and C. cumingii populations. There are varying results from other palm studies, where stem density was higher along ridges in Costa Rica (Clark et al., 1995) and in the Amazonian terra firme forest (Kahn & Mejia, 1987), while palm species distribution along topographic variation differed between species in Peruvian Amazon forest (Vormisto et al., 2004). Different habitat requirements of palm species along topographic position can be linked to their morphological and physiological adaptability to either a wet or dry environment, soil structure,
and light requirement (Salm et al., 2007; Svenning, 2001). The palms in Palanan FDP are more suited along valleys due to the vulnerability of ridge habitat to cyclone windthrow, especially for *P. maculata*, highlighting the species to prefer close canopy and wetter habitats.

We did not find substantial mortality and recruitment patterns along topographic positions, meaning demographic changes are not influenced by the topographic gradient of Palanan FDP. Strong topographic effects found in other studies were due to a wider elevational gradient at a larger spatial scale (Salm et al., 2007; Eiserhardt et al., 2011), compared to elevational differences between topographic positions in Palanan FDP that only range between 77 and 118 m a.s.l. conforming local scale studies in *terra firme* and *restinga* forest of Southern America (Vormisto et al., 2004). While mortality and recruitment of palms are not influenced by topographic position in Palanan FDP, the topographic aspect of either facing a leeward or windward direction was found to influence demographic patterns on trees in the plot (Yap et al., 2016). There are valleys and midslope topographic positions that are also in the leeward and windward direction, and the result of Yap et al. (2016) showed that trees in the windward direction were more affected by cyclones, resulting in higher mortality and recruitment between census years, especially during the 2016 census, as observed in this study.

## Conclusion

This study is the first to investigate the population dynamics of palms in the Philippines. While our result is still preliminary, it is apparent that the palm population may change over a short time, indicating the importance of palms in understanding short temporal responses of plant communities to changes in the environment. We suggest that other aspects of population dynamics should also be explored within the Palanan FDP, such as population responses linked to soil properties, water table depth, climate, and biotic structure. A more detailed study on palm phenology and dispersal ecology can also be conducted in addition to the demographic studies currently being monitored in the plot.

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## Author contributions

BP and PO discussed and conceived the ideas of the manuscript. PO, MRD, and EF provided the data. BP performed the analyses and prepared the original draft. BP, MRD, and EF edited and approved the final manuscript for submission.

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## Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

### Conflict of interest

The authors have no conflicts of interest to declare relevant to this article’s content.

### Informed consent

All authors agree to participate. All authors agree to publication.

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