Replanting reduces frog diversity in oil palm

David J. Kurz[1,5,6], Edgar C. Turner[1], Agung A.K. Aryawan[2], Hannah C. Barkley[3], Jean-Pierre Caliman[2], Oliver Konopik[4], Sudharto Ps.[2], and William A. Foster[1]

[1]Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

[2]SMART Research Institute, PT SMART Tbk, Jalan Tenku Umar 19, 28112 Pekan Baru, Indonesia

[3]Massachusetts Institute of Technology-Woods Hole Oceanographic Institution Joint Program in Oceanography, Woods Hole, MA 02543, U.S.A.

[4]Department of Animal Ecology and Tropical Biology, University of Würzburg, Theodor-Boveri-Institut, Biozentrum, Am Hubland, D-97074 Würzburg, Germany

[5]Current: Department of Environmental Science, Policy & Management, University of California – Berkeley, Berkeley, CA, U.S.A. 94720

[6]Corresponding author: dave.kurz@gmail.com

Word count: 4029 (excluding title page, abstract, literature cited, tables, and figures)

Received _________; Revision accepted _________.

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 yr 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 yr old) and recently replanted (1-2 yr 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: alpha diversity; amphibian; biodiversity loss; plantation management; SE Asia; Sumatra; tropical agriculture; working landscapes

Indonesian Abstract

Semakin banyak publikasi (tulisan ilmiah) yang menyebutkan bahwa terjadi kehilangan biodiversitas yang nyata, ketika hutan dikonversi menjadi perkebunan kelapa sawit. Namun belum ada studi yang langsung ditujukan untuk meneliti perubahan biodiversitas sepanjang siklus hidup kelapa sawit, yakni selama periode 25-30 tahun sebelum akhirnya kelapa sawit tersebut dilakukan penanaman ulang (replanting). Proses tersebut akan mengakibatkan perubahan besar tata ruang di dalam perkebunan kelapa sawit yang mungkin akan mempengaruhi keragaman jenis organisme dan fungsi dari ekosistem. Kami membandingkan keragaman katak pada areal kelapa sawit menghasilkan (TM) (umur 21-27 tahun) dengan areal kelapa sawit yang belum menghasilkan (TBM) bekas tanam ulang (ex replanting) (umur 1-2 tahun) di Sumatra, Indonesia. Dari pengamatan yang dilakukan pada 18 petak pengamatan, masing-masing seluas 2,25 ha kelapa sawit, kami menemukan 719 ekor katak dari 14 jenis katak. Kekayaan jenis katak 31 persen lebih rendah pada areal kelapa sawit TBM bekas tanam ulang (9 jenis) dibandingkan dengan pada areal kelapa sawit TM (13 jenis). Total kelimpahan jenis katak 47 persen lebih rendah pada areal tanaman kelapa sawit TBM bekas tanam ulang, dan komposisi kumpulan katak berbeda nyata antara kedua lokasi pengamatan tersebut. Sebagian besar jenis katak tersebut adalah jenis yang toleran terhadap gangguan lingkungan. Walaupun demikian, kami juga menjumpai 4 jenis katak yang berasosiasi dengan habitat hutan, di dalam areal kelapa sawit TM, meskipun jarak antara tempat studi kami dengan hamparan hutan terdekat minimum 28 km.

Walaupun jelas bahwa perlindungan hutan adalah hal yang paling penting untuk melindungi keberadaan binatang (fauna) di daerah tropis, namun hasil penelitian kami menunjukkan bahwa keputusan pengelolaan tata ruang pertanian juga dapat memberikan dampak yang besar di dalam biodiversitas fauna tersebut.

Praktek pengelolaan perkebunan seperti pengaturan giliran tanam ulang atau perbedaan panjang masa produksi kelapa sawit dapat membantu pengelolaan diversitas katak di dalam perkebunan kelapa sawit.

DEFORESTATION TO MAKE ROOM FOR EXPANDING AGRICULTURE IS WIDELY RECOGNIZED AS A leading threat to terrestrial biodiversity (Koh & Wilcove 2008, Rudel *et al.* 2009, Vié *et al.* 2009, Wilcove & 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: (1) have been shown to play a role in conserving biodiversity (Brockerhoff *et al.* 2008, Pawson *et al.* 2013); (2) can be readily modified to better accommodate biodiversity (Mang & Brodie 2015); and (3) 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 yr 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 rainfall of 2.4 m/yr, 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 yr old) and six plots of recently replanted oil palm (1-2 yr 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. S1). 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 wk 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 1 January 2012 – 31 August 2014). 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 h 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 h 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, 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 d at each plot, collecting readings every three h.

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. 1A), as was per-plot frog abundance (Welch's *t*-test, $P = 0.02$, Fig. 1B). Rarefaction curves for all samples combined across sites also showed higher species accumulation in mature oil palm (Fig. 2), 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. 3). 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 (+3.3ºC), and lower night-time temperatures (-1.6ºC).

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 yr 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 yr 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 and 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 SE 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 SE Asia (Gillespie *et al.* 2012, Faruk *et al.* 2013, Konopik *et al.* 2015). Like Faruk *et al.* (2013) but unlike Gillespie *et al.* (2012) and Konopik *et al.* (2015), 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.

Acknowledgments

We are very grateful to Dr. Mohd Naim and the SMARTRI leadership for their generosity in allowing us to conduct research at SMARTRI alongside their team. We also thank bp Ade Netral, Kurniadi, Darma, Jaka, Bambang, and all the others on the exceptional SMARTRI research assistant team for their assistance in the field. We are indebted to bp Agus and bp Sukardi for kindly driving us to the field sites. We also thank Aude Verwilghen for her advice and details of forest cover in the region, and Evelyne St-Louis for her help with figures. The Isaac Newton Trust and Sinar Mas Agro Resources and Technology funded both the fieldwork and the BEFTA Project. We thank RISTEK for permission for the BEFTA Project and ECT to conduct research in Indonesia (number 426/SIP/FRP/SM/XI/2012, 72/EXT/SIP/FRP/SM/IX/2013).

Literature Cited

Agamuthu, P., and W. J. Broughton. 1985. Nutrient cycling within the developing oil palm-legume ecosystem. Agric. Ecosyst. Environ. 13: 111–123.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26: 32-46.

Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9: 1146-1156.

Barlow, J., T. A. Gardner, I. S. Araujo, T. C. Ávila-Pires, A. B. Bonaldo, J. E. Costa, M. C. Esposito, L. V. Ferreira, J. Hawes, M. I. M. Hernandez, M. S. Hoogmoed, R. N. Leite, N. F. Lo-Man-Hung, J. R. Malcolm, M. B. Martins, L. A. M. Mestre, R. Miranda-Santos, A. L. Nunes-Gutjahr, W. L. Overal, L. Parry, S. L. Peters, M. A. Ribeiro-Junior, M. N. F. da Silva, C. da Silva Motta, and C. A. Peres. 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Nat. Acad. Sci. USA 104: 18555–18560.

Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv. 17: 925-951.

Chao, A. 1984. Non-parametric estimation of the number of classes in a population. Scand. J. Stat. 11: 265-270.

Chee, K. H. 2007. Mucuna bracteata – a cover crop and living green manure. Agroworld 188: 30-34.

Chivian, E. 2002. Biodiversity: its importance to human health. Boston: Center for Health and the Global Environment, Harvard Medical School.

Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates>.

Corley, R. H. V., and P. B. Tinker. 2003. The Oil Palm. Oxford: Blackwell Science Ltd.

Daily, G. C, P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of Southern Costa Rica. Ecol. Appl. 11: 1-13.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity, ecosystem change, and resilience. Front. Ecol. Environ. 1: 488–494.

Faruk, A., D. Belabut, N. Ahmad, R. J. Knell, and T. W. J. Garner. 2013. Effects of oil-palm plantations on diversity of tropical anurans. Conserv. Biol. 27: 615–624.

Foster, W. A, J. L. Snaddon, E. C. Turner, T. M. Fayle, T. D. Cockerill, M. D. F. Ellwood, G. R. Broad, A. Y. C. Chung, P. Eggleton, C. V. Khen, and K. M. Yusah. 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function in the oil palm landscapes of South East Asia. Philos. Trans. R. Soc. B. 366: 3277–3291.

Foster, W. A, J. L. Snaddon, A. D. Advento, A. A. K. Aryawan, H. Barclay, J-P. Caliman, C. Kurniawan, D. J. Kurz, D. Mann, M. Naim, P. Dedi, Pujianto, T. S. R. Dzulfikar, E. M. Slade, Soeprapto, Suhardi, P. S. Sudharto, S. T. Ribka, W. Resti, H. W. Rudi, and E. C. Turner. 2014. The Biodiversity and Ecosystem Function in Tropical Agriculture (BEFTA) Project. The Planter, Kuala Lumpur, 90: 581-591.

Gallmetzer, N., and C. H. Schulze. 2015. Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective. Global Ecology and Conservation 4: 95-109.

GIBSON, L, T. M. LEE, L. P. KOH, B. W. BROOK, T. A. GARDNER, J. BARLOW, C. A. PERES, C. J. A. BRADSHAW, W. F. LAURANCE, T. E. LOVEJOY, AND N. S. SODHI. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478: 378–383.

GILLESPIE, G. R, E. AHMAD, B. ELAHAN, A. EVANS, M. ANCRENAZ, B. GOOSSENS, AND M. P. SCROGGIE. 2012. Conservation of amphibians in Borneo: relative value of secondary tropical forest and non-forest habitats. Biol. Conserv. 152: 136–144.

GOH, K. J., H. H. GAN, AND H. C. PATRICK NG. 2007. Agronomy of *Mucuna bracteata* under oil palm. *In* K. J. GOH, AND S. B. CHIU (Eds.). *Mucuna bracteata* – A cover crop and living green manure, pp. 45-84. Agricultural Crop Trust, Kuala Lumpur, Malaysia.

HARDWICK, S. R., R. TOUMI, M. PFEIFER, E. C. TURNER, R. NILUS, AND R. EWERS. 2015. The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives change in microclimate. Agric. For. Meteorol. 201: 187-195.

HARTLEY, M. J. 2002. Rationale and methods for conserving biodiversity in plantation forests. For. Ecol. Manage. 155: 81–95.

INGER, R. F, AND R. B. STUEBING. 2005. A field guide to the frogs of Borneo (Second Edition). Natural History Publications, Kota Kinabalu, Malaysia.

IUCN 2015. The IUCN Red List of Threatened Species. Version 2015-3. <http://www.iucnredlist.org>. Downloaded on 9 September 2015.

JANSEN, A., AND M. HEALEY. 2003. Frog communities and wetland condition: relationships with grazing by domestic livestock along an Australian floodplain river. Biol. Conserv. 109: 207–219.

KANOWSKI, J. J, T. M. REIS, C. P. CATTERALL, AND S. D. PIPER. 2006. Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. Restor. Ecol. 4: 67–76.

Keller, A., M.-O. Rödel, K. E. Linsenmair, and T. U. Grafe. 2009. The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. J. Anim. Ecol. 78: 305–314.

Kindt, R., and R. Coe. 2005. Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi, Kenya.

Koh, L. P, and D. S. Wilcove. 2008. Is oil palm agriculture really destroying tropical biodiversity? Conserv. Lett. 1: 60–64.

Konopik, O., I. Steffan-Dewenter, and T. U. Grafe. 2015. Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. Biotropica 47: 636-643.

Kurz, D. J, A. J. Nowakowski, M. W. Tingley, M. A. Donnelly, and D. S. Wilcove. 2014. Forest-land use complementarity modifies community structure of a tropical herpetofauna. Biol. Conserv. 170: 246–255.

Laurance, W. F, J. Sayer, and K. G. Cassman. 2014. Agricultural expansion and its impacts on tropical nature. Trends Ecol. Evol. 29: 107–116.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. For. Sci. 2: 314–320.

Luskin, M. S, and M. D. Potts. 2011. Microclimate and habitat heterogeneity through the oil palm lifecycle. Basic Appl. Ecol. 12: 540–551.

Mang, S. L., and J. F. Brodie. 2015. Impacts of non-oil tree plantations on biodiversity in Southeast Asia. Biodivers. Conserv. 24: 3431-3447.

Mayhew, J. E, M. Andrew, J. H. Sandom, S. Thayaparan, and A. C. Newton. 2003. Silvicultural systems for big-leaf mahogany plantations. *In* A. E. Lugo, J. C. Figueroa, and M. Alayón (Eds.). Big-Leaf Mahogany: Genetics, Ecology, and Management, pp. 261–277. Springer, New York, U.S.A.

Noor, H. H., Z. A. C. M. Rizuan, and H. Suhaidi. 2013. Control measures and integrated approach for major pests of oil palm in FELDA. Malaysia Palm Oil Board Congress (PIPOC) 2013.

Noor, M. 2003. Zero burning techniques in oil palm cultivation: an economic perspective. Oil Palm Industry Economic Journal 3: 16-24.

Nowakowski, A. J., M. Veiman-Echeverria, D. J. Kurz, and M. A. Donnelly. 2015. Evaluating connectivity for tropical amphibians using empirically derived resistance surfaces. Ecol. Appl. 25: 928-942.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2013. vegan: Community Ecology Package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan

Ooi, L-H, and S. P. Heriansyah. 2005. Palm pulverisation in sustainable oil palm replanting. Plant Production Science 8: 345–348.

Parris, K. M, and M. A. McCarthy. 1999. What influences the structure of frog assemblages at forest streams? Aust. J. Ecol. 24: 495-502.

PAWSON, S. M., A. BRIN, E. G. BROCKERHOFF, D. LAMB, T. W. PAYN, A. PAQUETTE, AND J. A. PARROTTA. 2013. Plantation forests, climate change and biodiversity. Biodivers. Conserv. 22: 1203-1227.

RAMAGE, B. S., E. C. MARSHALEK, J. KITZES, AND M. D. POTTS. 2013. Conserving tropical biodiversity via strategic spatiotemporal harvest planning. J. Appl. Ecol. 50: 1301-1310.

RAMDANI, F, AND M. HINO. 2013. Land use changes and GHG emissions from tropical forest conversion by oil palm plantations in Riau Province, Indonesia. PLoS ONE 8: e70323.

RITTENHOUSE, T. A. G, E. B. HARPER, L. R. REHARD, AND R. D. SEMLITSCH. 2008. The role of microhabitats in the desiccation and survival of anurans in recently harvested oak-hickory forest. Copeia 4: 807-814.

ROUNTABLE ON SUSTAINABLE PALM OIL. 2007. RSPO Principles and Criteria for Sustainable Palm Oil Production. RSPO Criteria Working Group.

RUDEL, T. K, R. DEFRIES, G. P. ASNER, AND W. F. LAURANCE. 2009. Changing drivers of deforestation and new opportunities for conservation. Conserv. Biol. 23: 1396-1405.

RUF, F., AND F. LANÇON. 2004. From Slash and Burn to Replanting: Green Revolutions in the Indonesian Uplands? Washington, D.C.: World Bank.

SIM, B. L., AND N. NYKVIST. 1991. Impact of forest harvesting and replanting. J. Trop. For. Sci. 3: 251–284.

SNADDON, J. L, K. J. WILLIS, AND D. W. MACDONALD. 2013. Biodiversity: oil-palm replanting raises ecology issues. Nature 502: 170–171.

STUART, S. N, J. S. CHANSON, N. A. COX, B. E. YOUNG, A. S. L. RODRIGUES, D. L. FISCHMAN, AND R. W. WALLER. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.

SUTHERLAND, W. J., A.S. PULLIN, P. M. DOLMAN, AND T. M. KNIGHT. 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19: 305–308.

TEAM R. 2013. R Development Core Team. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. http://www.R-project.org/

TURNER, E. C., J. L. SNADDON, T. M. FAYLE, AND W. A. FOSTER. 2008. Oil palm research in context: identifying the need for biodiversity assessment. PloS One 3: e1572.

URBINA-CARDONA, J. N., M. OLIVARES-PEREZ, AND V. H. REYNOSO. 2006. Herpetofauna diversity and microenvironment correlates across a pasture–edge–interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. Biol. Conserv. 132: 61–75.

VIÉ, J. C., C. HILTON-TAYLOR, AND S. N. STUART. 2009. Wildlife in a changing world – An analysis of the 2008 IUCN Red List of Threatened Species. IUCN, Gland, Switzerland.

VON MAY, R., J. M. JACOBS, R. SANTA-CRUZ, J. VALDIVIA, J. M. HUAMAN, AND M. A. DONNELLY. 2010. Amphibian community structure as a function of forest type in Amazonian Peru. J. Trop. Ecol. 26: 509-519.

WHILES, M. R, K. R. LIPS, C. M. PRINGLE, S. S. KILHAM, R. J. BIXBY, R. BRENES, S. CONNELLY, J. C. COLON-GAUD, M. HUNTE-BROWN, A. D. HURYN, C. MONTGOMERY, AND S. PETERSON. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Front. Ecol. Environ. 4: 27–34.

WHITLOCK, M., AND D. SCHLUTER. 2009. The analysis of biological data. Roberts and Co. Publishers, Greenwood Village, U.S.A.

WILCOVE, D. S., AND L. P. KOH. 2010. Addressing the threats to biodiversity from oil-palm agriculture. Biodivers. Conserv. 19: 999-1007.

WISSINGER, S. A, H. H. WHITEMAN, G. B. SPARKS, G. L. ROUSE, AND W. S. BROWN. 1999. Foraging trade-offs along a predator–permanence gradient in subalpine wetlands. Ecology 80: 2102–2116.

WOOD, B. J. 2002. Pest control in Malaysia's perennial crops: a half century perspective tracking the pathway to Integrated Pest Management. Integrated Pest Management Reviews 7: 173–190.

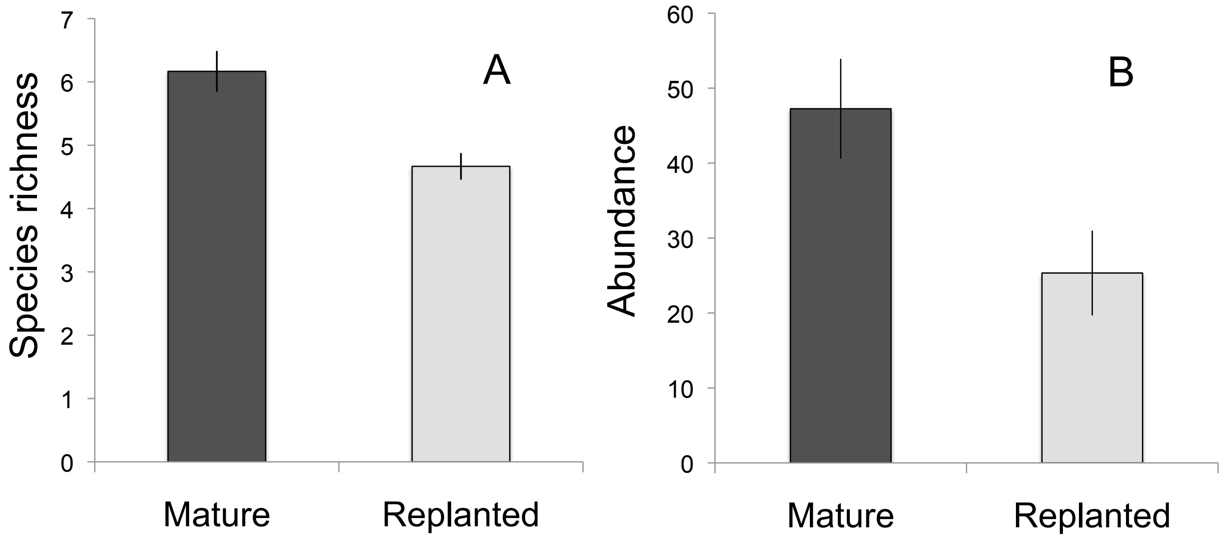
TABLE 1. *Species list of all frogs encountered on transects in mature and replanted oil palm plots in Riau province, Sumatra, Indonesia. Because of the unequal sample size between mature (n=12) and replanted (n=6) plots, and to facilitate direct comparisons between columns, we have divided the numbers 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

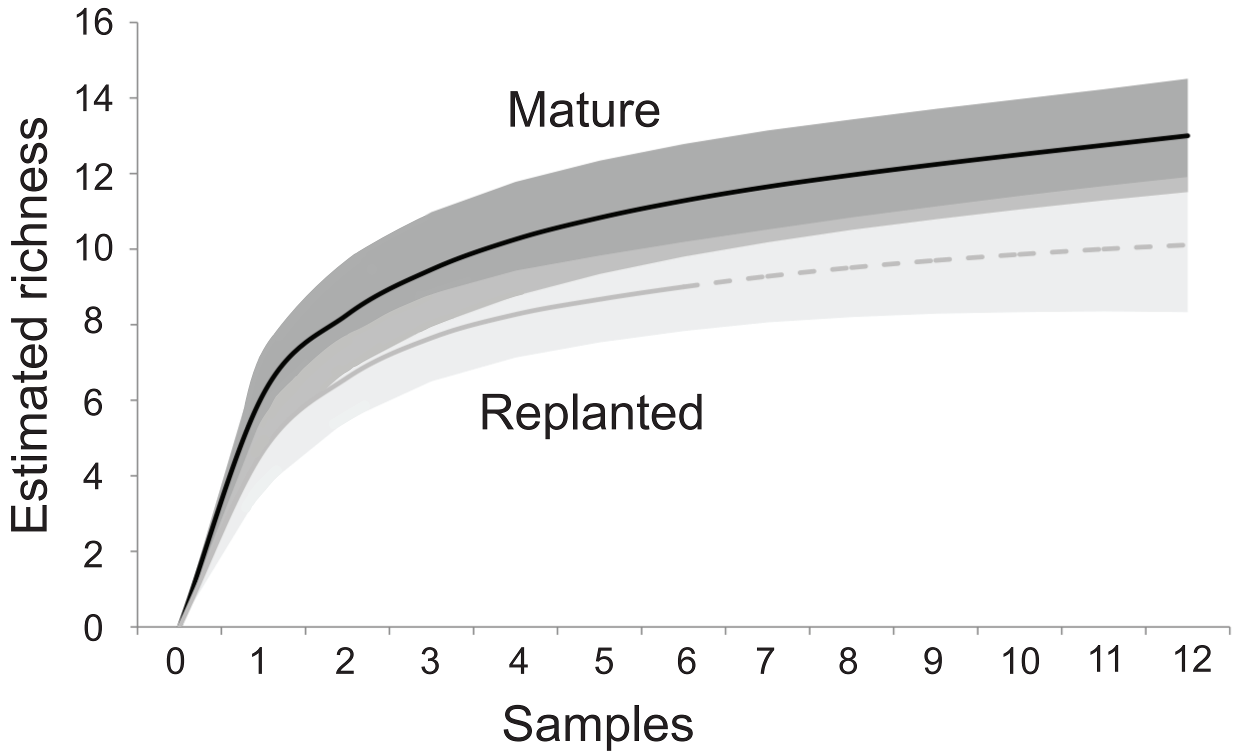
FIGURE 1. Average (±SE) frog species richness (A) and abundance (B) per plot in mature (dark gray, n=12) and replanted (light gray, n=6) oil palm plots, based on data collected in Riau province, Sumatra, Indonesia after three rounds of visual encounter surveys at each plot.

FIGURE 2. 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.

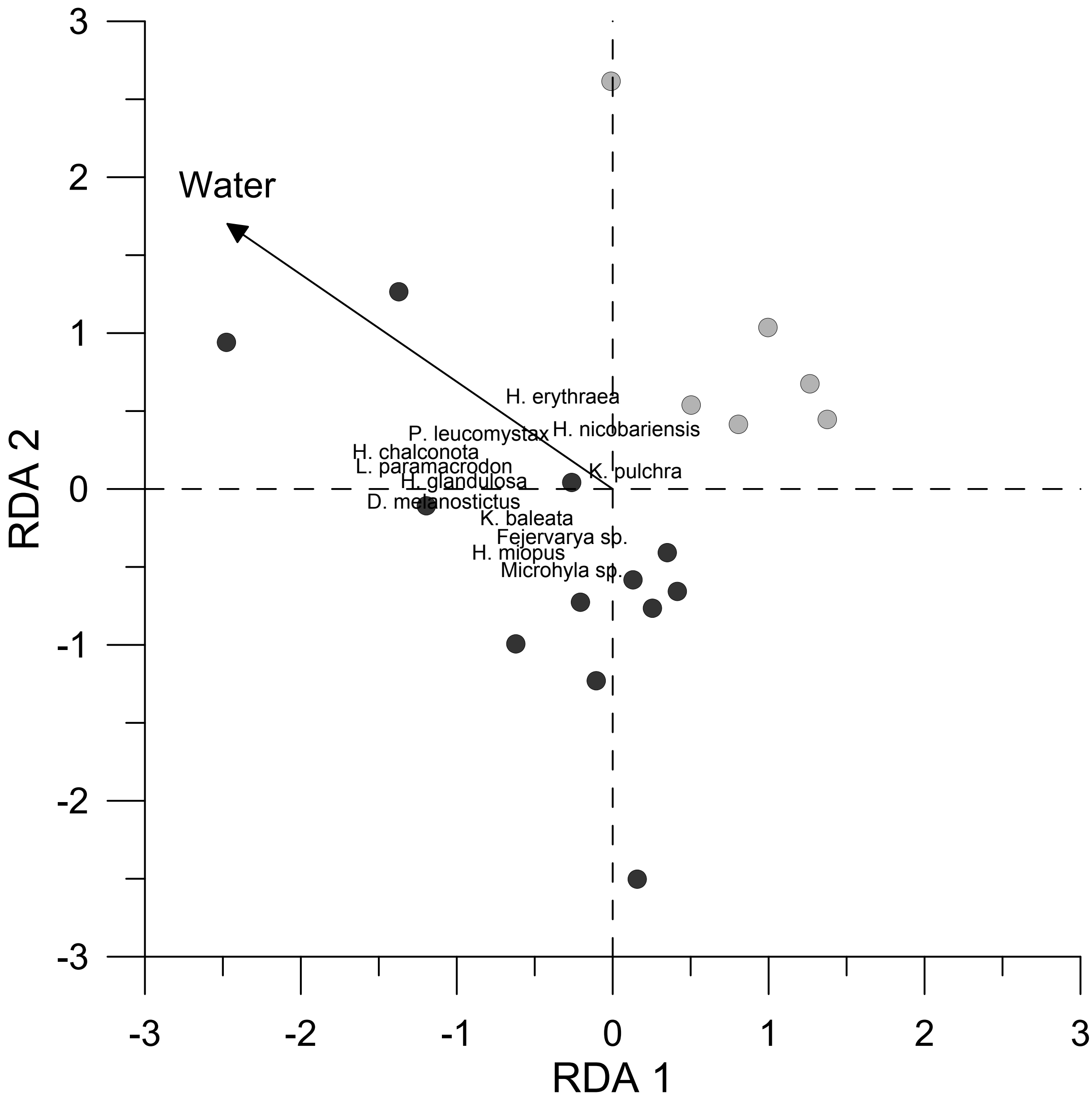
FIGURE 3. Redundancy analysis ordination plot based on transect data, showing the Euclidean distance between frog species, oil palm plots (circles; dark gray = mature plots, light gray = replanted plots), and water. Plot points closer together contain more similar frog assemblage compositions.



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


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

642



Water
H. erythraea
H. nicobariensis
P. leucomystax
H. chalconota
L. paramacrodon
H. glandulosa
K. pulchra
D. melanostictus
K. baleata
Fejervarya sp.
H. miopus
Microhyla sp.
RDA 2
RDA 1
3
2
1
0
-1
-2
-3

643

644