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Replanting reduces frog diversity in oil palm

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Abstract

A growing body of literature has demonstrated significant biodiversity losses for many taxa when forest is converted to oil palm. However, no studies have directly investigated changes to biodiversity throughout the oil palm life cycle, in which oil palm matures for 25-30 years before replanting. This process leads to major changes in the oil palm landscape that likely influence species assemblages and ecosystem function. We compare frog assemblages between mature (21-27 year old) and recently replanted (1-2 year old) oil palm in Sumatra, Indonesia. Across eighteen 2.25-ha oil palm plots, we found 719 frogs from 14 species. Frog richness was 31 percent lower in replanted oil palm (9 species) than mature oil palm (13 species). Total frog abundance was 47 percent lower in replanted oil palm, and frog assemblage composition differed significantly between the two ages of oil palm. The majority of frog species were disturbance-tolerant, although we encountered four forest-associated frog species within mature oil palm despite a distance of 28 km between our study sites and the nearest extensive tract of forest. Although it is clear that protection of forest is of paramount importance for the conservation of tropical fauna, our results indicate that management decisions within tropical agricultural landscapes also have a profound impact on biodiversity. Practices such as staggered replanting or variable retention of mature oil palm patches could help maintain frog diversity in the oil palm landscape.

Key words: amphibian; biodiversity loss; management; SE Asia; tropical agriculture

DEFORESTATION TO MAKE ROOM FOR EXPANDING AGRICULTURE IS WIDELY recognized as a leading threat to terrestrial biodiversity (Rudel *et al.* 2009, Vié et al. 2009, Wilcove and Koh 2010, Laurance *et al.* 2014). Nonetheless, agricultural areas can support substantial biodiversity, which is valuable inherently as well as for the sustainable function of agricultural landscapes (Balvanera et al. 2006), increased ecosystem resilience (Elmqvist *et al.* 2003), and better human health (Chivian 2002). Plantations are particularly important, as they: (a) have been shown to play a role in conserving biodiversity (Brockerhoff et al. 2008, Pawson et al. 2013); (b) can be readily modified to better accommodate biodiversity (Mang & Brodie, in press); and (c) will occupy an increasingly large proportion of human-modified landscapes (Hartley 2002). A major characteristic of plantation crops such as coffee, mahogany, rubber, and oil palm is that they are routinely clear-cut and replanted (Sim & Nykvist 1991, Mayhew *et al.* 2003, Ruf & Lançon 2004, Ooi & Heriansyah 2005). Thus, it is critical that more research be done to develop intelligent replanting schemes that are as biodiversity-friendly as possible while also balancing factors such as yield effects, cost, and disease (Luskin & Potts 2011). This is particularly true for oil palm (*Elaeis guineensis*), which, owing to its high structural complexity and long life span in comparison to other forms of agriculture, has the potential to support relatively high levels of biodiversity (Foster *et al.* 2011).

Understanding the best ways to replant oil palm is also urgent, as a disproportionate area of senescent oil palm is currently due for replanting, given the boom in oil palm cultivation in the mid-1980s and the 25-30 year life cycle of the crop (Snaddon *et al.* 2013). Replanting allows growers to more easily assess fruit ripeness and also typically increases crop production, as a block of aging oil palm is replaced with a newer, hardier, and higher-yielding strain (Corley & Tinker 2003). Replanting usually occurs through felling of oil palm trees followed by either stacking or chipping the trunks and then planting oil palm seedlings. Prevailing wisdom within the oil palm industry also recommends the planting of leguminous vegetation, which increases biological nitrogen fixation, stores nutrients, and then slow-releases organic matter back into the oil palm as the legumes die following closure of the oil palm canopy (Agamuthu & Broughton 1985). Legumes are also thought to help prevent beetle invasions, stem soil runoff, and reduce disease spread (Chee 2007, Goh *et al.* 2007, Noor *et al.* 2013).

While there has been significant attention paid to best practices for replanting in terms of oil palm health, there has been very little research focused on the relationship between replanting methods and biodiversity. As is the case with much decision-making in the conservation world at large (Sutherland et al. 2004), there is a great need for more scientific evidence behind oil palm-related conservation decisions (Turner *et al.* 2008, Foster *et al.* 2011). As it currently stands, the oil palm industry typically makes management decisions based primarily on economic factors (*e.g.* Noor 2003, Ruf & Lançon 2004), although sustainability efforts are increasing (*e.g.* RSPO 2007).

The current *modus operandi* of replanting involves clearing large (1-5 km) swaths of mature oil palm all at once, leading to extensive areas of homogeneous vegetation (Luskin & Potts 2011). Luskin & Potts therefore advocate novel, staggered replanting schemes designed to increase vegetative heterogeneity at the landscape scale. They argue that greater vegetative diversity in the oil palm landscape will increase habitat heterogeneity, thereby supporting a greater diversity of species. While their conceptual models have yet to be tested, they accord with empirical studies that link increased vegetative complexity in the matrix to increased biodiversity (Kanowski *et al.* 2006, Kurz *et al.* 2014).

While it is clear that preserving large tracts of forest is the top priority for conserving tropical biodiversity (Barlow *et al.* 2007; Gibson *et al.* 2011), management in plantations and other agricultural areas is also important as part of a comprehensive conservation strategy to support biodiversity and ecosystem function within and across landscapes (Daily *et al.* 2001, Hartley 2002, Foster *et al.* 2011). Although several studies have found differences in frog assemblages in forest and oil palm (Gillespie *et al.* 2012, Faruk *et al.* 2013, Gallmetzer & Schulze 2015, Konopik et al. 2015), ours is the first to examine changes in frog assemblages between mature and recently replanted oil palm. We also suggest ways that conservation practitioners and oil palm estate managers can identify which species are being harmed by current management methods and better conserve frog assemblages in tropical working landscapes through more biodiversity-friendly replanting practices.

METHODS

STUDY AREA AND SAMPLING DESIGN.— Fieldwork took place in Sumatra, Indonesia, in partnership with the Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Project collaboration between the University of Cambridge and the Sinar Mas Agro Resources and Technology Research Institute, SMARTRI (Foster et al. 2014; www.oilpalmbiodiversity.com). The BEFTA Project is located in actively managed oil palm estates owned and managed by Pt Ivo Mas Tunggal, a company owned by Golden Agri Resources and with technical advice from Pt Smart. The estates are located in the Siak regency of Riau province, Sumatra (0º55'56" N, 101º11'62" E). This area receives an average of 2.4 m of rainfall per year, with the natural landscape characterized by wet lowland forest on sedimentary soils. Our study area was logged in the 1970s and the resulting degraded logged forest was converted to oil palm from 1985-1995. At the regional scale, between 1990 and 2012 tropical forest cover in Riau declined from 63 percent to 22 percent mainly due to oil palm expansion (Ramdani & Hino 2013).

The estates are a mixture of mature and recently replanted oil palm. The area surrounding the estates is mainly mature oil palm, with varying amounts of other crops. Our study included twelve 2.25-ha plots of mature oil palm (21-27 years old) and six plots of recently replanted oil palm (1-2 years old). We obtained different sample sizes for the two ages of oil palm because data for the mature plots was collected as part of a larger manipulative study (Foster *et al.* 2014). To minimise variation among plots, all plots were established in flat areas 40-60 m asl. Understory vegetation is generally abundant in between the oil palm trees, except along harvesting paths, which are located along every other oil palm row and are kept open to facilitate access to the palms. In the replanted plots, this vegetation is dominated by *Mucuna bracteata* that is planted between the oil palm rows. Replanted plots also contain logs and litter from the previous mature oil palm trees, which are cut and stacked between the new replanted rows. Mature plots contained palm trees 12-15 m in height with a closed canopy and replanted areas contained trees 2.5-4 m in height with an open canopy. Due to the replanting schedule, recently replanted plots could not be paired with mature plots, but were selected to be no more than 15 km from the mature plots (Fig. 1). The sole remnant forest patch within the oil palm estates is a 112 ha fragment of low-quality secondary swamp forest located 1 km from our nearest sampling site. The closest extensive forest area (>5000 ha) is >28 km from all our sites. One-third of replanted plots and one-fourth of mature plots contained some form of standing or slow-moving water (*i.e.* stream, spring, or pond) at the time of the study.

AMPHIBIAN SAMPLING.—In both replanted and mature plots we conducted frog surveys around the perimeter of a 50 x 50 m square area. Each square transect was sampled three times over the course of six weeks and all sampling occurred at night between 1900-0200 h. Sampling took place during the dry season in February and March 2014; weather during the sampling period averaged only 0.007 mm/d rain in Libo Estate in February 2014 and 1.81 mm/d in March, compared to a monthly average of 5.51 mm/d (calculated over the period 01/01/12 - 31/08/14). These consistently dry conditions meant that weather was comparable for all sampling of plots throughout the study period. In addition, we rotated sampling between mature and replanted plots to help control for any minor weather-related variability. We used distance- and time-constrained visual encounter surveys to sample frogs (Kurz *et al.* 2014). For each transect, one observer (DJK) walked slowly for one hour along the perimeter of the 50 x 50 m square, lightly disturbing vegetation and searching for frogs within 2 m of either side of the perimeter and from 0–2.5 m above the ground (von May *et al.* 2010). Each frog observed was captured and identified with the help of a field guide for Borneo (Inger & Stuebing 2005, the best available resource for the identification of the frogs of Sumatra) and then released. Photographs were taken as necessary for further identification. Time needed for capture and identification was excluded from the one-hour limit. The observer noted the microhabitat in which each frog was found (categories included: fern, ground, forb, palm litter, empty fruit bunch, or other), the height of the frog off the ground (0, 0-0.5 m, 0.5-1 m, etc), and whether the frog was within 5 m of a water source.

ENVIRONMENTAL VARIABLES.—Environmental variables were also recorded along the perimeter of the 50 x 50 m square area. We collected data on vegetation cover, canopy cover, and temperature. Vegetation cover was recorded at 20 points along the 200 m transect perimeter. At each point, a single observer (AAKA) estimated vegetation cover in a 16 m^2 plot to the nearest 5 percent according to seven categories: bare ground, fern, forb, fallen palm frond, empty fruit bunch (EFB), dead vegetation, and other. Vegetation estimates were then averaged across the 20 points to give a score for each plot.

Percent canopy cover was collected using a convex spherical densiometer (Lemmon 1956). Night and daytime temperature data were collected using high-capacity Thermochron® iButtons (Maxim Integrated, San Jose, California) placed 1 m above the ground and set for an average of seven days and nights at each plot, collecting readings every three hours.

DATA ANALYSIS.—Statistical analyses were conducted in the 'vegan' and 'BiodiversityR' (Kindt & Coe 2005) packages in R (Team R 2013), and EstimateS Version 9.1.0 (Colwell 2013) was used to construct rarefaction curves. Survey data from all three transect visits at each plot were pooled before analysis. We tested for spatial autocorrelation of species richness results within the datasets for each plot type and found no spatial autocorrelation for either mature plots (Moran's $I = 0.08$, $p = 0.35$) or replanted plots (Moran's $I = -0.39$, $p = 0.51$). Because richness data did not meet assumptions for normality and homoscedasticity, we used Mann-Whitney U tests to compare species richness and a Welch's *t*-test to compare abundance between mature and replanted plots. To estimate species richness in each oil palm type, we used Chao 1, a simple species richness estimator based on the number of rare species in the sample (Chao 1984).

To test for differences in community composition between mature and replanted plots, we ran a permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) with 10,000 permutations on fourth-root standardized Bray-Curtis dissimilarities. We then calculated the contributions of each species to overall dissimilarity using the 'simper' function in the R package 'vegan' (Oksanen *et al.* 2013). We used redundancy analysis (RDA) to visualise relationships among frog species, mature and replanted oil palm plots, and water availability in the plots (Kindt & Coe 2005). Because water sources were variable and difficult to quantify precisely across oil palm plots, we used the average number of frogs per transect observed within 5 m of water as a proxy for water availability.

To compare the environmental variables across habitat types, we first tested the data for each environmental variable for normality and homoscedasticity. We then ran Welch's *t*-tests on variables with normal and homoscedastic data and Mann-Whitney U tests on variables with non-normal and non-homoscedastic data, and applied a Bonferonni correction to account for multiple comparisons (Whitlock & Schluter 2009).

RESULTS

FROG ASSEMBLAGES.—Across 18 oil palm plots, we sampled 719 individual frogs representing 14 species from 6 families. We found a total of 13 species in mature plots and 9 species in replanted plots (Table 1). Of the nine species found in replanted palm, only one (*Hylarana nicobariensis*) was not found in mature palm as well. However, five species occurred in mature plots that were not encountered in replanted oil palm: *Duttaphrynus melanostictus, Humerana miopus, Leptobrachium nigrops, Limnonectes paramacrodon,* and *Polypedates colletti*. Most species recorded were generalists that are known to thrive in various types of forest and agricultural habitats, although three of the species found only in mature oil palm – *L. nigrops*, *L. paramacrodon*, and *P. colletti* – are thought to dwell almost exclusively in forest (Inger & Stuebing 2005; IUCN 2015). We could not assign a species to frogs of the genus

Microhyla given the lack of clear frog identification resources for Sumatra. Because of this significant lack of regional information as well as the varying habitat preferences of frogs in the genus *Microhyla*, we did not consider the *Microhyla* sp. in our study as either generalist or predominantly forest-associated. Additionally, we opportunistically encountered *Kalophrynus punctatus* (a forest-associated, IUCN-listed 'Vulnerable' species) outside of our transect area in mature oil palm. One half of the species we encountered on our transects – *H. chalconota, H. glandulosa, H. miopus, H. nicobariensis, L. nigrops, L. paramacrodon,* and *P. colletti* – are endemic to Sundaland, as is *K. punctatus*.

Per-plot frog species richness was higher in mature oil palm than in replanted palm (Mann-Whitney U test, U = 63, $P = 0.01$; Fig. 2), as was per-plot frog abundance (Welch's *t*-test, $P = 0.02$, Fig. 2). Rarefaction curves for all samples combined across sites also showed higher species accumulation in mature oil palm (Fig. 3), with an estimated richness (given by Chao 1) of 13.5 species for mature plots and 10 species for replanted plots. There was also a significant difference in frog assemblage composition between plot types (PERMANOVA, $F_{1,16} = 5.34$, $P = 0.001$).

The first two axes in the redundancy analysis explained 43.6 percent of the variation in frog assemblages among sites (Fig. 4). More species were positively associated with mature plots compared to replanted plots. *P. leucomystax* and *H. chalconota* clustered towards water. Similarity percentages (SIMPER) showed that *P. leucomystax*, *H. chalconota*, *H. miopus*, and *Microhyla sp.* contributed most to the average overall Bray-Curtis dissimilarity between mature and replanted plots (Table S1).

ENVIRONMENTAL VARIABLES.—All environmental variables differed significantly ($p < 0.001$) between mature and replanted oil palm. Replanted plots contained less fern cover (-94%), canopy cover (-96%), bare ground (-63%), palm fronds (-100%), and empty fruit bunches (-92%). Replanted plots were also characterized by more herbaceous plant cover (+341%), higher day-time temperatures (+3.3 ºC), and lower night-time temperatures (-1.6 ºC).

MICROHABITAT PREFERENCES.—In mature plots, we found more frogs on bare ground than in any other microhabitat, whereas in replanted oil palm we found frogs most commonly on the ground-cover legume *M. bracteata.* Frogs in mature plots were also commonly found in fern, forb, and fallen palm frond microhabitats. The average height at which frogs were encountered was significantly higher in replanted oil palm (0.60 m) than mature oil palm (0.38 m) (Mann-Whitney U Test, W = 37070, $P < 0.001$). For the four species of frogs found four or more times in both mature and replanted oil palm, three showed a change in most commonly occupied microhabitat: *Microhyla* sp. (ground in mature, forb in replanted); *H. chalconota* (fern in mature, forb in replanted); and *P. leucomystax* (fern in mature, forb in replanted).

DISCUSSION

Our study is the first to examine and demonstrate the loss of frog diversity and a change in frog assemblage composition between mature and recently replanted oil palm. These findings add an additional layer of understanding to several others that show lower frog richness (Gallmetzer & Schulze 2015, Konopik et al. 2015) and a difference in frog assemblages (Gillespie et al. 2012, Faruk et al. 2013, Gallmetzer & Schulze 2015, Konopik et al. 2015) in oil palm as compared to forest. Our results point to new ways that conservation of tropical frogs can move forward via a more nuanced understanding of tropical plantation systems and their potential value for preserving frog diversity and function in agricultural landscapes.

THE INFLUENCE OF ENVIRONMENTAL VARIABLES ON FROG ASSEMBLAGES.— Environmental variables seemed to be a major driver behind the significantly more abundant and species-rich frog assemblages in mature oil palm. Critically, mature plots contained closed canopies with 73.8-89.1 percent canopy cover, compared to replanted palm plots, which essentially lacked any canopy cover. The open canopy and resulting lack of temperature stability that we saw in our replanted oil palm plots could make it difficult for frogs to colonize, survive, and reproduce in replanted oil palm patches, particularly during warm or dry spells. Other studies show that replanted oil palm is hotter and drier than mature oil palm (Luskin & Potts 2011; Hardwick *et al.* 2015), and frogs are susceptible to desiccation as temperature increases and humidity decreases (Rittenhouse *et al.* 2008, Nowakowski *et al.* 2015).

Vegetation cover was another major environmental factor that likely contributed to observed differences in frog assemblage structure. Across a broad range of ecosystems, vegetation structure is known to play a role in shaping frog ensembles (*e.g.*, Parris & McCarthy 1999, Jansen & Healey 2003, Urbina-Cardona *et al.* 2006). The *M. bracteata* legume that is widely planted in Sumatra between rows of replanted palm was by far the most common type of vegetation in replanted oil palm (>80% cover across all replanted plots). By comparison, mature plots had a greater mixture of bare ground, fern, fallen palm fronds, forbs, and empty fruit bunches. It is possible that the homogeneity of the forbaceous cover in replanted palm plots is not as conducive to attracting as diverse a suite of frog species as the more heterogeneous vegetative structure of mature plots.

THE IMPORTANCE OF MICROHABITAT OPTIONS.—For the four frog species found commonly in both types of oil palm, three showed a change in their most frequently occupied microhabitat between mature and replanted palm. This pattern was likely due to decreased microhabitat diversity in replanted palm. Replanted oil palm contained an overwhelming majority of *M. bracteata* forbaceous cover and therefore contained far less fern cover, far fewer patches of bare ground, and no palm trunks (as old palm trunks were chipped at replanting) as compared to the older oil palm. Also, frogs were found significantly higher off the ground in replanted palm plots, further indication of shifting niches. Environmental heterogeneity has been shown to influence species diversity and assemblage structure in other tropical amphibian assemblages (Keller *et al.* 2009).

OIL PALM AND FROG ASSEMBLAGE COMPOSITION.—Replanted palm plots were 20-25 years younger than mature plots, and thus did not have time to recover from the severe disturbance event of replanting and develop the greater microclimate buffering, increased canopy cover, and greater leaf litter cover of older oil palm plots (Luskin & Potts 2011). Perhaps because of the more favorable microclimate conditions in mature oil palm, older plots may be more accessible to not only a broader assemblage of disturbance-tolerant species, but also species that typically thrive in forested areas. On our transects we encountered *L. paramacrodon*, *L. nigrops*, and *P. colletti*, three forest-associated species (Inger & Stuebing 2005), as well as an opportunistic sighting of the forest species *Kalophrynus punctatus*. The presence of these species indicates that species traditionally considered forest-associated can inhabit oil palm. Furthermore, the lack of any extensive (> 5000 ha) forest tracts within 28 km of our oil palm plots, and the fact that the plots were originally established 20-30 years ago, suggests that some forest-associated frogs are able to sustain populations in oil palm independent of a forest source population.

In several ways, our results align with the findings of other studies on frog assemblages in oil palm. As in our study, Gillespie *et al.* (2012), Faruk *et al.* (2013), Gallmetzer & Schulze (2015), and Konopik et al. (2015) encountered frog assemblages in oil palm dominated by disturbance-tolerant species. Thus, across all studies on frogs in oil palm including ours, frog ensembles were impoverished in their reflection of known endemic and forest-associated species. Several of the same Southeast Asian generalist frog species, including *Hylarana erythraea, Hylarana nicobariensis, Fejervarya limnocharis* (recorded as *Fejervarya* sp. in our study given the similarity between *F. limnocharis* and *F. cancrivora* and the lack of frog ID guides for Sumatra), and *Polypedates leucomystax*, were common in oil palm plantations in our study as well as other studies on frogs in oil palm in Southeast Asia (Gillespie et al. 2012, Faruk et al. 2013, Konopik et al. 2015). Like Faruk *et al.* but unlike Gillespie *et al.* and Konopik *et al.*, we found multiple microhylid species in oil palm. We found four forest-associated species within mature oil palm located >28 km from any large tracts of forest, which lends additional support to the possibility that untapped potential exists for frog conservation in oil palm landscapes (Konopik et al. 2015).

CONSERVATION RECOMMENDATIONS.—Based on our findings, it seems that the process of clear-cutting and replanting mature oil palm results in the loss of frog species richness and abundance and presumably the loss of ecological functions performed by those frogs. If further studies establish that these results are typical for frogs as well as other taxa, then it will be important to consider replanting strategies that preserve biodiversity in the oil palm landscape, provided that these management practices do not significantly compromise net yield. These strategies might include: reducing the size of areas that are clear-cut and replanted so that habitat heterogeneity is increased at smaller scales (Ramage et al. 2013); maintaining connectivity among swaths of mature oil palm; replanting in continuous bands so that swaths of habitat of the same age are maintained (Luskin & Potts 2011); and replanting away from waterways in an effort to reduce erosion and thereby maintain “appropriate riparian buffer zones” (RSPO 2007).

By increasing both small-scale heterogeneity and connectivity of mature oil palm, it may be possible to avoid the turnover of frog assemblages between mature and replanted plots that, based on our data, included the loss of five species (three of them forest-associated) and greatly decreased abundance of five others (Table 1). While feasible in terms of the machinery required, novel replanting techniques could call for a substantial financial investment on the part of oil palm companies.

Amphibians are of central importance in many ecosystems (Wissinger *et al.* 1999, Whiles *et al.* 2006), and frogs are among the most abundant vertebrate groups in our study system. Among their many functions, predation in particular may be important; it is generally recognized that maintaining diverse and abundant natural predators in agricultural areas can help reduce pest outbreaks (Wood 2002). Furthermore, the protection of amphibian diversity is urgent given amphibian declines worldwide (Stuart *et al.* 2004). Our study shows that mature oil palm can sustain substantial frog diversity and abundance, including three species typically considered forest-associated, and indicates that frog assemblages are likely harmed in the replanting process. We therefore suggest that it is worthwhile to consider how frog populations and their functions might be better conserved during and after replanting in oil palm landscapes.

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Table 1. *Species list of all frogs encountered on transects in mature and replanted oil palm plots in Riau province, Sumatra, Indonesia. Because of the unequal sample size between mature (n=12) and replanted (n=6) plots, and to facilitate direct comparisons between columns, we have divided the numbers in the "Mature" column by two. The "G/F" column indicates whether the species is typically described in the literature as a habitat generalist (G) or forest-associated (F) species (Inger & Stuebing 2005; IUCN 2015). We use "habitat generalist" to refer to species that can be found in forests and/or various types of disturbed habitats, whereas we use "forest-associated" to refer to species that have been thought to dwell almost exclusively in rain forest. We have not classified* Microhyla sp. *as either generalist or forest-associated because of the varying habitat preferences of similar species in the genus* Microhyla *and the lack of detailed frog identification resources for Sumatra.* In *addition to the species listed here, we opportunistically encountered* Kalophrynus punctatus*, a forest-associated species listed as "Vulnerable" by the IUCN, outside of our transects, in mature oil palm.*

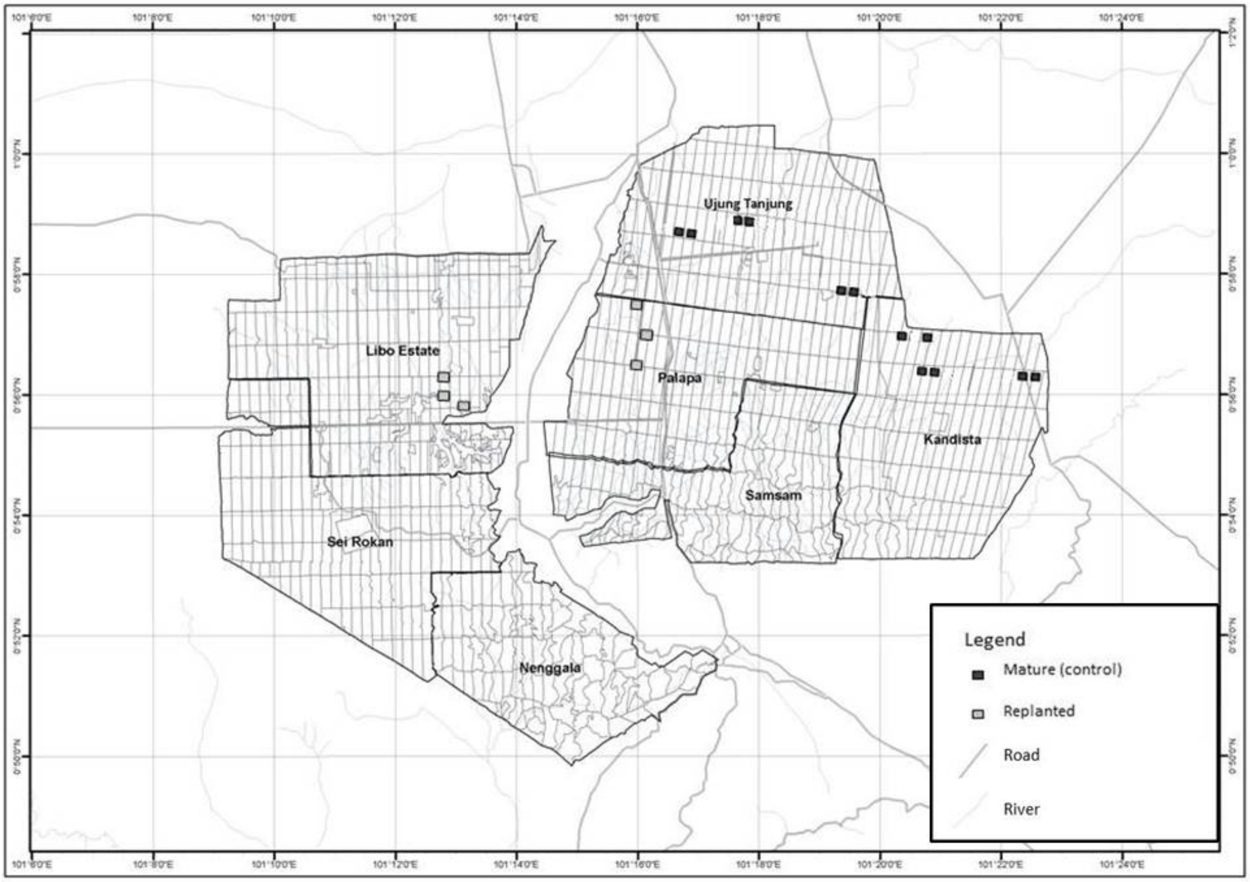
Family	Species	G/F	Mature	Replanted
Bufonidae	*Duttaphrynus melanostictus*	G	3	0
Dicroglossidae	*Fejervarya* sp.	G	18	9
Dicroglossidae	*Limnonectes paramacrodon*	F	3	0
Megophryidae	*Leptobrachium nigrops*	F	1	0
Microhylidae	*Kaloula baleata*	G	6	1
Microhylidae	*Kaloula pulchra*	G	3	9
Microhylidae	*Microhyla* sp.	N/A	28	11
Ranidae	*Hylarana chalconota*	G	63	1
Ranidae	*Hylarana erythraea*	G	1	7
Ranidae	*Hylarana glandulosa*	G	17	3
Ranidae	*Humerana miopus*	G	40	0
Ranidae	*Hylarana nicobariensis*	G	0	5
Rhacophoridae	*Polypedates colletti*	F	1	0
Rhacophoridae	*Polypedates leucomystax*	G	102	106

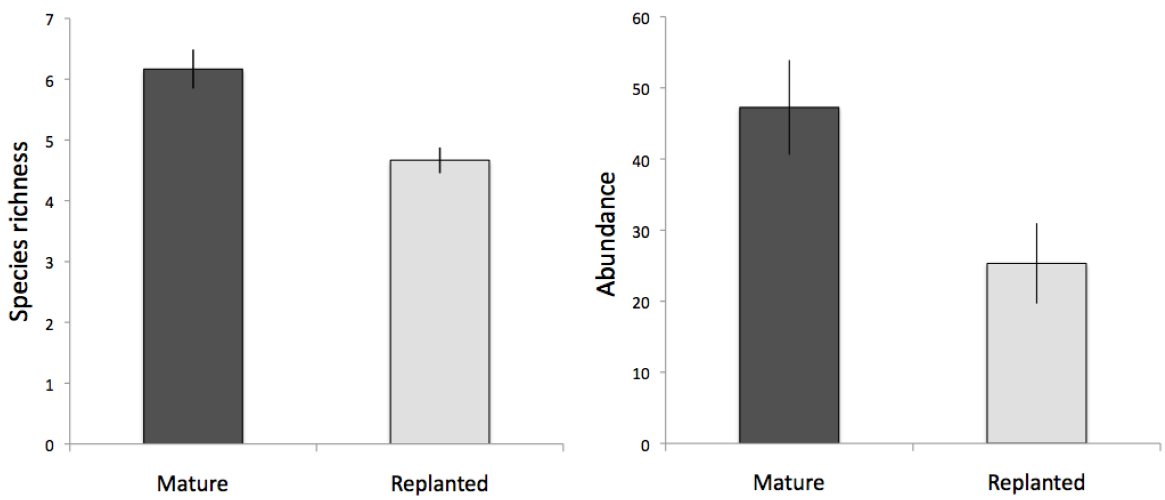
FIGURE 1. Location of mature (dark gray) and replanted (light gray) oil palm plots in Riau province, Sumatra, Indonesia. Dark lines show the borders between estates and gray lines show oil palm harvesting blocks. Libo, Palapa, Ujung Tanjung, and Kandista estates are owned and managed by Pt Ivo Mas Tunggal, a company owned by Golden Agri Resources. The width of one square grid is ~3.75 km.

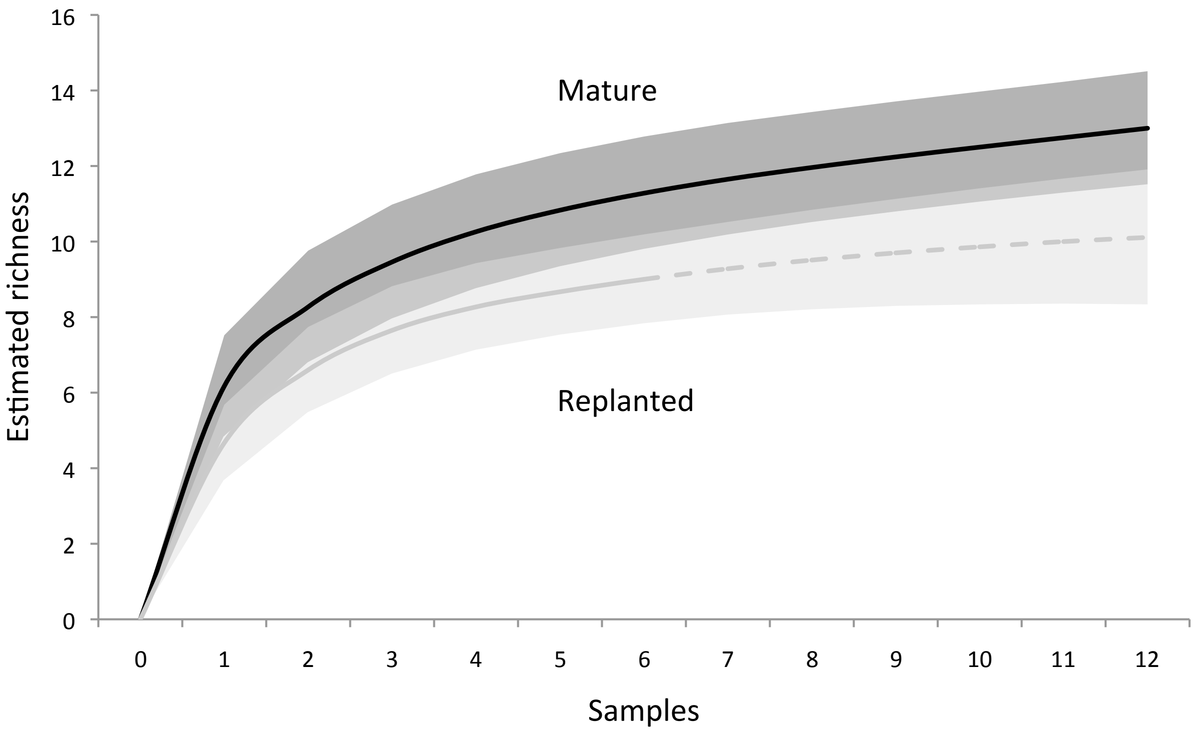
FIGURE 2. Average (±SE) frog species richness (top) and abundance (bottom) per plot in mature (dark gray, n=12) and replanted (light gray, n=6) oil palm plots, based on data collected in Riau province, Sumatra, Indonesia after three rounds of visual encounter surveys at each plot.

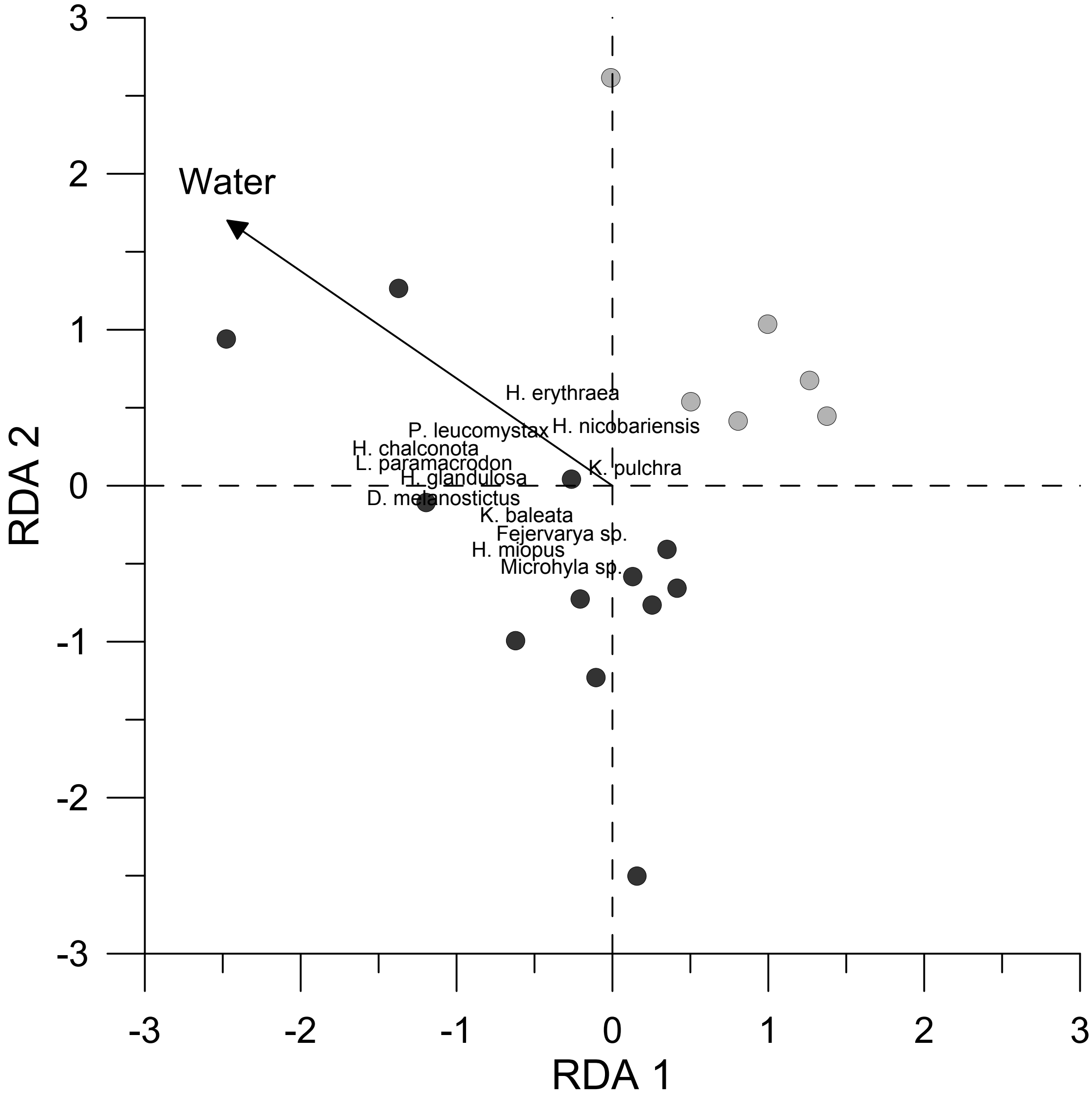
FIGURE 3. Sample-based rarefaction curves for mature (dark gray) and replanted (light gray) plot types, showing higher species accumulation in mature oil palm. The dashed line shows the extrapolated species richness estimate given more sample sites for replanted oil palm. Data were randomized 100 times. Error bands show standard deviation.

FIGURE 4. Redundancy analysis ordination plot based on transect data, showing the Euclidean distance between frog species, oil palm plots (circles; dark gray = mature plots, light gray = replanted plots), and water. Plot points closer together contain more similar frog assemblage compositions.


Ujung Tanjung
Libo Estate
Palapa
Kandista
Samsam
Sei Rokan
Nenggala
Legend
Mature (control)
Replanted
Road
River


7
6
5
4
3
2
1
0
Species richness
Mature
Replanted
60
50
40
30
20
10
0
Abundance
Mature
Replanted


Mature
Replanted
Estimated richness
Samples
0
2
4
6
8
10
12
14
16
0
1
2
3
4
5
6
7
8
9
10
11
12


Water
H. erythraea
P. leucomystax
H. nicobariensis
H. chalconota
L. paramacrodon
H. glandulosa
K. pulchra
D. melanostictus
K. baleata
Fejervarya sp.
H. miopus
Microhyla sp.
RDA 2
RDA 1