



## Prolific fruit output by the invasive tree *Bellucia pentamera* Naudin (Melastomataceae) is enhanced by selective logging disturbance

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### ABSTRACT

Selective logging in tropical rain forests may promote population growth of invasive plants. The ability of invaders to respond, specifically in reproductive traits, to increase in resource abundance may allow them to increase their presence in the seed rain of recipient communities. The invasive pioneer tree *Bellucia pentamera* (Melastomataceae) is currently spreading within Gunung Palung National Park in West Kalimantan, Indonesia. The park has also experienced periods of illegal, small-scale, selective logging that seem to have facilitated population growth and spread of this invader. We first used fruiting frequency as a proxy for fruit output to make comparisons between *B. pentamera* and the native tree community of over 200 genera. We then constructed two Generalized Linear Autoregressive Moving Average (GLARMA) models using 13 months of phenology data to predict both fruiting frequency and crop size of *B. pentamera* under selective logging versus natural treefall disturbance regimes. *Bellucia pentamera* fruited at considerably higher frequency than all 200 native genera considered. This invader also responded positively to selective logging with both odds of being in fruit and crop sizes at least doubling in logged plots. Prolific seed output of *B. pentamera* is especially problematic within the lottery competition of tropical rain forest gap tree communities, in which prominence in the seed rain is particularly important. Furthermore, the reproductive response of *B. pentamera* to selective logging suggests that this harvesting practice may have a considerable role in facilitating this invasion in Southeast Asia.

*Key words:* GLARMA model; Indonesia; seed output; selective logging; tropical invasion.

PROLIFIC SEED OUTPUT IS ONE OF THE MANY TRAITS ASSOCIATED WITH INVASIVE PLANTS (Rejmánek & Richardson 1996, Mason *et al.* 2008, van Kleunen *et al.* 2010, Burns *et al.* 2013, Jelbert *et al.* 2015). This high fecundity can lead to high abundance in the seed rain, a major factor in many invasions (Rouget & Richardson 2003, Holle & Simberloff 2005). High seed input of an invasive species may even overwhelm native communities thought to be relatively resistant to invasion (D'Antonio *et al.* 2001). Tropical rain forest, for instance, is thought to be difficult to invade because of high biodiversity at least at small scales (1–10 m<sup>2</sup>; Levine *et al.* 2004, Fridley *et al.* 2007, Maron & Marler 2007). However, given the stochastic nature of colonization in rain forest gap tree communities (Brokaw & Busing 2000, Lusk *et al.* 2006), high seed input might be particularly effective for a potential invasive species.

Gap creation and regeneration are fundamental processes within tropical rain forests (Brokaw 1985, 1987). Disturbance in

the form of treefalls creates gaps for pioneer species, including small, light-demanding trees that quickly colonize these spaces (Denslow 1987). Although there is some evidence for niche differentiation as a function of gap size, pioneer tree assemblages are largely shaped by chance arrival at a gap, rather than competitive outcomes tracking slight differences in abiotic conditions (Hubbell *et al.* 1999, Schnitzer & Carson 2001, Stevens & Carson 2002, Letten *et al.* 2013). The resulting lottery of colonization by these pioneer species may make propagule pressure particularly important in tropical rain forest pioneer tree communities. Quantitative and qualitative changes to the natural treefall gap disturbance regime created by selective logging may increase the chance of introduced species entering the colonization lottery, facilitating invasion by such species with prolific reproductive output (Britton-Simmons & Abbott 2008, Eschtruth & Battles 2009).

In addition to a higher baseline rate of seed output, invasive species often show greater plasticity relative to native species in responding to increase in resource availability (Davidson *et al.* 2011) that often accompany disturbances to the canopy, such as

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selective logging. This response may be shown in reproductive traits in particular (Ruprecht *et al.* 2014), increasing seed output, and ultimately, relative presence in the seed rain of native communities. Therefore, an already prolific invasive species that further increases seed output in response to disturbance could be especially successful in tropical rain forest gap communities, considering the colonization lottery discussed above.

The invasive Neotropical pioneer tree *Bellucia pentamera* Naudin (Melastomataceae) is currently spreading at a significant rate within Gunung Palung National Park (GPNP) in West Kalimantan, Indonesia. First observations of this invader at GPNP were noted roughly 20 years ago, and the presence has steadily increased since then. The park experienced a period of intense selective logging in 2000–2002 that produced many canopy gaps of equivalent size to natural treefall gaps (*i.e.*, only a single tree is felled). Previous work has demonstrated that these selective logging gaps support significantly more *B. pentamera* than natural treefall gaps (Dillis *et al.* 2017). Furthermore, adult individuals within these selective logging gaps experience increased light levels due to the process of monodominant stands recruiting followed by self-thinning with age, leaving few conspecific competitors and even fewer heterospecific competitors (*personal obs.*). This process therefore may result in ambient conditions that influence the reproductive potential of *B. pentamera* individuals.

We collected phenology and crop size data for *B. pentamera* over the course of 13 months to study seed output in its invaded range. Ongoing projects at the Cabang Panti Research Station (CPRS) within GPNP have collected similar phenology data on over 200 genera of native trees, thus allowing comparisons between *B. pentamera* and the native community. Furthermore, the lack of selective logging within the CPRS allowed us to compare the seed output of *B. pentamera* in natural treefall gaps to seed output in logging gaps that occurred in close proximity to the research area. We first hypothesized that *B. pentamera* trees would demonstrate relatively high fruiting frequency compared to the rest of the community. We also hypothesized that *B. pentamera* adults in plots that contained selective logging would produce fruit more frequently and in greater abundance than *B. pentamera* adults in plots without selective logging disturbance.

## METHODS

**FIELD SITE AND STUDY SPECIES.**—This study was conducted in and around the Cabang Panti Research Station (CPRS) at Gunung Palung National Park (GPNP), West Kalimantan, Indonesia. CPRS comprises approximately 2100 ha of the 90,000 ha that makes up GPNP (Marshall 2004). Phenology data have been recorded for over 20 years within CPRS (Cannon *et al.* 2007a,b, Marshall *et al.* 2014). The trail grid system of CPRS is situated along the western slope of Gunung Palung and is intersected by two small rivers (Sungai Bayas and Sungai Air Putih) that drain westward to the South China Sea. A third river (Sungai Rankong) flows roughly parallel to these, several kilometers south of the

trail grid system. Logging occurred between the Sungai Rankong and the trail grid system, as well as several kilometers further to the west. The trail grid system was frequently walked by CPRS staff, which had the effect of discouraging any illegal logging within CPRS. The trail grid system therefore constituted a boundary, separating the undisturbed CPRS forest from this adjacent area in which illegal loggers operated.

*Bellucia pentamera* has a wide native range extending from southern Mexico to the Brazilian Amazon. Reproductive maturity can occur in as few as three years of age (Renner 1990) after which point individuals almost continuously produce flowers along main woody branches (cauliflorous fruiting habit). Reproduction of *Bellucia* spp. is characterized by self-incompatibility and evidence of asexual reproduction (*i.e.*, apomixis; Renner 1986). Its globose fruits contain thousands of small seeds and are eaten by a wide range of vertebrates in its native range including monkeys, birds, terrestrial mammals, and humans, who are thought to have introduced *B. pentamera* to Southeast Asia as a potential crop fruit (Renner 1989).

**SAMPLING DESIGN.**—Phenology routes were created in six separate locations. There were three routes within the undisturbed trail system of CPRS: one along each river (Sungai Bayas and Sungai Air Putih), beginning at 50 m elevation and extending 5 km downstream, as well as a third route comprising all other known *B. pentamera* adult individuals within the trail grid system ( $N = 15$ ). There were also three routes within areas that had experienced selective logging: one along the Sungai Rankong (also extending 5 km downstream from 50 m elevation) and two along established paths (~2 km long) to the south and to the west of CPRS. Individuals along the paths were included in the study if they were 10–50 m off the path. Sampling along rivers included individuals within 20 m of the shoreline. Only adult *Bellucia pentamera* individuals were included in this study. Individuals were classed as adult by the presence of fruiting scars, which occurred as a result of the cauliflorous fruiting habit of this species. The presence/absence of buds, flowers, immature fruit, and mature ripe fruit was recorded monthly for each individual stem. Mature ripe fruits were also counted to record monthly crop sizes. No immature fruits were included, and all observable mature ripe fruits were counted (*i.e.*, no proxy was used to infer crop sizes). Diameter at breast height (dbh) of each individual was also measured at the beginning of the study. The study lasted for 13 months from March 2014 through April 2015, with a two-month hiatus in data collection in September and October caused by administrative complications. Attempts to quantify the relative presence of *B. pentamera* propagules within the seed rain were unsuccessful.

Although all adult *B. pentamera* in CPRS were included in the study, the large size of the population in the adjacent disturbed areas necessitated that a subset of these were randomly selected for sampling. Along all six routes, trees were grouped into plots, which consisted of all individuals <20 m apart (*i.e.*, a distance of >20 m would designate a separate plot). Within the disturbed forest, identification numbers of individual plots were selected for study using a random number generator. The maximum number

of trees sampled within each plot was five, even though some plots contained far more than five individuals. Therefore, a random number generator was also used to select individual trees within plots when necessary. Each plot was also searched for evidence of prior selective logging (*i.e.*, remnant boards which remain for years after felled trees are processed on site) to designate each plot as 'logging' or 'non-logging'. No plots within CPRS contained selective logging, while in the adjacent area there were both plots with and without prior selective logging.

**STATISTICAL ANALYSIS.**—Our first analysis compared the fruit frequency of *B. pentamera* to native trees within CPRS. Fruit frequency was calculated monthly for *B. pentamera* as the number of individuals with mature or ripe fruit divided by the total number of individuals at CPRS. Similar data had been collected for 200 native genera from the period of October 2007 through April 2013 by AJM (for justification of using genera instead of species, see [Marshall & Leighton 2006, Dillis *et al.* 2015]). These existing data from native genera included only stems of sufficient diameter to produce fruit (Marshall & Leighton 2006). Preliminary fruiting frequency comparisons between *B. pentamera* and native trees indicated that only descriptive statistics would be appropriate and necessary (*i.e.*, there was a substantial empirical difference that was immediately obvious). We discuss individual comparisons below, including the overall forest average, the most common pioneer trees, and the most frequent fruiter other than *B. pentamera*.

We considered fruiting frequency as the most appropriate tool for comparison between *B. pentamera* and the native community, given the enormous amount of variation in fruit types (*e.g.*, size, nutritional content, seeds per fruit), as well as evidence from this forest that fruiting frequency may be one of the best predictors of consumption by fruit dispersers (Dillis *et al.* 2015). We additionally determined frequencies with which *B. pentamera* trees had buds, flowers, and immature fruit, to address whether the frequency of ripe fruit was a result of frequent reproduction or an artifact of persistence across months.

It should be noted that data on fruiting in logged sites were only available for *B. pentamera*, rather than the entire tree community, so comparisons of native responses to selective logging cannot be made. The purpose of including the initial comparison with the native community was to establish whether *B. pentamera* has a substantially higher fruiting frequency than other species.

The second analysis compared the fruiting frequency of *B. pentamera* trees in plots containing evidence of selective logging versus those without. The dataset consisted of monthly observations of the fruiting status of each tree, with trees nested in plots and locations; therefore, a statistical model that accommodated temporal and nested spatial structure was required. A Generalized Linear Autoregressive Moving Average (GLARMA) model was a suitable choice (Dunsmuir 2016). We fitted a GLARMA model estimating the log odds that a tree was in fruit in a given month, including an overall intercept, fixed effects for the presence of logging (predictor referred to hereafter as *logging*), log-transformed *DBH*, and membership in either the riverside or forest zones

(referred to hereafter as *zone*). The regression model further included nested random effects (varying intercepts) for tree, plot, and location; finally, the model included a lag-one moving average term, which captures the dependence of each monthly observation on the previous month's observation. To incorporate the September–October hiatus in data collection, the moving average residuals used to predict fruiting status in November 2014 were equated to zero; in effect, this re-started the moving average process anew in November 2014.

The third analysis used a GLARMA model for fruit counts to compare crop sizes of *B. pentamera* individuals in plots containing evidence of selective logging versus undisturbed plots. In place of the log odds above, the crop size model predicted log fruit count for each tree in each month of observation. All other details are as above.

The GLARMA models were fitted by computationally intensive Bayesian methods, using the general purpose Gibbs sampler JAGS (Plummer 2003), called from the statistical programming language R (R Development Core Team 2012) via the package *rjags* (Plummer 2015). One million posterior samples were generated from each Markov chain and discarded for burn in, and an additional one million samples were generated, thinned at an interval of 100, and saved. Two independent Markov chains were run for each model, producing 20,000 samples for posterior analysis.

## RESULTS

**COMMUNITY COMPARISON.**—Monthly fruiting frequency (proportion of stems in fruit) of *B. pentamera* at CPRS (Mean = 0.56, SD = 0.23) was consistently and dramatically higher than the overall forest average (Mean = 0.04, SD = 0.01; Fig. 1A). Even the most frequently fruiting native genus at CPRS (*Pternandra* spp: Mean = 0.25, SD = 0.13) fruited only half as often as *B. pentamera* (Fig. 1A). More importantly, the fruiting frequency of the most abundant native pioneer tree competitor (*Macaranga* spp: Mean = 0.03, SD = 0.05) was in order of magnitude lower than *B. pentamera* (Fig. 1B). Finally, *B. pentamera* also had high frequencies of buds (Mean = 0.87, SD = 0.15), flowers (Mean = 0.83, SD = 0.11), and immature fruit (Mean = 0.91, SD = 0.12).

**SELECTIVE LOGGING AND *BELLUCLA PENTAMERA* FRUIT FREQUENCY.**—Estimated coefficients for the longitudinal binary fruit frequency model are shown in Table 1. Coefficients refer to the log odds of fruiting, but are converted to interpretable effect sizes by exponentiation. All else being equal, the odds of a tree being in fruit in a selectively logged plot were two times as large as in an unlogged plot: exponentiating the coefficient estimate, upper and lower limits for *logging* from Table 1, the odds are  $\exp(0.69) = 1.99$ , with 95% credibility interval ( $\exp(0.30) = 1.35$ ,  $\exp(1.09) = 2.97$ ). Tree size also positively influenced the odds it was in fruit, with a 10 cm dbh increase from the overall mean value (15.66 cm, overall observed dbh range: 5–37 cm) doubling the odds of fruiting (*DBH* estimate = 2.00, 95% CI (1.63, 2.44)). Figure 2 depicts observations and model estimates for these

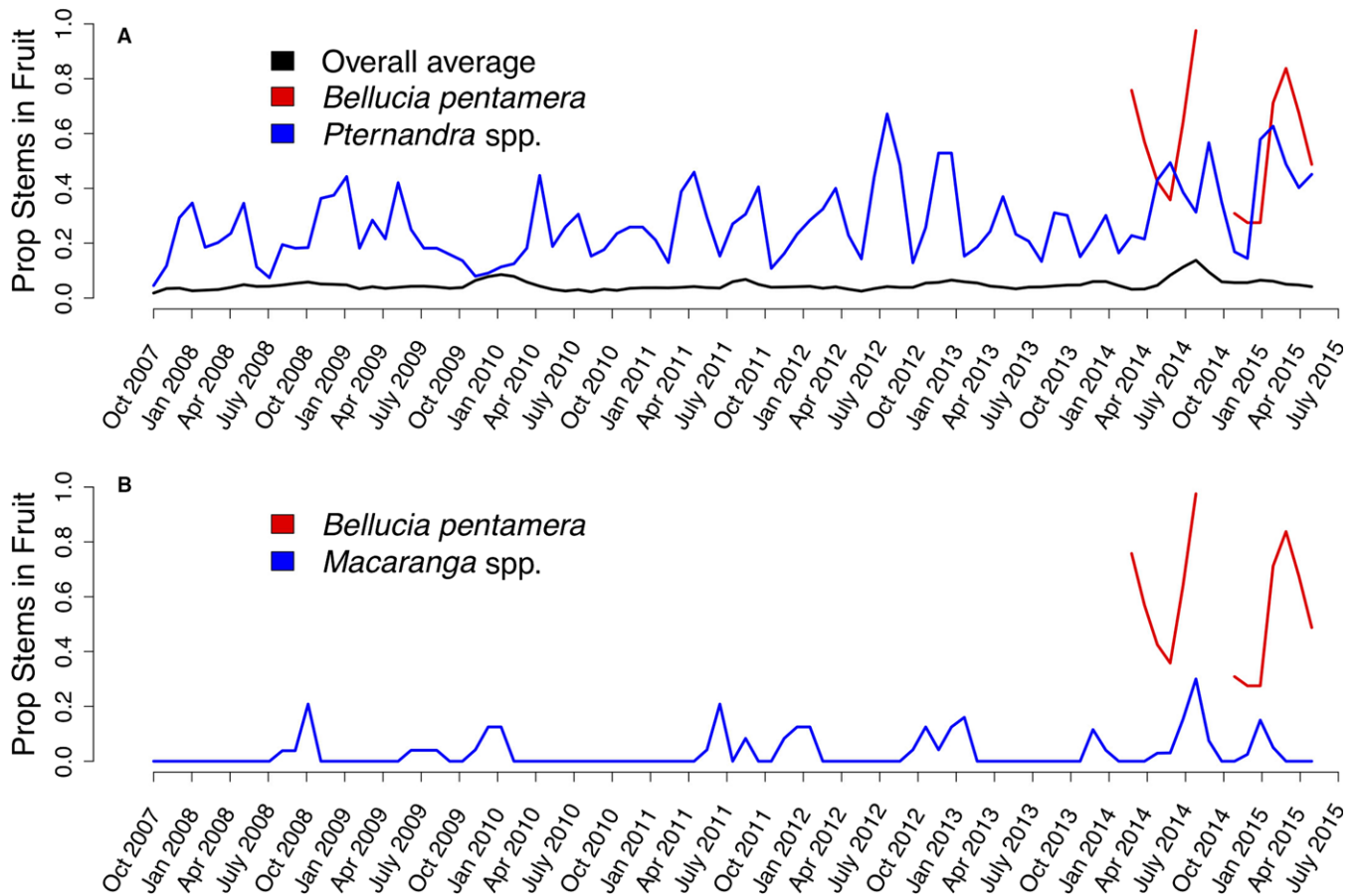


FIGURE 1. Monthly mean proportions of stems in fruit at CPRS. Data from *Bellucia pentamera* at CPRS are compared against the overall monthly means of all genera under observation and that of the most frequently fruiting genus (*Pternandra* spp.) at CPRS (A). Monthly means of the most common native pioneer tree competitor of *B. pentamera* (*Macaranga* spp.) is also shown in (B). Data for the *B. pentamera* were first collected in April 2014, and no data were available for September or October 2014.

effects. *Logging* and *DBH* are independently significant (see Table 1), although the figure shows considerable overlap in confidence bands. This is likely because the bands incorporate several sources of uncertainty, notably from the intercept. *Zone* had a weakly supported effect on the odds of being in fruit (estimate = 0.24), as the 95% credibility interval (0.47, 3.40) includes the null value 1. The random-effect standard deviations suggest that there was more variation in fruiting frequency among locations than among either plots or individual trees. Finally, the time-lag parameter implies a positive temporal autocorrelation in fruiting observations from month to month, so that a tree in fruit in month *m* had greater odds of being in fruit in month *m* + 1, all else being equal (Table 2).

**SELECTIVE LOGGING AND *BELLUCIA PENTAMERA* CROP SIZE.**—Estimated coefficients for the longitudinal crop size model are shown in Table 1. As above, coefficients are converted to effect sizes by exponentiation. All else being equal, the predicted fruit counts were more than twice (*logging* estimate = 2.51, 95% CI (1.26, 4.87)) as large for trees in selectively logged plots compared to natural treefall gaps. A

10 cm increase in the mean dbh nearly doubled the predicted fruit count (*DBH* estimate = 1.84, 95% CI (1.18, 2.70)). Figure 3 depicts observations and model estimates for these effects. *Logging* and *DBH* are once again individually significant, although the figure

TABLE 1. Estimated coefficients for the fixed effects of both the binary longitudinal model for fruit frequency and the longitudinal count model for crop size.

	Fruiting frequency model (Posterior mean, 95% Credibility Interval)	Crop size model (Posterior mean, 95% Credibility Interval)
Fixed effects		
Log <i>DBH</i>	1.40 (1.00, 1.81)	1.24 (0.34, 2.01)
<i>Logging</i>	0.69 (0.30, 1.09)	0.92 (0.23, 1.58)
<i>Zone</i> = Forest	0.24 (−0.75, 1.22)	−0.95 (−1.79, −0.13)
Intercept	−3.30 (−4.57, −2.05)	−1.88 (−4.06, 0.70)
Time-lag effect		
One-month lag	0.52 (0.43, 0.61)	0.09 (0.09, 0.10)

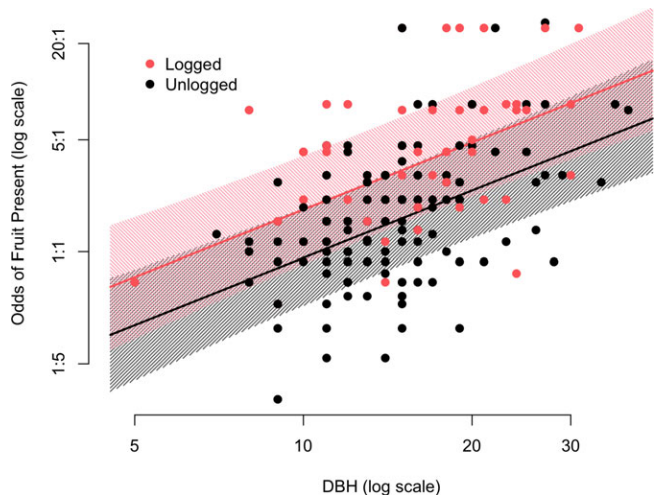


FIGURE 2. Scatter plot of odds of fruit present versus DBH with model predictions. Observations are displayed as the number of months each tree had fruits present divided by the number of months fruits were absent, equivalent to a time-averaged odds that a tree was in fruit. The boundary correction 0.5 was added to both the numerator and denominator. Trees in logged and unlogged plots are marked with red and black circles, respectively. Central tendency lines depict posterior mean regressions, with the fixed effect *zone* held at ‘river’. Shaded regions depict 95% credibility bands for regressions, incorporating combined uncertainty in the intercept and coefficients of *DBH* and *logging*.

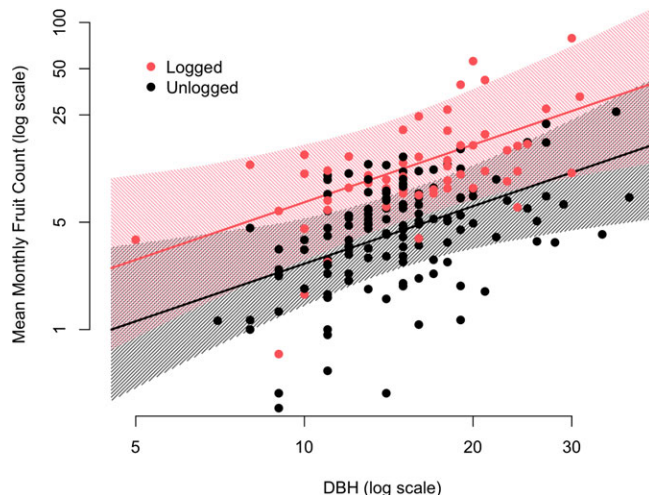


FIGURE 3. Scatter plot of mean monthly fruit count versus DBH with model predictions. Observations are displayed as the mean monthly fruit count for each individual. See Fig. 2 for all other details.

TABLE 2. Estimated coefficients for random effects for both the binary longitudinal model for fruit frequency and the longitudinal count model for crop size.

Random effect standard deviations	Mean estimate	Mean estimate
Location	0.51	0.26
Plot	0.34	0.62
Tree	0.12	1.48

again shows considerable overlap in confidence bands. The effect of *zone* was reliably negative, with crop sizes within the forest less than half as large (estimate = 0.39, 95% CI (0.17, 0.88)) as those along the river. The random effects suggest most variation was among trees, followed in order by plots and locations. Finally, the time-lag parameter implies a positive temporal autocorrelation in fruit count from month to month, so that a tree with elevated fruit count in month *m* was likely to have elevated fruit count in month *m* + 1, all else being equal.

## DISCUSSION

FRUITING FREQUENCY WITHIN THE COMMUNITY.—The fruiting frequency of *Bellucia pentamera* is distinctly higher than all native trees considered in this study. Given the high frequencies of all reproductive phases, it appears that this species is frequently producing new fruit, rather than a single crop remaining on stems for

extended periods of time. Although some trees, such as *Pternandra* spp., produced fruit almost half as often, there were no native pioneer trees (*i.e.*, potential competitors of *B. pentamera*) that were even close to the frequency with which *B. pentamera* produced fruit. Ideally, we would have been able to directly quantify the proportion of *B. pentamera* within the seed rain; however, our proxy of seed output indicates a significant advantage of *B. pentamera* over its native competitors within the colonization lottery of rain forest gaps.

In comparison with availability of native fruits, which is spread over many different taxa of relatively rarely fruiting trees, *B. pentamera* represents a consistent source of fruit for seed dispersers. The ability to maintain a constant presence in the plant–seed disperser market may provide an attractive target for frugivores (Dillis *et al.* 2015), as it may ease their task of tracking fruiting schedules over space and time (Howe & Smallwood 1982). Furthermore, the fruit of *B. pentamera* is of relatively high quality (*i.e.*, high sugar content and low in defensive compounds; Renner 1986), and production of new fruit appears to be relatively frequent. Although there have been no formal studies yet of frugivory of *B. pentamera*, field observations suggest its fruit is eaten by a wide variety of vertebrates including birds, terrestrial mammals, as well as human and non-human primates (Marshall *pers. comm*). Therefore, the second component of propagule pressure, dispersal, does not appear to be lacking in this invasion.

RESPONSES TO SELECTIVE LOGGING.—There was a strong relationship between *B. pentamera* reproduction and selective logging disturbance, with individuals in old logging sites producing fruit at a much higher frequency. Even though the model indicated that larger trees produced fruit more frequently and trees in selective logging sites may have in fact been larger (which this model did not explicitly address), they still had higher fruiting frequency

after accounting for size (dbh; Fig. 2). The same result was found for crop sizes (Fig. 3), with reliably larger predicted counts for trees in plots that had experienced selective logging, even after accounting for differences in size.

Taken together, increases in the frequency and quantity with which *B. pentamera* produces fruit suggest a strong positive response to selective logging. The specific mechanism for selective logging disturbance facilitating this phenotypic response in *B. pentamera* was not determined by the current study. Previous work, however, demonstrated that *B. pentamera* recruits in higher densities in selective logging gaps than in natural treefalls, perhaps responding to increased substrate available to epiphytic seedlings of this species (the epiphytic growth habit of *B. pentamera* is discussed in detail by Dillis *et al.* 2017). Subsequent field observations suggest that high seedling recruitment may lead to an environment with reduced light competition, as a result of dense recruitment followed by self-thinning and a lack of interspecific competition (Dillis *et al.* 2017). This invader has traits associated with fast growth in response to increased light availability (Poorter 2001), such as high specific leaf area (Poorter 1999), much like many other invaders (Dahler 2003). The importance of light availability was also evidenced by the result that crop sizes and fruiting frequency were greater in riverine zones, which inherently had more light. Further work will be valuable in determining the precise mechanism by which selective logging is facilitating the recruitment and reproductive output of this invader. It should be noted that the current study did not analyze reproductive responses of native trees in this forest, which may also respond to changes in light environments in a similar way. A systematic comparison is needed.

**CUMULATIVE IMPACTS.**—Instances of disturbance are known to facilitate invasions (Lozon & MacIsaac 1997, Lockwood *et al.* 2007, Moles *et al.* 2012). Canopy disturbance is a particularly important prerequisite for many tropical plant invasions (Denslow & DeWalt 2008). Considering the invasion described herein, it appears that in addition to a population increase of *B. pentamera* in response to selective logging (Dillis *et al.* 2017), this invader is rendered more successful on an individual basis as well. The cumulative impacts of individual and population-level responses to selective logging may create a scenario in which the lottery of gap colonization is overrun (Britton-Simmons & Abbott 2008) with *B. pentamera* propagules. There is evidence that selective logging has the potential to indirectly alter the structure and composition of forests (Slik *et al.* 2002, Rutten *et al.* 2015). Although relatively little has been determined about reproductive responses of invasive tree species to selective logging disturbance in tropical rain forests, population level responses to gaps created by timber harvesting have been documented (Padmanaba & Corlett 2014). Therefore, additional work quantifying the relative proportion of *B. pentamera* in the seed rain and seed bank would be valuable to determine whether the responses in fruit output may carry through and pose a significant threat to the biodiversity of this forest.

## CONCLUSION

The invasion of *B. pentamera* in Southeast Asia represents a potential threat to its biodiversity, the extent of which we currently can only speculate. Our study has provided evidence that this invasion may be exacerbated by selective logging, a practice that may otherwise superficially appear relatively benign (Bicknell *et al.* 2015). That is, negative impacts to biodiversity and forest health may be occurring in the absence of noticeable habitat loss. The threat of *B. pentamera* is most likely of concern to biodiversity of pioneer tree species in recipient communities, via the potential for inundation of the lottery of colonization. Although there has not been systematic work on succession and replacement of *B. pentamera*, the sapling layer under monodominant *B. pentamera* canopies is often almost entirely barren. Therefore, unlike some invaders that do not disrupt succession (Viisteensaari *et al.* 2000), such a pattern may not exist within the current invasion. More work is urgently needed to determine how severe this invasion may become and how broad of a threat it is to the plant community. *Bellucia pentamera* is now widely distributed on many islands in Southeast Asia. Similar to other emerging plant invasions in the region, such as that of *Cecropia* spp. (Sheil & Padmanaba 2011), the current priority should be mapping the extent and developing management strategies.

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## DATA AVAILABILITY

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.t2j2r>

## LITERATURE CITED

- BICKNELL, J., M. STRUEBIG, AND Z. DAVIES. 2015. Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *J. App. Ecol.* 52: 379–388.
- BRITTON-SIMMONS, K., AND K. ABBOTT. 2008. Short- and long-term effects of disturbance and propagule pressure on a biological invasion. *J. Ecol.* 96: 68–77.

- BROKAW, N. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- BROKAW, N. 1987. Gap-phase regeneration of three pioneer species in a tropical forest. *J. Ecol.* 75: 9–19.
- BROKAW, N., AND R. BUSING. 2000. Niche versus chance and tree diversity in forest gaps. *Trends Ecol. Evol.* 15: 183–188.
- BURNS, J., E. PARDINI, M. SCHUTZENHOFER, Y. CHUNG, K. SEIDLER, AND T. KNIGHT. 2013. Greater sexual reproduction contributes to differences in demography of invasive plants and their noninvasive relatives. *Ecology* 94: 995–1004.
- CANNON, C. H., L. M. CURRAN, A. J. MARSHALL, AND M. LEIGHTON. 2007a. Beyond mast-fruiting events: Community asynchrony and individual dormancy dominate woody plant reproductive behavior across seven Bornean forest types. *Curr. Sci.* 93: 1558–1566.
- CANNON, C. H., L. M. CURRAN, A. J. MARSHALL, AND M. LEIGHTON. 2007b. Long-term reproductive behavior of woody plants across seven Bornean forest types in the Gunung Palung National Park, Indonesia: suprannal synchrony, temporal productivity, and fruiting diversity. *Ecol. Letters* 10: 956–969.
- DAHLER, C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annu. Rev. Ecol. Syst.* 34: 183–211.
- D'ANTONIO, C., J. LEVINE, AND M. THOMSEN. 2001. Ecosystem resistance to invasion and the role of propagule supply: A California perspective. *J. Mediterranean Ecol.* 2: 233–245.
- DAVIDSON, A., M. JENNIONS, AND A. NICOTRA. 2011. Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis. *Ecol. Letters* 43: 419–431.
- DENSLOW, J. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431–451.
- DENSLOW, J., AND S. DEWALT. 2008. Exotic plant invasions in tropical forests: patterns and hypotheses. In W. P. Carson, and S. A. Schnitzer (Eds.). *Tropical forest community ecology*, pp. 409–426. Blackwell Scientific, Oxford, UK.
- DILLIS, C., L. BEAUDROT, K. FEILEN, D. CLINK, H. WITTMER, AND A. J. MARSHALL. 2015. Modeling the ecological and phenological predictors of fruit consumptions by gibbons (*Hylobates albibarbis*). *Biotropica* 47: 85–93.
- DILLIS, C., A. J. MARSHALL, AND M. REJMÁNEK. 2017. Change in disturbance regime facilitates invasion by *Bellucia pentamera* Naudin (Melastomataceae) at Gunung Palung National Park, Indonesia. *Biol. Invasions* 19: 1329–1337.
- DUNSMUIR, W. T. M. 2016. Generalized linear autoregressive moving average models. In R. A. Davis, S. H. Holan, R. Lund, and N. Ravishanker (Eds.). *Handbook of discrete-valued time series*, pp. 61–62. CRC Press, Boca Raton, FL.
- ESCHTRUTH, A., AND J. BATTLES. 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecol. Monographs* 79: 265–280.
- FRIDLEY, J., J. STACHOWICZ, S. NAEEM, D. SAX, E. SEABLOOM, M. SMITH, T. STOHLGREN, D. TILMAN, AND B. VON HOLLE. 2007. The invasion paradox: Reconciling pattern and process in species invasions. *Ecology* 88: 3–17.
- HOLLE, B., AND D. SIMBERLOFF. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 88: 3212–3218.
- HOWE, H., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13: 201–228.
- HUBBELL, S., R. FOSTER, S. O'BRIEN, K. HARMS, R. CONDIT, B. WECHSLER, S. WRIGHT, AND S. de LAO. 1999. Light-gap disturbance, recruitment limitation, and tree diversity in a Neotropical forest. *Science* 283: 554–557.
- JELBERT, K., I. STOTT, R. McDONALD, AND D. HODGSON. 2015. Invasiveness of plants is predicted by size and fecundity in the native range. *Ecol. Evol.* 5: 1933–1943.
- van KLEUNEN, M., E. WEBER, AND M. FISCHER. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Letters* 13: 235–245.
- LETTEN, A., K. LYONS, AND A. MOLES. 2013. The mid-domain effect: It's not just about space. *J. Biogeogr.* 40: 2017–2019.
- LEVINE, J., P. ADLER, AND S. YELENIK. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Letters* 7: 975–989.
- LOCKWOOD, J. L., M. F. HOOPEES, AND M. P. MARCHETTI. 2007. *Invasion ecology*. Blackwell Publishing, Oxford, UK.
- LOZON, J., AND H. MACISAAC. 1997. Biological invasions: Are they dependent on disturbance? *Environmental Review* 5: 131–144.
- LUSK, C., R. CHAZDON, G. HOFMANN, AND J. MEMMOTT. 2006. A bounded null model explains juvenile tree community structure along light availability gradients in a temperate rain forest. *Oikos* 112: 131–137.
- MARON, J., AND M. MARLER. 2007. Native plant diversity resists invasion at both low and high resource levels. *Ecology* 88: 2651–2661.
- MARSHALL, A. J. 2004. Population ecology of gibbons and leaf monkeys across a gradient of Bornean forest types. PhD Dissertation. Harvard University, Cambridge, MA.
- MARSHALL, A. J., L. BEAUDROT, AND H. U. WITTMER. 2014. Responses of primates and other frugivorous vertebrates to plant resource variability over space and time at Gunung Palung National Park. *Int. J. Primatol.* 35: 1178–1201.
- MARSHALL, A. J., AND M. LEIGHTON. 2006. How does food availability limit the population density of white bearded gibbons? In G. Hohmann, M. M. Robbins, and C. Boesch (Eds.). *Feeding ecology in apes and other primates: Ecological, physical, and behavioral aspects*. Cambridge University Press, Cambridge, UK.
- MASON, R., J. COOKE, A. MOLES, AND M. LEISHMAN. 2008. Reproductive output of invasive versus native plants. *Glob. Ecol. Biogeogr.* 17: 633–640.
- MOLES, A., H. FLORES-MORENO, S. P. BONSER, D. I. WARTON, A. HELM, L. WARMAN, D. J. ELDRIDGE, E. JURADO, F. A. HEMMINGS, P. B. REICH, J. CAVENDER-BARES. 2012. Invasions: The trail behind, the path ahead, and a test of a disturbing idea. *J. Ecol.* 100: 116–127.
- PADMANABA, M., AND R. CORLETT. 2014. Minimizing risks of invasive alien plant species in tropical production forest management. *Forests* 5: 1982–1988.
- PLUMMER, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs Sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, Vienna, Austria, ISSN 1609-395X.
- PLUMMER, M. 2015. rjags: Bayesian graphical models using MCMC. R package version 4.4. <https://CRAN.R-project/package=rjags>
- POORTER, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: The relative importance of morphological and physiological traits. *Funct. Ecol.* 13: 396–410.
- POORTER, L. 2001. Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Funct. Ecol.* 15: 113–123.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- REJMÁNEK, M., AND D. RICHARDSON. 1996. What attributes make some plant species more invasive? *Ecology* 77: 1655–1661.
- RENNER, S. 1986. Reproductive biology of *Bellucia* (Melastomataceae). *Acta Amazon* 16(17): 197–208.
- RENNER, S. 1989. Systematic studies in the Melastomataceae. *Mem. N. Y. Bot. Gard.* 50: 2–97.
- RENNER, S. 1990. Reproduction and evolution in some genera of Neotropical Melastomataceae. *Mem. N. Y. Bot. Gard.* 55: 143–152.
- ROUGET, M., AND D. RICHARDSON. 2003. Inferring process from pattern in plant invasions: A semimechanistic model incorporating propagule pressure and environmental factors. *Am. Nat.* 162: 712–724.

- RUPRECHT, E., A. FENESI, AND I. NIJS. 2014. Are plasticity in functional traits and constancy in performance traits linked with invasiveness? An experimental test comparing invasive and naturalized plant species. *Biol. Invasions* 16: 1359–1372.
- RUTTEN, G., A. ENSSLIN, A. HEMP, AND M. FISCHER. 2015. Forest structure and composition of previously selectively logged and non-logged montane forests at Mt. Kilimanjaro. *Forest Ecol. Manag.* 337: 61–66.
- SCHNITZER, S., AND W. CARSON. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919.
- SHEIL, D., AND M. PADMANABA. 2011. Innocent invaders? A preliminary assessment of *Cecropia*, an American tree, in Java. *Plant Ecol. Divers* 4: 279–288.
- SLIK, J., R. VERBURG, AND P. KEBLER. 2002. Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodiversity Conserv.* 11: 85–98.
- STEVENS, M., AND W. CARSON. 2002. Resource quality, not resource heterogeneity, maintains plant diversity. *Ecol. Letters* 5: 420–426.
- VIESTEENSAARI, J., S. JOHANSSON, V. KAARAKKA, AND O. LUUKKANEN. 2000. Is the alien tree species *Maesopsis eminii* Engl. (Rhamnaceae) a threat to tropical forest conservation in the East Usambaras, Tanzania? *Environ. Conserv.* 27: 76–81.