Wild Pigs (*Sus scrofa*) Mediate Large-Scale Edge Effects in a Lowland Tropical Rainforest in Peninsular Malaysia

Junichi Fujinuma[1], Rhett D. Harrison[2]*

1 Graduate School of Environmental Science, Hokkaido University, Sapporo, Hokkaido, Japan, **2** Key Laboratory for Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Science, Mengla, Yunnan, China

Abstract

Edge-effects greatly extend the area of tropical forests degraded through human activities. At Pasoh, Peninsular Malaysia, it has been suggested that soil disturbance by highly abundant wild pigs (*Sus scrofa*), which feed in adjacent Oil Palm plantations, may have mediated the invasion of *Clidemia hirta* (Melastomataceae) into the diverse tropical lowland rain forest. To investigate this hypothesis, we established three 1 km transects from the forest/Oil Palm plantation boundary into the forest interior. We recorded the distribution of soil disturbance by wild pigs, *C. hirta* abundance, and environmental variables. These data were analyzed using a hierarchical Bayesian model that incorporated spatial auto-correlation in the environmental variables. As predicted, soil disturbance by wild pigs declined with distance from forest edge and *C. hirta* abundance was correlated with the level of soil disturbance. Importantly there was no effect of distance on *C. hirta* abundance, after controlling for the effect of soil disturbance. *Clidemia hirta* abundance was also correlated with the presence of canopy openings, but there was no significant association between the occurrence of canopy openings and distance from the edge. Increased levels of soil disturbance and *C. hirta* abundance were still detectable approximately 1 km from the edge, demonstrating the potential for exceptionally large-scale animal mediated edge effects.

Introduction

Tropical forests are threatened by deforestation and forest degradation [1]. Forest degradation arises when factors such as hunting, logging, fire, invasive species, and pollution, often acting in concert, alter the ecology of the forest and reduce its capacity to maintain biodiversity [2,3]. Whereas the area of deforestation is relatively easily defined, forest degradation varies hugely in spatial extent and the severity of its consequences depending on the agents responsible [4,5]. Edge effects occur where a sharp boundary is created between the forest and an open habitat, such as a road, cattle pasture or Oil Palm plantation [6]. The microclimate of the forest edge is changed, particularly with respect to temperature, humidity, wind shear and turbulence [7,8], and these microclimatic changes alter ecological processes at the edge [5,8,9,10]. Irregularly shaped forest fragments and linear cuttings, such as roads, power-line corridors, and pipelines, create a large proportion of edge and can, therefore, lead to forest degradation over substantial areas.

Nevertheless, direct edge effects are usually confined to within 400 m of the edge [5,11]. However, animals may also respond to edges and as a consequence of their mobility can potentially alter plant communities over much larger scales [4,11,12]. Changes in animal abundances at edges have been reported and these are predicted to affect animal-mediate ecological functions, such as pollination [13,14], decomposition [15], predation [16,17], herbivory [16,18], and seed dispersal [19]. However, to date, animal mediated edge effects have rarely been studied [11,16].

Colonization of habitats by exotic species is a major problem for biodiversity conservation [20,21]. Through release from natural enemies [22] or functional traits that confer a competitive advantage over native species [23,24], exotic species may become invasive. Such species command a large proportion of the energy flow through an ecosystem, altering its ecology and displacing native species [25]. Invasive plants are most common in open habitats and in particular those that have been highly disturbed [2]. In general, diverse natural communities, such as undisturbed continental tropical rain forests, rarely suffer from such crises [26,27]. However, contrary to expectations, Pasoh Forest Reserve, Peninsular Malaysia, a highly diverse lowland dipterocarp forest, has been invaded by the South American pioneer shrub *Clidemia hirta* (L.) D. Don. (Melastomataceae). It has been suggested that this invasion may have been mediated by the activities of wild pigs (*Sus scrofa*), which are very abundant at Pasoh [18]. It is thought that soil disturbance caused by the wild pigs, when they root and grub for food, may create colonization micro-sites for *C. hirta* and thereby have abetted the invasion of the rain forest by this alien plant. Moreover, as the pigs are known to feed in the Oil Palm surrounding the reserve, Peters [18] predicted the existence of a gradient of soil disturbance frequency with distance from forest/Oil Palm plantation boundary, and suggested that the abundance of *C. hirta* would decline in a similar fashion. If this conjecture is correct, the invasion of the rain forest at Pasoh by *C. hirta* may be considered a consequence of a large-scale edge effect mediated by wild pigs.

Wild pigs are native throughout Europe and Asia, including tropical SE Asia. Their activities, including feeding, wallowing, and nest construction, have important effects on the ecology of forests [28–30]. Where abundant, their feeding activities can disturb the soil surface over large areas [31]. Pigs grub for insect larvae and fruit in the leaf litter and surface soil using their noses to turnover the soil. Trampling with their sharp hooves further churns the soil, particularly where it is water-logged. In addition, a single pig may cut over 50 seedlings in the construction of a sleeping nest [28]. The activities of wild pigs have shaped invasive plant community composition on oceanic islands [32] and where wild pigs have been introduced they are often considered invasive.

Two possible factors have been put forward to explain the high abundance of wild pigs in the forest at Pasoh: the local extinction of tigers who would previously have been the main predator of pigs [33] and a super-abundance of food in the Oil Palm plantations around reserve [34]. However, tigers have been extirpated over much of their former range in SE Asia and are rare where they still occur, but high abundances of wild pigs are localized phenomena. Moreover, during the early 2000s the Oil Palm plantations around Pasoh were cut down and replanted and during this period the populations of wild pigs declined drastically, before recovering again after the young Oil Palms began fruiting [34]. Thus, a super-abundance of food in the surrounding Oil Palm plantations is strongly suspected as being the primary cause of the high abundance of pigs at Pasoh.

We set out to examine Peters (2001) hypothesis that the invasion of Pasoh by *C. hirta* may have been mediated by wild pigs and their soil disturbing activities. We therefore investigated the spatial pattern of wild pig activity and its impact on *C. hirta* abundance in relation to the forest/Oil Palm plantation boundary. Specifically, we hypothesized that (i) soil disturbance cause by wild pigs activity would decline with distance from the forest/Oil Palm boundary and (ii) *C. hirta* abundance would be correlated with soil disturbance by wild pigs and therefore also decline with distance from the edge of the forest.

Methods

Study site

The study was conducted at Pasoh Forest Reserve, Peninsular Malaysia (2°59′N, 102°18′E) in August 2008. The reserve consists of a primary lowland dipterocarp forest with an area of forest that was lightly selectively-logged in the late 1950s [35]. Three sides of the reserve are surrounded by Oil Palm plantations and the northern side is adjacent to an extensive area of primary hill dipterocarp forest. The emergent layer averages 46 m and the main canopy is from 20 to 30 m in height [36]. Annual rainfall ranges from 1469 to 2350 mm with a mean of 1810 mm [37].

We set up three 1-km long transects from the center of the southern edge of the reserve, adjacent to the Oil Palm plantation, running northwards towards the middle of the forest reserve and its undisturbed northern boundary. Each transect was 6 m wide and there was an interval of 200 m between transects (Figure 1). We elected to use this orientation and positioning of the transects to avoid interference from edge effects of the western and eastern boundaries of the reserve and other fragments of forest located nearby. It should be pointed out that the selective logging took place over 50 yrs prior to the study and, therefore, that logging history is unlikely to have any affect on wild pig behavior today.

Study species

Clidemia hirta originates in humid tropics of Central and South America, extending from southern Mexico to northern Argentina,
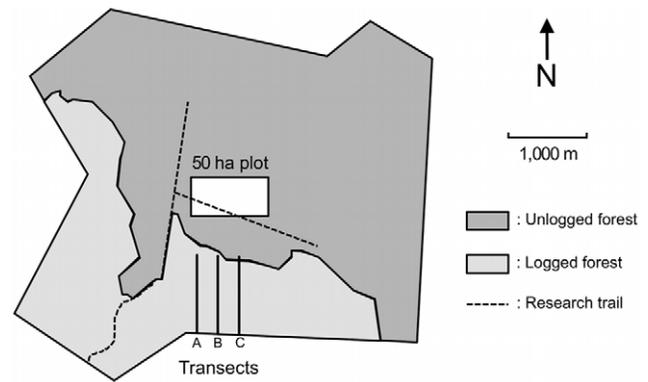

Figure 1. Map of Pasoh Forest Reserve, Peninsular Malaysia. The dark gray area represents unlogged forest and the light gray area represents forest that was lightly selectively logged in the 1950s. The rectangle at the center of the reserve is the CTFS 50 ha permanent plot. Broken lines represent research trails. Solid lines marked A to C are the transects along which our observations were conducted.
doi:10.1371/journal.pone.0037321.g001

and including the islands of the West Indies [38]. It is known to have invaded wet and dry regions of the tropics and subtropics [38]. *Clidemia hirta* is a densely branching woody shrub with a maximum height of 2–3 m and occurs in mesic to wet areas from sea level to about 1500 m asl in both its native and introduced ranges [38]. Although the species re-sprouts vigorously when damaged and may root along fallen stems, it does not exhibit clonal growth. The breeding system of *C. hirta* may include both sexual reproduction and apomixis [39], and the fruits are sweet pulpy, dark-blue berries that are produced year-round [38]. A fruit may contain between 200 and 900 seeds, about 0.5 mm in diameter [40], which are animal dispersed, especially by small birds. Individuals may become reproductive after reaching approximately 0.5 m height. As a pioneer shrub *C. hirta* establishes best in large gaps, but can reach reproductive size across a substantial range of light levels in the forest understorey. In some non-native habitats, in the absence of the herbivorous insects, fungi, and fast-growing competitors, *C. hirta* forms dense tall (3 m height), monotypic thickets that shade out virtually all vegetation below them [41]. In Pasoh, seedlings of *C. hirta* have been observed since 1979 and mature individuals have been present throughout the forest since at least 1997 [18] However, dense thickets of *C. hirta* have not been recorded at Pasoh.

Wild pigs (*Sus scrofa*) have a natural geographical range that extends from Europe to Asia and SE Asia, including Peninsular Malaysia and the islands of Sumatra and Java. Wild pigs have also been domesticated and naturalized in numerous locations. They are omnivorous and a large part of their diet is subterranean in origin. In addition to rooting for their food, they are known to cause disturbance through nest construction and wallowing [29]. At Pasoh large numbers of wild pigs feed on fallen Oil Palm fruit in the Oil Palm plantations surrounding the reserve at night, but return to the forest, which has more cover, during the day [34]. Abundant evidence of their sleeping nests and feeding activities may be found in the forest at Pasoh [28].

Data collection

We divided each of the three transects (Figure 1) into two hundred 5-m sections and recorded the following five parameters in each section: (1) distance from the forest/Oil Palm boundary to the center point of the section; (2) number of *C. hirta* individuals, including seedlings with first leaves; (3) level of soil disturbance by

wild pigs; (4) presence or absence of swampy ground; and (5) presence or absence of open canopy. Soil disturbance level was evaluated from following steps: (a) the section was divided into five 1-m subsections; (b) in each subsection the length of the central line of the transect that crossed soil disturbed by wild pigs was assessed; (c) the subsection was scored as "disturbed" if this length amounted to more than half (50 cm); and finally (d) the "disturbed" subsections were counted up to give the disturbance level for each 5-m section (range 0–5). Soil disturbance by wild pigs can be easily recognized, as pigs turnover the soil leaving an uneven surface of loose soil without a litter layer or any vegetation cover [18]. There are no other animals in Pasoh that disturb soil in this characteristic manner. A section was scored as "swamp present" if water-logged mud or standing water crossed the center line of the transect. Similarly, a section was scored as "canopy opening present" if there was a gap in the foliage ≥1 m in diameter at any point directly above the central line of the section as measured using a canopy densiometer. Foliage lower than the observer's eye was ignored. We recorded the presence of swampy ground and canopy openings, because these factors are known to affect the abundance of wild pigs and *C. hirta*, respectively. All data were conducted by the same observer to assure consistency.

Data analysis

We used a hierarchical Bayesian model to elucidate the causal relationships among *C. hirta* distribution, wild pig activity and environmental factors. We used a Bayesian approach, instead of alternative simpler models, for two reasons. First, there was a possibility of complex effects among factors and, therefore, analysis by simple linear regressions might have produced misleading results or difficult to interpret interactive parameters. Second, it was obvious that there was strong spatial auto-correlation of environmental factors that would have been difficult to parameterize in a simple linear regression. The Bayesian modeling approach, combined with Gibbs sampling of the posterior distribution using a Markov Chain Monty-Carlo (MCMC) process, provides a flexibility that can handle these two conditions with ease [42]. Our Bayesian model is represented in Figure 2. We used Gibbs sampling software WinBUGS to sample the posterior distributions of model parameters from 16000 iterations of a Markov Chain Monty Carlo process, where the first 8000 were discarded as burn-in and the remainder thinned out by sampling once in every ten chains. All analyses were conducted using R 2.14 [43] and the model code and details of the parameter settings are given in Text S1 and Table S1.

Clidemia hirta abundance (log link function) was modeled as a function of distance and environmental factors (top row of Figure 2).

$$\log(\text{CLIDEMIA}) \sim a_{1,k} + d_1 \cdot \text{DISTANCE} + \text{ENVIRONMENT}_1 \tag{1}$$

where the abundance of *C. hirta* (CLIDEMIA) was assumed to follow a Poisson distribution; $a_{1,k}$ is the intercept estimated separately for each transect k; d_1 is the coefficient of DISTANCE, the centralized distance from the forest/Oil Palm boundary, and ENVIRONMENT$_1$ is a virtual variable, representing the observed environmental parameters. ENVIRONMENT$_1$ was estimated as follows (the second row of Figure 2).

$$\text{ENVIRONMENT}_1 \sim \text{SMOOTH}_1 + b_1 \cdot \overset{predicted}{\text{disturbance}} + b_2 \cdot \text{OPEN} + b_3 \cdot \text{SWAMP} \tag{2}$$

where SMOOTH$_1$ is a smoothing device to deal with spatial auto-correlation of environmental factors; $b1$ is the coefficient for the effect of soil disturbance by wild pigs (disturbance), the value of which is predicted from the model of DISTURBANCE (see below); b_2 is the coefficient for the presence or absence of canopy openings (OPEN); and b_3 is the coefficient for the presence or absence of swamp (SWAMP). SMOOTH$_1$ was calculated as follows (third row of Figure 2).

$$\text{SMOOTH}_{1,(i)} = (c_1 - 0.5) \cdot \left(\text{ENVIRONMENT}_{1,(i-1)} + \text{ENVIRONMENT}_{1,(i+1)} \right) \tag{3}$$

where c_1 is the coefficient determining the strength of spatial auto-correlation and takes a range of $0 < c_1 < 1$; and the two ENVIRONMENT$_1$ parameters are from the neighboring sections of the transect. Thus, SMOOTH$_1$ is a certain fraction of averaged neighboring environmental factors and takes a range of -ENVIRONMENT$_1$ < SMOOTH$_1$ < ENVIRONMENT$_1$. If spatial auto-correlation is strong ($c_1 = > 1$), the impact of SMOOTH$_1$ on the estimation of ENVIORNMENT$_1$ of the focal section would be substantial. Disturbance by wild pigs was itself treated as a response variable (forth row of Figure 2).

$$\text{logit}(\text{DISTURBANCE}) \sim a_{2,k} + d_2 \cdot \text{DISTANCE} + \text{ENVIRONMENT}_2 \tag{4}$$

where DISTURBANCE is observed wild pig disturbance, which is a binomial factor of five trials (five subsections per section), and other variables are estimated in the same way as in the CLIDEMIA model (except that the "disturbance" term is removed from ENVIRONMENT).

$$\text{ENVIRONMENT}_2 \sim \text{SMOOTH}_2 + b_4 \cdot \text{OPEN} + b_5 \cdot \text{SWAMP} \tag{5}$$

$$\text{SMOOTH}_{2,(i)} = (c_2 - 0.5) \cdot \left(\text{ENVIRONMENT}_{2,(i-1)} + \text{ENVIRONMENT}_{2,(i+1)} \right) \tag{6}$$

a, b and d were assigned non-informative Gaussian prior probability distributions with a mean of 0 and precision of 10^{-4} (Table S1). c was assigned a non-informative beta distribution with a mean of 0.5 and precision of 12 (Table S1). All the parameters were connected in the same model and thus their posterior distributions were simultaneously estimated based on likelihood.

Results

A total of 1956 individuals of *C. hirta* were recorded in the three transects (1087 plants/ha) (Figure 3). Approximated 18% of the total transect length was categorized as disturbed by wild pigs (Figure 3). Fourteen sections had swamp and 17 sections had canopy openings (Figure 3).

The results of the Bayesian model are presented in Figure 4 and Table S2. For soil disturbance, >97.5% of the posterior distribution of the coefficient of Distance was less than zero (Figure 4; median $d_2 = -4.55$). Thus, there was a significant decline in soil disturbance with increasing distance from the forest/Oil Palm plantation boundary. Soil disturbance was also significantly positively correlated with the presence of swampy ground (Figure 4; median $b_5 = 1.11$), but was not associated with the presence of canopy gaps (95% credible interval incorporates zero, Figure 4).
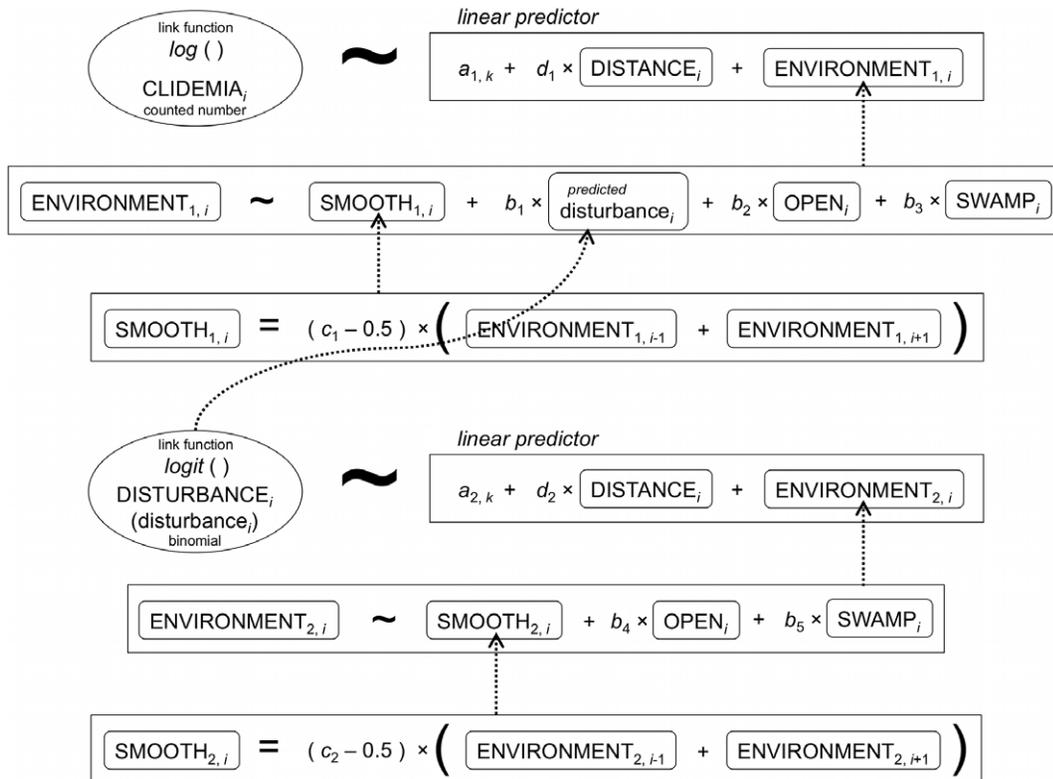
Figure 2. Scheme of Bayesian model. i, section number (5 m transect sections numbered sequentially from forest/Oil Palm boundary for 1 km into the forest); k, transect number (three parallel transects spaced at 200 m intervals). Arrows indicate the origins of parameters.
doi:10.1371/journal.pone.0037321.g002

As suggested by Peters [18], there was a significant correlation between soil disturbance and *C. hirta* abundance (>97.5% of the coefficient's posterior distribution is greater than zero, Figure 4, median $b_1 = 0.17$). *Clidemia hirta* was also significantly associated with canopy openings (Figure 4; median $b_2 = 1.08$), but not swampy ground. Moreover, there was no direct correlation

between distance from the forest edge and the abundance of *C. hirta* (Figure 4; median $d_1 = 0.41$), when the effect of soil disturbance by wild pigs was controlled for in the model.

The estimated posterior distributions of the coefficients for Smooth, c_1 and c_2, were approximately 0.95, indicating a prominent role of spatial auto-correlation in the model (if spatial
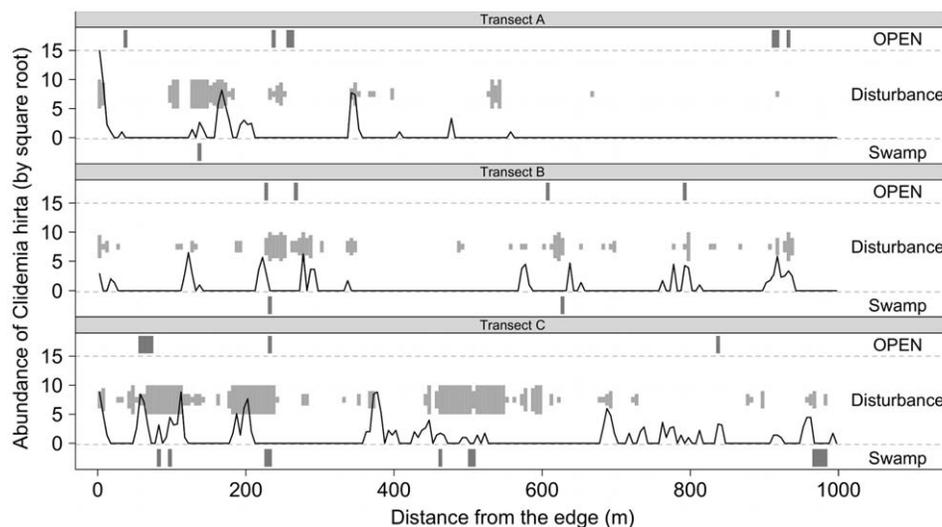

Figure 3. Distribution of measured parameters along each transect. The x-axis represents the distance from the forest edge. The solid line in the middle of each panel represents the abundance of *Clidemia hirta*. The bar in the middle of each panel represents intensity of soil disturbance (scale 0–5). Bars at the top and bottom of each panel represent the location of canopy openings and swampy areas, respectively.
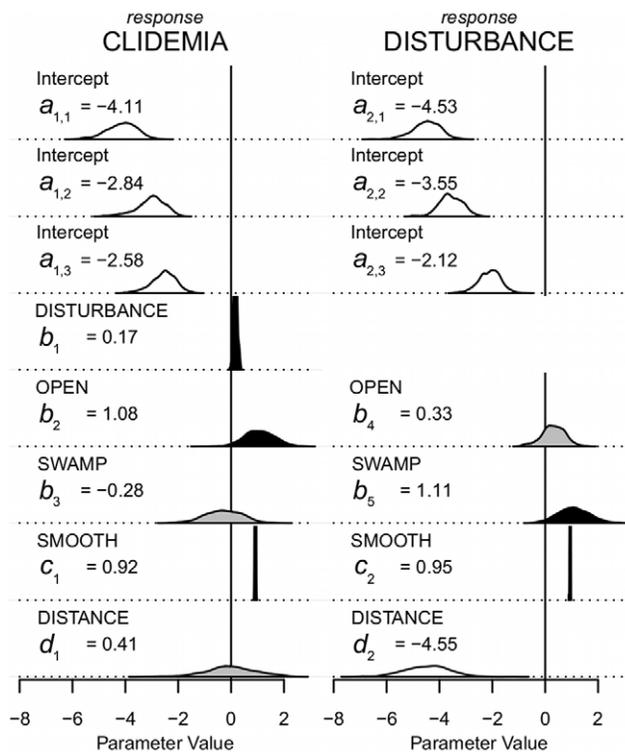doi:10.1371/journal.pone.0037321.g003

Figure 4. Posterior distributions of parameter values for *Clidemia hirta* abundance (left) and soil disturbance (right). Colors were assigned based on the 95% credible interval: Black<0; Grey, incorporating zero; White >0. The median values are given beside each distribution. The x-axis represents the parameter value and the y-axis the probability (some peaks are truncated).
doi:10.1371/journal.pone.0037321.g004

Figure 5. Estimated decline in soil disturbance (A) and *Clidemia hirta* abundance (m-2) (B). Soil disturbance is given as the percentage of 1 m segments affected per 5 m section. The broken lines represent confidence intervals.
doi:10.1371/journal.pone.0037321.g005

auto-correlation had no effect, the values would be expected to converge to 0.5).

Discussion

Our hierarchical Bayesian model detected a significant pattern of declining soil disturbance by wild pigs with increasing distance from the forest/Oil Palm plantation boundary and a positive association between soil disturbance and *C. hirta* abundance. Moreover, there was no correlation between the abundance of *C. hirta* and distance from the forest/Oil Palm boundary, after controlling for the effect of soil disturbance by wild pigs. These results lend support to the suggestion of that there was a cascade of causation from Oil Palm plantations to a high abundance of wild pigs, especially at the edge of the forest, to the *C. hirta* invasion of Pasoh [18]. The large-scale gradient of soil disturbance (Figure 4; median $d_2 = -4.55$) indicates substantially increased levels of wild pig activity in Pasoh around the edge of the forest (Figure 5), and this mostly likely reflects the availability of food in the Oil Palm plantations. Increased levels of soil disturbance and *C. hirta* abundance were still evident approximately 1 km into the forest (Figure 5).

Through their soil disturbing activities, wild pigs act as mobile ecosystem engineers and their activities at Pasoh can be regarded as an indirect biological edge-effect [4,44] that acts over exceptionally large spatial scales (Figure 5). Edge effects in forests usually attenuate within a few tens of meters of the forest/clearing boundary, and almost all measurable effects on plant community composition or dynamics have been confined to within 400 m of
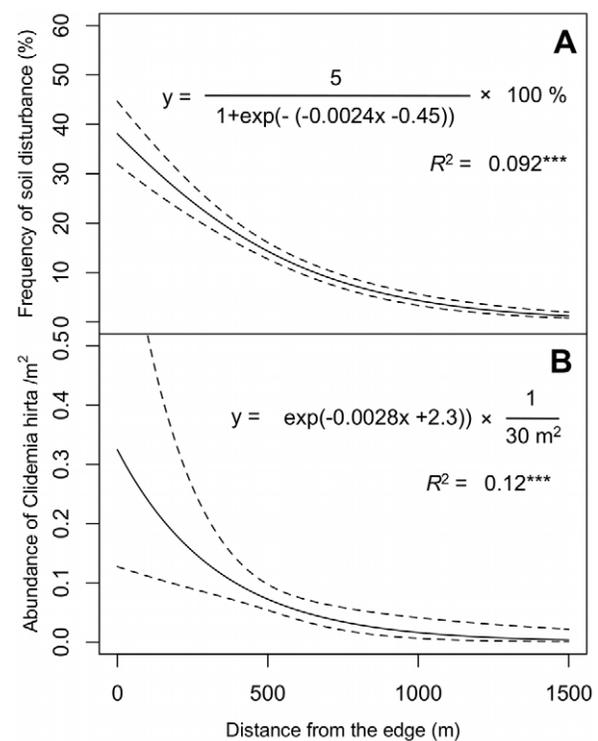
the edge of the forest [5,11]. The spatial extent of the increased soil disturbance by wild pigs at Pasoh is therefore one of the largest among previously reported edge-effects in tropical forests. Moreover, it is likely that these soil disturbing activities are having a profound effect on the plant community [28,32].

It should be noted that a different pattern of soil disturbance might be expected during a mast fruiting year at Pasoh, when more food will be available inside the forest [45,46], or when food resources in the Oil Palm decline, as occurred when the plantation was replanted in the early 2000s [34]. In general, the strength of this type of edge effect is expected to be dependent on the relative difference in food resources between the forest and the surrounding matrix.

The distribution of soil disturbance was also associated with the presence of swampy ground, which is compatible with general observations of wild pig activity [47]. *Clidemia hirta* abundance was also correlated with the presence of canopy gaps. Again, this is compatible with what is understood about the ecology of this plant. Previous studies have found that canopy gaps are more frequent near forest edges over scales of less than 500 m [48,49]. However, we did not find any significant association between the frequency of canopy openings and distance from the forest/Oil Palm boundary (Figure 3).

Our study took place in an area of forest that was lightly selectively logged during the 1950s (Figure 1) [35]. It is possible that an increased incidence of canopy openings, as a consequence of logging, may have helped *C. hirta* colonize the forest. However, the logging occurred over 20 yrs before the first *C. hirta* seedlings were observed and today the logged forest at Pasoh has a higher tree density than the primary forest [35]. Therefore, we believe this scenario to be unlikely. Several researchers have reported an

increased gapiness in the forest interior at Pasoh since the 1980s, when several large windstorms were recorded, and it is likely that such gaps have contributed to *C. hirta*'s persistence. Hence, we support Peters [18]'s suggestion that increased soil disturbance by wild pigs may have enabled *C. hirta* to colonize the forest initially, particularly nearer the edge, and facilitated its movement between canopy gaps within the forest.

Conclusions

We found a highly significant decline in the level of soil disturbance by wild pigs with increasing distance from the forest/ Oil Palm plantation boundary, and a significant positive association between the level of soil disturbance and *C. hirta* abundance. These effects were detectable approximately 1 km into the interior of the forest. This demonstrates a capacity for exceptionally large-scale animal mediated edge effects in tropical forests.

Supporting Information

Table S1 Prior probability distributions used in our hierarchical Bayesian model. The symbols in the left-most column correspond to those used in the model (see Methods section, Text S1). *k* subscript refers to the transect number. (PDF)

Table S2 Results of the estimated posterior distributions from our hierarchical Bayesian model. The symbols in left-most column correspond to those used in the model (see Methods section, Text S1). Significant parameters, whose 95% credible interval does not incorporate zero, are in bold. (PDF)

Text S1 WinBUGS code for the analysis of *Clidemia hirta* abundance and soil disturbance by Wild pigs. (PDF)

Author Contributions

Conceived and designed the experiments: JF RDH. Performed the experiments: JF. Analyzed the data: JF. Wrote the paper: JF RDH.

References

1. Wright SJ (2010) The future of tropical forests. Ann NY Acad Sci 1195: 1–27.
2. Hobbs RJ, Huenneke LF (1992) Disturbance, diversity, and invasion: Implications for conservation. Conserv Biol 6: 324–337.
3. Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: A synthesis. Global Ecol Biogeogr 16: 265–280.
4. Murcia C (1995) Edge effects in fragmented forests: Implications for conservation. Trends Ecol Evol 10: 58–62.
5. Laurance WF, Lovejoy TE, Vasconcelos HL, Bruna EM, Didham RK, et al. (2002) Ecosystem decay of Amazonian forest fragments: A 22-year investigation. Conserv Biol 16: 605–618.
6. Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: A review. Conserv Biol 5: 18–32.
7. Malcolm JR (1998) A model of conductive heat flowin forest edges and fragmented landscapes. Clim Change 39: 487–502.
8. Laurance WF, Curran TJ (2008) Impacts of wind disturbance on fragmented tropical forests: A review and synthesis. Austral Ecol 33: 399–408.
9. Harper KA, Macdonald SE, Burton PJ, Chen J, Brosofske KD, et al. (2005) Edge influence on forest structure and composition in fragmented landscapes. Conserv Biol 19: 768–782.
10. Laurance WF, Camargo JLC, Luizão RCC, Laurance SG, Pimm SL, et al. (2011) The fate of Amazonian forest fragments: A 32-year investigation. Biol Conserv 144: 56–67.
11. Broadbent EN, Asner GP, Keller M, Knapp DE, Oliveira PJC, et al. (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biol Conserv 141: 1745–1757.
12. Prevedello JA, Marcus VV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19: 1205–1223.
13. Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine 'Chaco Serrano.' Ecol Appl 4: 378–392.
14. Chacoff NP, Aizen MA (2006) Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. J Appl Ecol 43: 18–27.
15. Didham RK (1998) Altered leaf-litter decomposition rates in tropical forest fragments. Oecologia 116: 397–406.
16. Kinnaird MF, Sanderson EW, O'Brien TG, Wibisono HT, Woolmer G (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. Conserv Biol 17: 245–257.
17. Herrera JM, Garcia D, Morales JM (2011) Matrix effects on plant-frugivore and plant-predator interactions in forest fragments. Landscape Ecol 26: 125–135.
18. Peters HA (2001) *Clidemia hirta* invasion at the Pasoh Forest Reserve: An unexpected plant invasion in an undisturbed tropical forest. Biotropica 33: 60–68.
19. Rodríguez-Cabal MA, Aizen MA, Novaro AJ (2007) Habitat fragmentation disrupts a plant-disperser mutualism in the temperate forest of South America. Biol Conserv 139: 195–202.
20. Batcheler CL (1983) The Possum and Rata-Kamahi Dieback in New Zealand: A Review. Pac Sci 37: 415–426.
21. Ramakrishnan PS, Vitousek PM (1989) Ecosystem-level processes and the consequences of biological invasions. In: Drake JA, ed. Biological invasions: a global perspective John Wiley & Sons. pp 281–300.
22. Liu H, Stiling P (2006) Testing the enemy release hypothesis: A review and meta-analysis. Biol Invasions 8: 1535–1545.
23. Prieur-Richard AH, Lavorel S (2000) Invasions: The perspective of diverse plant communities. Austral Ecol 25: 1–7.
24. Blumenthal DM (2006) Interactions between resource availability and enemy release in plant invasion. Ecol Lett 9: 887–895.
25. Levine JM, Vilà M, D'Antonio CM, Dukes JS, Grigulis K, et al. (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond 270: 775–781.
26. Levine JM (2000) Species diversity and biological invasions: Relating local process to community pattern. Science 288: 852–854.
27. Fine PVA (2002) The invasibility of tropical forests by exotic plants. J Trop Ecol 18: 687–705.
28. Ickes K, Dewalt SJ, Appanah S (2001) Effects of native pigs (*Sus scrofa*) on woody understorey vegetation in a Malaysian lowland rain forest. J Trop Ecol 17: 191–206.
29. Ickes K, Paciorek CJ, Thomas SC (2005) Impacts of nest construction by native pigs (*Sus scrofa*) on lowland Malaysian rain forest saplings. Ecology 86: 1540–1547.
30. Siemann E, Carrillo JA, Gabler CA, Zipp R, Roger WE (2009) Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US. Forest Ecol Manag 258: 546–554.
31. Singer FJ, Swank WT, Clebsch EE (1984) Effects of wild pig rooting in a deciduous forest. J Wildl Manage 48: 464–473.
32. Aplet GH, Anderson SJ, Stone CP (1991) Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. Vegetatio 95: 55–62.
33. Ickes K (2001) Hyper-abundance of native wild pigs (*Sus scrofa*) in a lowland dipterocarp rain forest of Peninsular Malaysia. Biotropica 33: 682–690.
34. Sun IF, Chen YY, Hubbell SP, Wright SJ, Noor NSM (2007) Seed predation during general flowering events of varying magnitude in a Malaysian rain forest. J Ecol 95: 818–827.
35. Okuda T, Suzuki M, Adachi N, Yoshida K, Niiyama K, et al. (2003) Logging history and its impact on forest structure and species composition in the Pasoh forest reserve — implications for the sustainable management of natural resources and landscapes. In Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC, et al., editor. Pasoh: Ecology of a lowland rain forest in Southeast Asia, Springer-Verlag, Tokyo. pp 15–34.
36. Manokaran N, Swaine MD (1994) Population Dynamics of Trees in Dipterocarp Forests of Peninsular Malaysia. No. 40 in Malayan Forest Records. Forest Research Institute of Malaysia.
37. Noguchi S, Nik AR, Tani M (2003) Rainfall characteristics of tropical rainforest at Pasoh forest reserve, Negeri Sembilan, Peninsular Malaysia. In Okuda T, Manokaran N, Matsumoto Y, Niiyama K, Thomas SC, et al., editor. Pasoh: Ecology of a lowland rain forest in Southeast Asia, Springer-Verlag, Tokyo. pp 51–58.

38. Wester LL, Wood HB (1977) Koster's Curse (*Clidemia hirta*), a weed pest in Hawaiian forests. Environ Conserv 4: 35–41.

39. Renner SS (1989) A survey of reproductive biology in neotropical Melastomataceae and Memecylaceae. Ann Missouri Bot Gard 76: 496–518.

40. Dewalt SJ, Denslow JS, Hamrick JL (2004) Biomass allocation, growth, and photosynthesis of genotypes from native and introduced ranges of the tropical shrub *Clidemia hirta*. Oecologia 138: 521–531.

41. Smith CW (1992) Distribution, status, phenology, rate of spread, and management of Clidemia in Hawai'i. In: Stone CP, Smith CW, Tunison JT, eds. Alien plant invasions in native ecosystems of Hawaii, management and research, University of Hawaii Cooperative, Hawaii, U.S.A. pp 241–253.

42. Clark JS (2005) Why environmental scientists are becoming Bayesians. Ecol Lett 8: 2–14.

43. R Development Core Team (2011) A Language and Environment for Statistical Computing. The R Project for Statistical Computing. Available: http://www.r-project.org/. Accessed 2011 Jul 08.

44. Ries L, Fletcher RJ, Battin Jr. J, Sisk TD (2004) Ecological responses to habitat edges: mechanisms, models, and variability explained. Annu Rev Ecol Evol Syst 35: 491–522.

45. Ashton PS, Givinish TJ, Appanah S (1988) Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. Am Nat 132: 44–66.

46. Sakai S, Momose K, Yumoto T, Nagamitsu T, Nagamasu H, et al. (1999) Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. Am J Bot 86: 1414–1436.

47. Graves HB (1984) Behavior and Ecology of Wild and Feral Swine (*Sus Scrofa*). J Anim Sci 58: 482–492.

48. Pereira Jr. R, Zweede J, Asner GP, Keller M (2002) Forest canopy damage and recovery in reduced-impact and conventional selective logging in eastern Para, Brazil. Forest Ecol Manag 168: 77–89.

49. Asner GP, Keller M, Silva JM (2004) Spatial and temporal dynamics of forest canopy gaps following selective logging in the eastern Amazon. Glob Change Biol 10: 765–783.