

UC Davis

UC Davis Previously Published Works

Title

Change in disturbance regime facilitates invasion by *Bellucia pentamera* Naudin (Melastomataceae) at Gunung Palung National Park, Indonesia

Permalink

<https://escholarship.org/uc/item/2g213201>

Journal

Biological Invasions, 19(4)

ISSN

1387-3547

Authors

Dillis, C
Marshall, AJ
Rejmánek, M

Publication Date

2017-04-01

DOI

10.1007/s10530-016-1345-5

Peer reviewed

Change in disturbance regime facilitates invasion by *Bellucia pentamera* Naudin (Melastomataceae) at Gunung Palung National Park, Indonesia

Christopher Dillis  · Andrew J. Marshall · Marcel Rejmánek

Received: 19 February 2016 / Accepted: 28 November 2016 / Published online: 30 January 2017
© Springer International Publishing Switzerland 2017

Abstract In tropical rainforests, gaps created by fallen canopy trees are the primary colonization sites for pioneer species. Selective logging mimics these natural disturbances in that only a single tree is felled, creating a gap of comparable size. Rates of tree felling greatly exceed natural mortality rates, however, changing disturbance regime by increasing the number of gaps in logged areas compared to intact forest. Little is known about whether gaps in logged forests are qualitatively different as well. At Gunung Palung National Park in West Kalimantan, Indonesia, a period of selective logging in areas adjacent to the research station created a natural experiment permitting comparison of populations of the invasive pioneer tree *Bellucia pentamera* in selectively logged and undisturbed forest. We sought to first establish whether canopy gaps are necessary for invasion by *B.*

pentamera. We then examined whether the type of gap (logging vs. natural treefall) had an effect on recruitment. Finally, we compared populations in natural treefall gaps in logged and undisturbed forest to estimate the effect of logging on population size. *Bellucia pentamera* was limited to gaps, regardless of canopy tree density. Furthermore, gaps created by selective logging supported significantly more *B. pentamera* individuals than natural gaps. Finally, natural treefall gaps in the disturbed area contained significantly more individuals than gaps in the undisturbed forest. Therefore, it appears that selective logging not only created more gaps for *B. pentamera*, these gaps in particular promoted greater abundance of this invader and led to a population increase throughout the disturbed habitat.

Keywords Tropical invasion · Disturbance · Selective logging · Tropical rainforest

C. Dillis (✉) · M. Rejmánek
Department of Ecology and Evolution, University of California-Davis, One Shields Avenue, Davis, CA 95616, USA
e-mail: cdillis@ucdavis.edu

C. Dillis · M. Rejmánek
Graduate Group in Ecology, University of California-Davis, One Shields Avenue, Davis, CA 95616, USA

A. J. Marshall
Department of Anthropology, Program in the Environment, and School of Natural Resources and Environment, University of Michigan, 500 S. State St., Ann Arbor, MI 48109, USA

Introduction

One of the most common maxims in the field of plant invasion biology is that disturbance facilitates invasion (Lozon and MacIsaac 1997; Lockwood et al. 2007). Invasions may occur when disturbance makes resources available (Davis et al. 2000) to particular introduced species that are well adapted to use them (Funk and Vitousek 2007). However, as a result of

treating disturbance as a generalized phenomenon, or even poorly defining it to begin with (Grime 1977), discrepancies have emerged regarding its role in invasions, leading to examples of studies finding a negative association (Cox and Allen 2008; Smart et al. 1985) or no association whatsoever (Hester and Hobbs 1992) between disturbance and invasion.

The inability to draw broad conclusions about the effects of disturbance stems from both idiosyncrasies in patterns of disturbance, such as frequency (Hobbs and Huenneke 1992), spatial scale (Allcock and Hik 2003; Dorough et al. 2007), or time since initial disturbance (Belote et al. 2012; Catford et al. 2012), as well as idiosyncrasies of the habitats in which invasions occur (Moles et al. 2012; Jauni et al. 2015). Moles et al. (2012) determined that changes in disturbance regimes were more explanatory than disturbance itself, suggesting that overlooking idiosyncrasies of invaded habitats may be particularly problematic. That is, failure to account for the original disturbance regime may ultimately result in misleading or inconclusive findings, as mentioned above (Hobbs and Huenneke 1992; Allcock and Hik 2003; Lake and Leishman 2004). Therefore, there is a need for studies to compare the natural regime against the novel regime in determining the effect of disturbance on invasion.

Within tropical rainforests, the most pervasive form of disturbance is gap creation by treefalls (Brokaw 1985; Denslow 1987). New gaps are colonized by pioneer species, followed by a continuum of increasingly shade tolerant species ending with large canopy trees (Brokaw 1987). Some invasions have been known to proceed in the absence of such disturbance (Reinhart et al. 2006) or with minimal disturbance, such as human-made trails (Totland et al. 2005). However, it is much more common that canopy gaps are required for establishment of invaders (Gorchov et al. 2011). This may be exacerbated by the presence of selective logging (Rutten et al. 2015; Silk et al. 2002; Xu et al. 2015), but not necessarily only because there are simply more gaps available.

Selective logging is similar to natural treefalls in that only a single tree is felled, creating a gap of comparable size. However, processing of lumber typically occurs on site (pers obs), altering the profile of ground cover and growth substrates in a manner unlike natural treefalls. For example, unusable remnant boards are left behind, increasing the surface area

of the fallen bole relative to natural treefalls. In this way, the gaps in logged forests may be qualitatively different, as well as more numerous. Determining the impact of changes in disturbance regime within a tropical rainforest requires exploration of how introduced species respond to both treefalls (i.e. natural disturbance) and selective logging (i.e. novel disturbance) within a single study site.

Gunung Palung National Park (GPNP) in Indonesia is currently an invasion front of the Neotropical pioneer tree, *Bellucia pentamera* Naudin (Melastomataceae: Renner 1986), which has begun to naturalize in the last 15-20 years (Cam Webb pers. comm.). This species was introduced to Indonesia in the early part of the twentieth century via Bogor Botanic Gardens (Heyne 1950, sec. de Kok et al. 2015). *Bellucia pentamera* is a fast growing gap species that reaches maturity at 2-4 years of age (Renner 1990). It produces large, sugar rich fruits capable of long distance dispersal by a variety of birds and mammals (Renner 1989), including humans. A number of frugivores including birds, primates, and boar have been observed eating the fruit of this newly naturalized species at the Cabang Panti Research Station (CPRS; Marshall pers. comm.). It has been observed to occasionally form monodominant stands and consistently remains in a continuous reproductive state once reaching maturity (Dillis unpublished data), a common trait of invasive woody species (Rejmánek and Richardson 1996). There were no observations of senescence, presumably because the invasion at GPNP is more recent than the natural lifespan of *B. pentamera*, although this information is currently unknown.

Between 2000 and 2002 a period of intense selective logging occurred adjacent to the Cabang Panti Research Station, with relatively little such activity occurring within the research trail system. This event therefore resulted in a sharp boundary between otherwise comparable logged and unlogged habitat in close proximity. The purpose of the current study was to use this opportunity for a quasi-experimental design, comparing CPRS to the adjacent selectively logged forest (referred to hereafter as *SLF*), to determine if the alteration to the natural disturbance regime created by selective logging was facilitating this invasion.

Although some invaders have been known to recruit beneath closed canopies (Reinhart et al. 2006), initial observations suggested *B. pentamera* is

a shade-intolerant pioneer species. Our first hypothesis was therefore that *B. pentamera* is limited to recruiting in gaps (i.e. treefalls and selective logging), thus making the presence of gaps particularly important. We further expected that qualitative differences between gaps created by natural treefalls versus selective logging may influence recruitment, based on observations of *B. pentamera* growing on decaying wood. Our second hypothesis was that selective logging gaps promote colonization by *B. pentamera* more than natural treefall gaps. We further expected that even natural treefall gaps could be prone to significant invasion given sufficient seed input. Our third hypothesis was thus that natural treefall gaps within the SLF area would contain significantly more *B. pentamera* than natural treefall gaps at CPRS, due to spillover from a large population of adults resulting from the logging period 12 years prior to this study.

Methods

Field site and study species

This study was conducted from October to December 2014, in and around the Cabang Panti Research Station (CPRS) at Gunung Palung National Park (GPNP), West Kalimantan, Indonesia. GPNP is comprised of 108,400 ha of tropical rainforest extending east from the southwest coast of Borneo inland up to an elevation of 1100 m. The research station is situated along the western slope of Gunung Palung within a trail grid system covering approximately 2100 ha, ranging from montane forest to upland forest to swamp (Marshall 2004). Plots established by other ongoing research projects were used for sampling (see below). These existing plots were either 0.1 or 0.2 ha in size, in which all trees larger than 14.5 cm dbh were identified and tagged (Marshall and Leighton 2006, Marshall 2010, Marshall et al. 2014). Work was also conducted in the selectively logged forest (SLF) adjacent to CPRS, within an area of an equivalent size to CPRS. The SLF was situated directly south of CPRS and ranged from lowland sandstone forest (~100 m elevation) to swamp forest (~0 m elevation). Both CPRS and the SLF contained walking trails (~1 m wide), however aside from selective logging, neither area has been subjected to major disturbance such as cyclones, landslides, or construction of roads.

Bellucia pentamera occurs naturally over a large range from Brazil to the Yucatan Peninsula of Mexico. One of its earliest recorded introductions into Indonesia was on the island of Java (via Bogor Botanic Gardens) in the early twentieth century (de Kok et al. 2015). It is a medium sized tree, with a maximum height of ~15 m (Renner 1989). Although the average lifespan is currently unknown, no senescent individuals were observed at GPNP. It is known to produce fruit as early as three years of age (Renner 1990). Following maturity, adult individuals maintain a nearly constant state of reproduction (Dillis unpublished data), although two peak fruiting periods were observed (January–February, August–September). Ripe fruits are ~5 cm in diameter and contain thousands of small seeds (0.5–1 mm long; Renner 1990).

Sampling design

New plots (70 plots; 50 m × 20 m) were established in the SLF, using the same method that was used for the 70 existing plots within CPRS (A. Marshall pers. comm.). A random number generator was used to establish coordinates within the borders of the SLF, as well a compass bearing along which each plot extended (50 m) from its predetermined origin. If an obstacle such as a river, cliff, or trail prevented reaching 50 m from the origin, the remaining distance was added in the opposite direction from the origin. Of the 70 existing plots at CPRS, 10 were discarded because they were at much higher elevations than those sampled within the SLF, leaving a comparison of 60 0.1 ha and 0.2 ha plots (30 of each) at CPRS to 70 0.1 ha plots in the adjacent forest. Plot size was taken into account when standardizing predictor variables in the statistical analysis (see below). Each plot was identified as either swamp (freshwater and peat swamp) or upland (alluvial bench, lowland sandstone, and lowland granite forests), with about equal proportions (30:70, swamp:upland) in CPRS and the adjacent forest.

C. Dillis and his field assistants carefully searched each plot for *B. pentamera* individuals, which were divided into four age classes: seedlings (stem distinctly red, leaf trichomes prominent), saplings (stem green, not yet woody above breast height), juveniles (stem woody above breast height, but lacking fruiting scars from cauliflorous inflorescence or active

reproduction), and adults (presence of fruiting scars or active reproduction). Dbh was measured for all adults.

All canopy trees (dbh > 31 cm) were counted and measured (dbh) to produce estimates of canopy basal area for each plot. We distinguished between two habitat types, swamp versus upland, in further describing the plots. Treefalls (canopy trees, dbh > 31 cm) were counted if any portion of the fallen bole was contained in the plot. Plots were identified as containing selective logging based on the presence of remnant boards.

For the purposes of analysis, plots were considered categorically as containing treefalls, selective logging, both, or neither. Although treefalls could be counted, the number of natural treefalls could not be specified in all plots that contained logging due to uncertainty over their cause (i.e. resulting from natural falls or as collateral damage from felling of selectively logged trees). However, plots that did contain treefalls in addition to selective logging were identified as such in the analysis. Finally, the number of selectively logged trees per plot could not be definitively determined in each case, given that boles are processed on site, often leaving only remnant boards. However, there rarely appeared to be more than a single logging gap per plot.

Statistical analysis

We used a model comparison approach to determine if *B. pentamera* appeared to be restricted to gaps specifically or if some lower threshold of canopy basal area existed, below which there may have been sufficient light for recruitment. We created five component models of increasing complexity (including a null model), which were then compared using Akaike's Information Criterion (AIC corrected; Burnham and Anderson 2002). These generalized linear models all used negative binomial distributions, reflecting over-dispersion in the observed counts. Model weights were used to produce an averaged model (Johnson and Omland 2004) with the MuMIn package (Barton 2012) in R (R Development Core Team 2012). The averaged model predicted counts of *B. pentamera* individuals per plot based on gap presence (yes, no), canopy basal area, location (CPRS vs. SLF), and habitat type (swamp vs. upland). Estimates of these predictor variables were considered reliable if 95% confidence intervals did not overlap zero. Seedlings were excluded from all analyses

because their counts did not correlate with any other age categories (which otherwise did all correlate with each other), likely because their numbers are much more ephemeral. Counts within individual age classes were prohibitively sparse to run separate analyses for each age class (particularly at CPRS), so age classes (aside from seedlings) were pooled for all analyses.

We conducted a second analysis to determine if the predicted counts of *B. pentamera* individuals were significantly different in logging and treefall plots. We again used a model comparison and averaging approach, including the same parameters (canopy basal area, location, habitat type), but specifying gap type (logging vs. treefall plots). Again, estimates of predictor variables were considered reliable if 95% confidence intervals did not overlap zero and seedlings were excluded from the analysis.

We also compared treefall plots in CPRS and the SLF to determine if *B. pentamera* is more prominent in treefalls within the latter. Considering only treefall plots reduced the sample size from $N = 130$ to $N = 76$. We again used a similar model comparison and averaging approach, predicting the number of individuals using the parameters of location (CPRS vs. SLF), canopy basal area, and habitat type. This analysis was restricted to only treefall plots, thus allowing for specific treefall totals, however, due to insufficient sample sizes across counts of treefalls per plot we were unable to include the number of treefalls per plot as a separate predictor variable. However, comparisons between average treefall totals in CPRS and the adjacent forest were included in our analysis and our interpretation of these results.

Results

Necessity of gaps

AICc model comparison favored the most complex model, including all four predictors: gap presence, canopy basal area, location, and habitat type (Table 1). This model received 83% model weight, while the null model received 0%. Presence of gaps had a reliably positive effect on predicted counts of *B. pentamera* (estimate = 2.46, SE 0.55). Canopy basal area also had a significant, yet negative effect on predicted counts (estimate = -0.94, SE 0.20). It was clear however that this relationship was strongly

Table 1 AICc comparison between component models for the first analysis (importance of gap presence/absence)

Model components	df	Log-likelihood	AICc	Δ AICc	Weight
Canopy BA, location, gap presence, habitat type	6	-286.17	585.03	0.00	0.83
Canopy BA, location, gap presence	5	-288.87	588.23	3.20	0.17
Location, gap presence	4	-298.10	604.52	19.49	0.00
Location	3	-303.49	613.16	28.13	0.00
Null	2	-325.24	654.58	69.55	0.00

An averaged model was created based on weights shown here

driven by plots with gaps rather than plots without gaps (Fig. 1). Predicted counts of *B. pentamera* were reliably higher in the SLF than at CPRS (estimate = 1.60, SE 0.37) and significantly lower in plots situated in swamp habitat type (estimate = -0.80, SE 0.32).

Natural versus novel disturbance types

Our second analysis, focusing specifically on gap type, the AICc model comparison revealed that gap type, canopy basal area, and location were all more useful predictors than habitat type (Table 2). The top model (66% model weight) included only the first three predictors. The null model again received 0% model weight. Gap type had a reliable effect, with logging plots having higher predicted counts of *B. pentamera* than plots with only natural treefalls (estimate = 1.31,

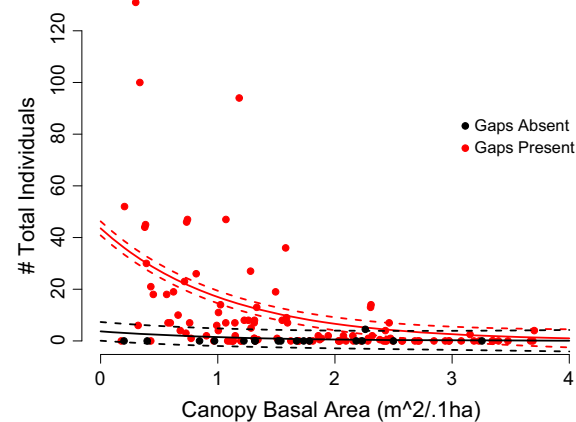


Fig. 1 Model estimated trends for counts of *B. pentamera* in plots without (black) and with (red/gray) canopy gaps. Individual counts are plotted against Canopy Basal Area to demonstrate differences between the two categories despite considerable overlap in canopy density. Estimated means are depicted as solid curves while dashed curves represent 95% confidence bands

SE 0.40). Canopy basal area had a reliably negative effect (estimate = -0.75, SE 0.22), similar to the first analysis described above. Similarly, by separating logging plots and treefall plots it was clear that the former had a stronger relationship, with lower values of canopy basal area in particular leading to much higher predicted counts of *B. pentamera* in logging plots (Fig. 2). There were again more *B. pentamera* in the SLF than at CPRS (estimate = 1.70, SE 0.39). Habitat type was least important, as demonstrated by the AICc comparison, and it was also unreliable as a predictor, with no discernable difference between swamp and upland habitats (estimate = 0.39, SE 0.37).

Population spillover into natural treefalls

There were clear differences in the size of the *B. pentamera* adult population between CPRS and the SLF. Within the CPRS plots there were only 12 adult individuals found, producing a mean of 0.2 per 0.1 ha (SD 0.68); however, in the adjacent forest there were 167 adults, with a mean of 2.38 per 0.1 ha (SD 4.55).

The AICc model comparison revealed that location of treefall plots, as well as the canopy basal area, were more useful predictors of counts of *B. pentamera* individuals than was habitat type (Table 3). The top model (receiving 66% model weight) included only the former two predictors, the model including habitat type was second (34% model weight), and the null model received 0% model weight. The effect of being located in the adjacent forest relative to CPRS was reliably positive (estimate = 1.90, SE 0.48) and the difference between these two locations was most pronounced at lower values of canopy basal area (Fig. 3), which once again had a reliably negative effect (estimate = -0.91, SE 0.31). Habitat type once again had no reliable effect (estimate = 0.52, SE

Table 2 AICc comparison between component models for the second analysis (importance of gap type)

Model components	df	Log-likelihood	AICc	Δ AICc	Weight
Canopy BA, location, gap type	5	-208.62	427.88	0.00	0.66
Canopy BA, location, gap type, habitat type	6	-208.14	429.19	1.31	0.34
Location, gap type	4	-216.04	440.50	12.62	0.00
Location	3	-221.04	448.33	20.46	0.00
Null	2	-241.68	487.49	59.61	0.00

An averaged model was created based on weights shown here

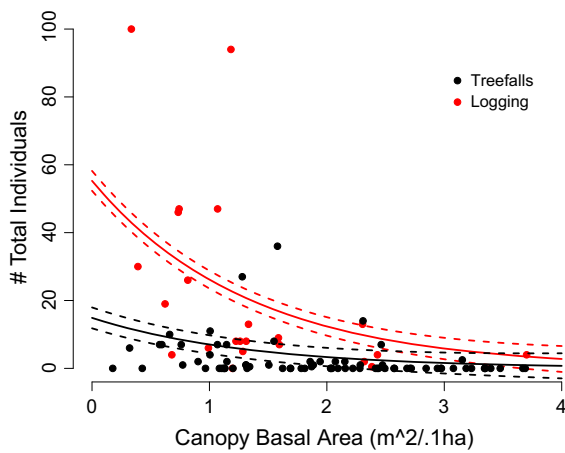


Fig. 2 Model estimated trends for counts of *B. pentamera* in plots with only treefalls (black) or only selective logging (red/gray). Individual counts are plotted against Canopy Basal Area to demonstrate differences between the two categories despite considerable overlap in canopy density. Estimated means are depicted as solid curves while dashed curves represent 95% confidence bands

0.47). There were no significant differences in the number of treefalls per plot between CPRS (Mean = 1.67, SD 0.85) and the SLF (Mean = 1.84, SD 0.90), removing this as a potential reason for differences in predicted *B. pentamera* counts of treefall plots in these two locations.

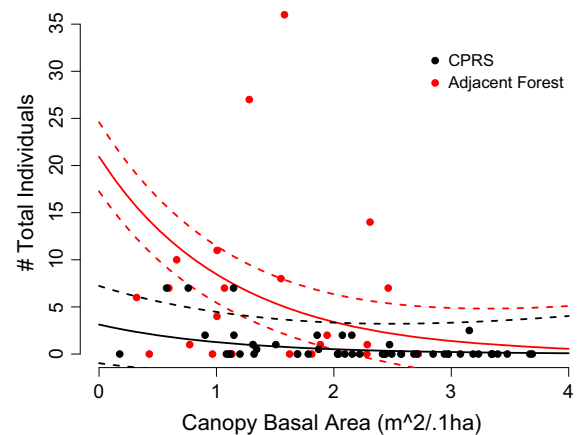


Fig. 3 Model estimated trends for counts of *B. pentamera* only in plots containing treefalls at CPRS (black) and adjacent forest (red/gray). Individual counts are plotted against Canopy Basal Area to demonstrate differences between the two categories despite considerable overlap in canopy density. Estimated means are depicted as solid curves while dashed curves represent 95% confidence bands

Discussion

Our results demonstrate that *B. pentamera* requires canopy gaps in order to recruit. Although canopy basal area had a negative effect on *B. pentamera* counts, this was almost entirely within plots that already had existing gaps. Furthermore, although reproductive

Table 3 AICc comparison between component models for the third analysis (spillover into natural treefalls)

Model components	df	Log-likelihood	AICc	Delta AICc	Weight
Canopy BA, location	5	-208.62	427.88	0.00	0.66
Canopy BA, location, habitat type	6	-208.14	429.19	1.31	0.34
Canopy BA	4	-216.04	440.50	12.62	0.00
Null	2	-241.68	487.49	59.61	0.00

An averaged model was created based on weights shown here

behavior was not the focus of this study, we did not observe any individuals sufficiently large enough to be adults that remained infertile. Thus, in contrast to other tropical invaders, such as *Chromolaena odorata* (Joshi 2006), there did not appear to be a lower light threshold below which *B. pentamera* was reproductively inactive.

The impact of selective logging on *B. pentamera* recruitment was also definitively positive. Relative to treefall gaps (i.e. the natural disturbance regime), selective logging gaps appeared to support much higher densities of *B. pentamera*. This effect was slightly muted as overall canopy cover increased, but over the range of canopy densities observed, plots with selective logging consistently had more *B. pentamera* individuals than treefall plots.

The presence of logging gaps appears to have created footholds for *B. pentamera*. The density of natural treefalls appears to be the same in the SLF and CPRS, however *B. pentamera* is spilling into these natural treefall gaps at much higher rates in the former than the latter. *Bellucia pentamera* apparently had a large population response to the 2000–2002 logging activity and the larger number of adults it produced has presumably increased the relative presence of *B. pentamera* in the seed rain. However, because we were unable to use seed traps or other such approaches to confirm this, we can currently only presume that this is the case.

Qualitative differences between selective logging and natural treefalls

We believe there may be several reasons the selective logging gaps appeared to support more *B. pentamera* than natural treefall gaps, owing to qualitative differences between the two. First, although selective logging removes more biomass from the gap, the remnant boards left behind actually increase the amount of available substrate for epiphytic growth. Over the course of our study we observed that seedlings of *B. pentamera* more readily grew on dead and decaying tree material rather than on bare ground, both on remnant boards (Fig. 4) and natural treefalls. These are currently only anecdotal observations and further systematic study of this growth habit will be needed to determine if the increased availability of growth substrate provided by selective logging may be partially responsible for facilitating this invasion.

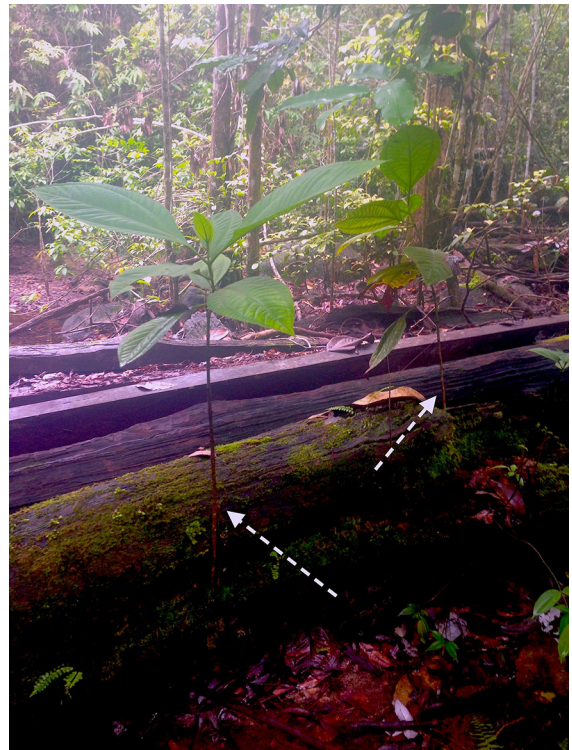


Fig. 4 Arrows highlight *Bellucia pentamera* saplings growing on remnant wood and boards left in gap following selective logging. Many instances of this epiphytic growth habit were observed

A second potential reason for *B. pentamera* recruiting more in logging gaps is due to human dispersal. *Bellucia pentamera* fruits are quite palatable (the species was reportedly introduced into Southeast Asia as a crop fruit; Renner 1989) and frequently encountered on the ground along trails. Additionally, we observed an instance in which a large adult tree had been felled in order to harvest its fruit, further suggesting that loggers may be dispersing fruits specifically to the canopy gaps they create and inhabit for several days while processing new lumber.

The third possibility is that there are qualitative differences we failed to account for, such as greater available light in plots with selective logging. Although we attempted to hold canopy cover constant in our analysis using canopy basal area, more fine-grained analysis might reveal differences in ambient light or microclimate in selective logging gaps versus natural treefall gaps, based on understory characteristics.

Long term effects of selective logging

Within the constraints of our current study (e.g. population is still far from equilibrium, no available comparisons of relative stem densities of native species within disturbed and undisturbed habitat) we are not able to determine if selective logging is necessary for an outright invasion. We are only able to suggest that the current invasion at Gunung Palung National Park is more extensive than it otherwise would have been without an alteration to the disturbance regime. Tropical primary rainforests are generally thought to be relatively resistant to invasions (Rejmánek 1996; Delnatte and Meyer 2012), yet anthropogenic impacts can help invaders overcome such resistance.

Although the immediate effects of selective logging may be relatively benign on faunal biodiversity (Bicknell et al. 2015), alterations to floral communities can be severe and persistent. Selective logging has the potential to provide opportunity for invaders by altering forest structure and composition for significant periods of time thereafter (Rutten et al. 2015; Silk et al. 2002). Recovery can be very slow (Xu et al. 2015), with some forests remaining affected more than 50 years after selective logging ceases (Yamada et al. 2013), possibly due to alterations to nutrient cycling (Villega et al. 2006). Additional work will be needed to determine the response of *B. pentamera* in the following decades to lingering effects of selective logging at Gunung Palung National Park.

Conclusion

By comparing the response of *B. pentamera* to natural as well as anthropogenic disturbances, we were able to determine that selective logging appears to have provided a foothold for *B. pentamera* at Gunung Palung National Park. Further work will be necessary to determine the most important mechanisms by which this invasion is taking place. Understanding the potential idiosyncrasies of this invasion, such as the substrate profile created by selective logging, growth habits of this particular invader, or the behavior of human dispersal agents in this area, might be just as important as considering the change in disturbance regime relative to the natural baseline. Therefore, although we have a preliminary picture of this

invasion, we are still lacking the level of detail necessary for inclusion in meta-analyses attempting to produce generalizations about how disturbance relates to biological invasions. We hope that further work will be able to produce this level of detail, but until then, the current work serves as a case study that assesses the effects of novel disturbance with a proper consideration of the natural regime.

Acknowledgements Permission to conduct research at Gunung Palung National Park was kindly granted by the Indonesian Institute of Sciences (LIPI), the State Ministry of Research and Technology (RISTEK), the Directorate General for Nature Conservation (PHKA) and the Gunung Palung National Park Bureau (BTNGP). CD would like to thank his research counterpart in Indonesia, Irwan Lovadi at Universitas Tanjungpura (UNTAN). This work was supported by grants from the British Ecological Society and the Davis Botanical Society. CD received support from a National Science Foundation Graduate Research Fellowship. CD would also like to thank his field assistants Sudi and Bacong for their help with this project. CD is also grateful for help and advice received from assistants at the Cabang Panti Research Station, as well as S.M. Jaffe, and lodging provided by AJM.

References

- Allcock KG, Hik DS (2003) What determines disturbance-productivity-diversity relationships? The effect of scale, species and environment on richness patterns in an Australian woodland. *Oikos* 102:173–185
- Barton K (2012) MuMIn: multi-model inference. R package version 0.12.2. <http://r-forge.r-project.org/projects/mumin/>
- Belote RT et al (2012) Compositional stability and diversity of vascular plant communities following logging disturbance in Appalachian forests. *Ecol Appl* 22:502–516
- Bicknell J, Struebig M, Davies Z (2015) Reconciling timber extraction with biodiversity conservation in tropical forests using reduced-impact logging. *J Appl Ecol* 52:379–388
- 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
- Burnham K, Anderson D (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York
- Catford JA et al (2012) The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. *Perspect Plant Ecol Evolut Syst* 14:231–241
- Cox RD, Allen EB (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *J Appl Ecol* 45:495–504
- Davis M, Grime J, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88:528–534
- de Kok R, Briggs M, Pirnanda D, Girmansyah D (2015) Identifying targets for plant conservation in Harapan rainforest, Sumatra. *Trop Conserv Sci* 8:28–32

- Delnatte C, Meyer JY (2012) Plant introduction, naturalization, and invasion in French Guiana. *Biol Invasions* 14:915–927
- Denslow J (1987) Tropical rainforest gaps and tree species diversity. *Ann Rev Ecol Syst* 18:431–451
- Dorough JW et al (2007) From plant neighbourhood to landscape scales: how grazing modifies native and exotic plant species richness in grassland. *Plant Ecol* 191:185–198
- Funk JL, Vitousek PM (2007) Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081
- Gorchov D, Thompson E, O’Neil J, Whigham D, Noe D (2011) Treefall gaps required for establishment, but not survival, of invasive *Rubus phoenicolasius* in deciduous forest, Maryland, USA. *Plant Species Biol* 26:221–234
- Grime JP (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194
- Hester A, Hobbs R (1992) Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheat-belt. *J Veg Sci* 3:101–108
- Hobbs R, Huenneke L (1992) Disturbance, diversity and invasion: implications for conservation. *Conserv Biol* 6:324–337
- Jauni M, Gripenberg S, Ramula S (2015) Non-native plant species benefit from disturbance: a meta-analysis. *Oikos* 124:122–129
- Johnson J, Omland K (2004) Model selection in ecology and evolution. *Trends Ecol Evol* 19:101–108
- Joshi C (2006) Mapping cryptic invaders and invasibility of tropical forest ecosystems: *Chromolaena odorata* in Nepal. PhD Dissertation, University of Wageningen, The Netherlands
- Lake JC, Leishman MR (2004) Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biol Conserv* 117:215–226
- Lockwood JL, Hoopes MF, Marchetti MP (2007) *Invasion ecology*. Blackwell Publishing, Oxford
- Lozon J, MacIsaac H (1997) Biological invasions: are they dependent on disturbance? *Environ Rev* 5:131–144
- Marshall AJ (2004) Population ecology of gibbons and leaf monkeys across a gradient of Bornean forest types. PhD Dissertation, Harvard University, Cambridge, MA
- Marshall AJ (2010) Effect of habitat quality on primate populations in Kalimantan: Gibbons and leaf monkeys as case studies. In: Gursky S, Supriatna J (eds) *Indonesian primates*. Springer, New York, pp 157–177
- Marshall AJ, Leighton M (2006) How does food availability limit the population density of white bearded gibbons? In: Hohmann G, Robbins MM, Boesch C (eds) *Feeding ecology in apes and other primates: Ecological, physical, and behavioral aspects*. Cambridge University Press, Cambridge, pp 313–335
- Marshall AJ, Beaudrot L, Wittmer HU (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
- Moles A et al (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *J Ecol* 100:116–127
- R Development Core Team (2012) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Reinhart K, Gurnee J, Tirado R et al (2006) Invasion through quantitative effects: intense shade drives native decline and invasive success. *Ecol Appl* 16:1821–1831
- Rejmánek M (1996) Species richness and resistance to invasions. In: Orians GH, Dirzo R, Cushman JH (eds) *Diversity and processes in tropical forest ecosystems*. Springer, Berlin, pp 153–172
- Rejmánek M, Richardson D (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 Garden* 50:2–97
- Renner S (1990) Reproduction and Evolution in some genera of Neotropical Melastomataceae. *Mem N Y Bot Garden* 55:143–152
- Rutten G, Ensslin A, Hemp A, Fischer M (2015) Forest structure and composition of previously selectively logged and non-logged montane forests at Mt. Kilimanjaro. *For Ecol Manag* 337:61–66
- Silk J, Verburg R, Kebler P (2002) Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodivers Conserv* 11:85–98
- Smart N, Hatton J, Spence C (1985) The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biol Conserv* 33:229–245
- Totland O, Nyeko P, Bjercknes AL, Hegland S, Nielsen A (2005) Does forest gap size affect population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? *For Ecol Manag* 215:329–338
- Villela D, Nascimento M, de Aragao L, da Gama D (2006) Effect of selective logging on forest structure and nutrient cycling in a seasonally dry Brazilian Atlantic Forest. *J Biogeogr* 33:506–516
- Xu H, Li Y, Liu S, Zang R, He F, Spence J (2015) Partial recovery of a tropical rainforest a half-century after clear-cut and selective logging. *J Appl Ecol* 52:1044–1052
- Yamada T, Hosaka T, Okuda T, Kassim AR (2013) Effects of 50 years of selective logging on demography of trees in a Malaysian lowland forest. *For Ecol Manag* 310:531–538