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Barriers to dispersal of rain forest butterflies in tropical agricultural landscapes

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ABSTRACT

Fragmentation of natural habitats can be detrimental for species if individuals fail to cross habitat boundaries to reach new locations, thereby reducing functional connectivity. Connectivity is crucial for species shifting their ranges under climate change, making it important to understand factors that might prevent movement through human-modified landscapes. In tropical regions, rain forests are being fragmented by agricultural expansion, potentially isolating populations of highly diverse forest-dependent species. The likelihood of crossing habitat boundaries is an important determinant of species dispersal through fragmented landscapes, and so we examined movement across rain forest-oil palm plantation boundaries on Borneo by using relatively mobile nymphalid butterflies as our model study taxon. We marked 1666 individuals from 65 species, and 19 percent (100/527) of recaptured individuals crossed the boundary. Boundary crossing was relatively frequent in some species, and net movement of individuals was from forest into plantation. However, boundary crossing from forest into plantation was detected in less than 50 percent (12/28) of recaptured species and was dominated by small-sized butterfly species whose larval host plants occurred within plantations. Thus, while oil palm plantations may be relatively permeable to some species, they may act as barriers to the movement of forest-dependent species (*i.e.*, species that require rain forest habitat to breed), highlighting the importance of maintaining forest connectivity for conserving rain forest species.

Abstract in Malay is available with online material.

ACROSS THE GLOBE, NATURAL HABITATS ARE BEING FRAGMENTED BY HUMAN ACTIVITIES WITH DETRIMENTAL CONSEQUENCES FOR BIODIVERSITY (Canale *et al.* 2012, Melo *et al.* 2013, Almeida-Gomes *et al.* 2016). Habitat connectivity is important for population persistence (Hanski 1999), and species are predicted to shift their ranges in response to climate change (Chen *et al.* 2011), making it important to understand the permeability of fragmented landscapes (Hodgson *et al.* 2011) and to maintain landscape connectivity (Martensen *et al.* 2008). Loss of connectivity is of particular concern in tropical regions (Wade *et al.* 2003) because rain forests are global hotspots for biodiversity but have already experienced extensive deforestation (Gibbs *et al.* 2010). For example, in parts of Southeast Asia, fragmentation of lowland forest is primarily due to the expansion of large-scale oil palm plantations (*Elaeis guineensis* Jacq.) (Gaveau *et al.* 2014), which can lead to the isolation of populations of forest-dependent species in the remaining areas of forest within these landscapes (Scriven *et al.* 2015).

The ability of species to move between habitat patches depends on species dispersal ability, a complex process that integrates the physical costs of movement through preferred habitat (Bonte *et al.* 2012), the response of species to habitat boundaries (Kallioniemi *et al.* 2014), and the permeability of the matrix (Perfecto & Vandermeer 2002). For tropical forest species to disperse

successfully through fragmented habitats, they need to cross forest–non-forest edges, which are frequently avoided by forest specialists (*e.g.*, Laurance 2004, Watson *et al.* 2004). Thus, an important component of dispersal involves species behavior upon reaching the forest edge, and responses to habitat boundaries affect emigration rates from suitable habitat (Ries & Debinski 2001). Boundary crossing by individuals (*e.g.*, butterflies) may be part of a random walk or movement (*e.g.*, see Schultz *et al.* 2012), although it is also likely that crossing may represent an active decision by an individual to leave areas of suitable habitat, and so the likelihood of crossing an edge may be an indicator of dispersal ability. However, leaving areas of suitable habitat may not always indicate longer distance dispersal (see review by Stevens *et al.* 2010), but boundary crossing is a prerequisite for individuals moving through highly fragmented landscapes.

While some tropical forest species avoid forest edges (Hansbauer *et al.* 2008), there is little information on the variation in boundary crossing among species. In temperate regions, species have been shown to recognize boundaries between suitable and unsuitable habitat and can actively control their rate of boundary crossing (Conradt & Roper 2006) and modify their movement behavior in response to boundaries (*e.g.*, birds: Rodríguez *et al.* 2001, butterflies: Schultz & Crone 2001, bush crickets: Berggren *et al.* 2002, and salamanders: Rittenhouse & Semlitsch 2006). Several temperate studies of butterflies have also reported species-specific differences in boundary-crossing ability (*e.g.*, Haddad

1999, Ries & Debinski 2001, Kallioniemi *et al.* 2014), and differences among species in their overall levels of activity can also affect rates of boundary crossing (Mair *et al.* 2015). Thus, current evidence implies that tropical species may vary in their sensitivity to habitat boundaries, and hence to rain forest fragmentation effects, but data quantifying movement of species across rain forest boundaries and how ecological traits influence edge-crossing behavior are lacking.

The movement of individuals across a habitat boundary is predicted to follow productivity (Rand *et al.* 2006) and population source-sink (Pulliam 1998, Tscharntke *et al.* 2005) gradients. In both tropical (*e.g.*, Lucey & Hill 2012) and temperate (*e.g.*, González *et al.* 2015) regions, there is evidence of spillover from natural habitats into managed systems, although spillover can also occur in the opposite direction (Barcelos *et al.* 2015). Studying net movement of individuals across rain forest-agricultural boundaries is important for understanding species diversity and ecosystem functioning; for example, if forest pests move into plantations and reduce crop yields or if crop-dwelling predators move into forests and reduce biodiversity (Rand *et al.* 2006).

Conversion of rain forest to oil palm agriculture reduces tropical biodiversity (Fitzherbert *et al.* 2008) and remaining tracts of rain forest become isolated within agricultural landscapes (Scriven *et al.* 2015). In order to develop effective conservation management, there is a pressing need to determine the permeability of forest-oil palm plantation boundaries to forest-dependent species (*i.e.*, species that are dependent on forest habitat to breed). If forest species are unable to cross forest boundaries, then plantations will form barriers to the movement of individuals among forest patches, thereby reducing habitat connectivity for these species. We investigated the movement of species at forest-oil palm plantation boundaries and tested the hypotheses that net flow of individuals is from forest into plantations, and that plantations are barriers to movement of many forest-dependent species; hence, we predicted fewer overall movements of species from forest into plantations compared with movements within forest. In addition, we predicted that plantations will be less of a barrier to species whose larval host plants occur within the plantation, and we also examined whether other species traits (forewing length, larval host plant specificity, and geographic range size) affected boundary crossing. We selected these traits for study because they have previously been shown to affect the sensitivity of tropical butterfly species to forest fragmentation (Benedick *et al.* 2006). Our study taxon was nymphalid butterflies, which are diverse (Benedick *et al.* 2006), relatively mobile (Marchant *et al.* 2015), and many species are dependent on closed-canopy forest (Hill *et al.* 2001). Butterfly distributions have also been shown to correlate well with observed patterns in other taxa (Schulze *et al.* 2004, Thomas 2005, Gardner *et al.* 2008), and so butterflies are considered sensitive ecological indicators of environmental changes (Cleary 2004).

METHODS

STUDY SITES.—Butterflies were sampled at four sites spanning forest-oil palm plantation boundaries in Sabah (Malaysian Borneo) between June–September 2013 and April–July 2014 (Fig. 1A). Our sampling design comprised two groups of two sites; groups were ~115 km apart, and sites within each group were more than 5 km apart (Fig. 1A). Sites were located at boundaries between mature fruiting oil palm (cleared and planted between 1998 and 2000) and production forest that had been selectively logged at least twice (Fig. S1), representing habitat mosaics and boundaries typical of plantation landscapes (Tawatao *et al.* 2014). We selected four forest sites that had experienced similar levels of disturbance (due to repeated commercial selective logging) and that were adjacent to oil palm plantations of similar age (~13–16 yr since planting). Thus, we minimized site-level differences in habitat structure, allowing us to focus on general patterns of boundary crossing. Oil palm plantations at sites 3 and 4 (adjacent to Tabin Wildlife Reserve; Nakashima *et al.* 2010) were members of the Roundtable for Sustainable Palm Oil (RSPO), but sites 1 and 2 (adjacent to the Ulu Segama Forest Reserve; Hector *et al.* 2011, Reynolds *et al.* 2011) were not (Fig. 1A). To characterize the structure of forest-oil palm plantation boundaries at the four study sites, we measured a number of variables in the two habitat types (detailed descriptions of structural habitat and abiotic measurements taken at study sites are given in Appendix S1). Differences in the means and standard errors of these variables among the four sites were small, showing that boundary characteristics were broadly similar (Table S1), thus minimizing any influence of site effects on our results.

SAMPLING TECHNIQUES.—At each of the four sites, 24 banana-baited traps (Dumbrell & Hill 2005, Benedick *et al.* 2006) were set up 50 m apart in a grid design spanning the boundary (Fig. 1B) and sampled for a total of 18 d per site (1728 trap-days in total). Traps were checked daily and trapped individuals were identified (following Otsuka 1988, Corbet & Pendlebury 1992), uniquely marked (Lucey & Hill 2012), and released. Some *Tanaecia* and *Euthalia* species cannot be identified in the field and so were grouped for analysis as *Tanaecia/Euthalia* sp.

SPECIES TRAITS.—To investigate factors affecting the likelihood of species crossing the forest boundary, we examined the importance of four species traits that are associated with dispersal and with specialist-generalist characteristics. Traits examined were (1) forewing length (mm), computed as the mean of male and female values quoted in Otsuka (1988), who measured the distance from the base of the forewing to the apex with a ruler; (2) larval host plant diet breadth (subsequently termed 'specificity') computed as the ln-transformed number of larval host plant genera each butterfly species has been recorded feeding on, based on information in Robinson *et al.* (2001); (3) presence/absence of larval host plants in oil palm plantations (subsequently termed 'availability') based on data from Lucey and Hill (2012), who recorded butterfly larval host plants in oil palm plantations in Sabah and assigned butterflies according to the presence/absence of host plant families occurring in plantations; and (4) geographic range size, analyzed according to three categories: narrow (restricted to Sundaland – Borneo, Sumatra, Java, and West Malaysia),
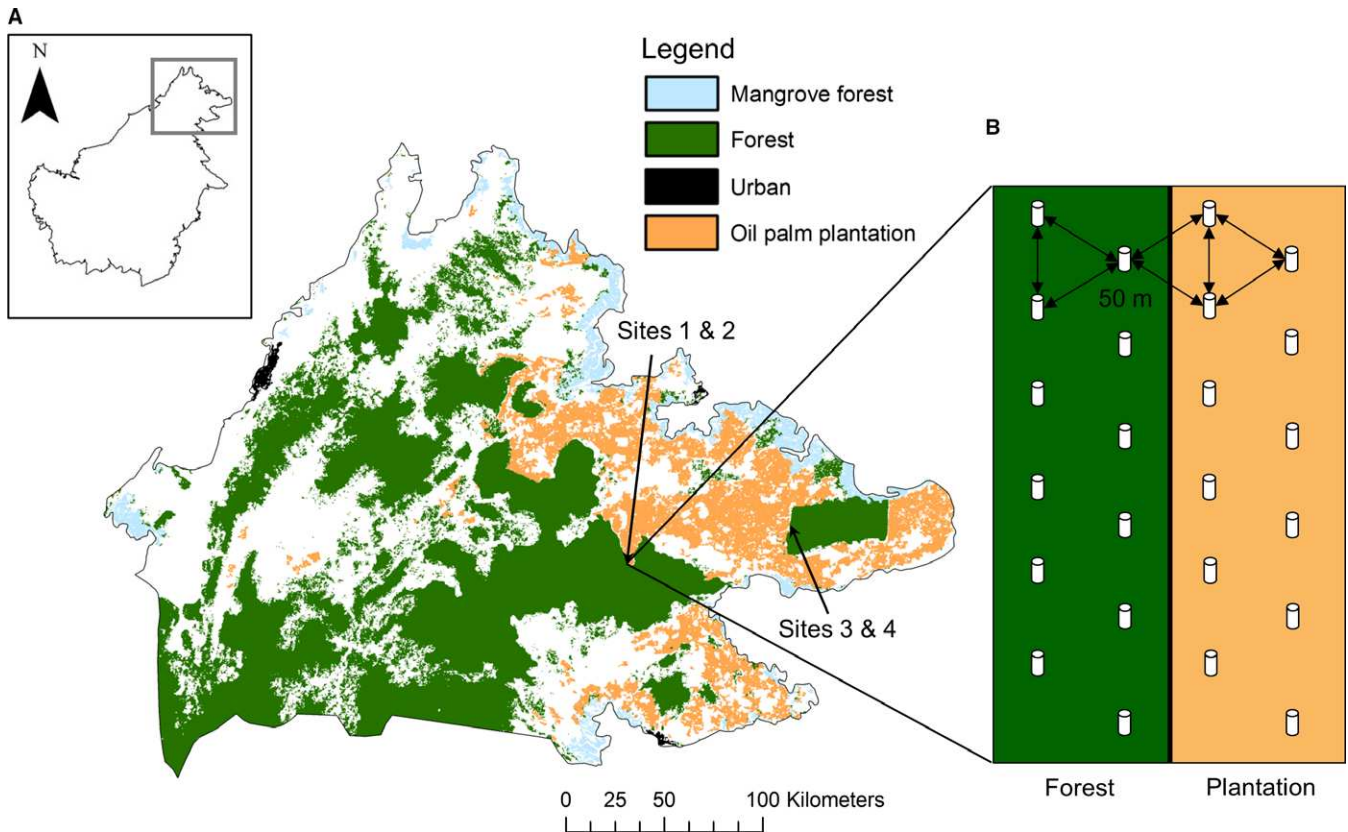
FIGURE 1. (A) Map of Sabah (North Borneo), arrows show study sites. The landcover category 'forest' consists of peat swamp forest, lowland evergreen forest, and lower and upper montane forest, and the category 'oil palm plantation' shows the extent of mature fruiting oil palm plantations (see Miettinen *et al.* 2012 for details). (B) Sampling design comprising 24 fruit-baited butterfly traps placed 50 m apart and sampled for a total of 18 d at each site.

intermediate (restricted to the Oriental region), and widespread (all other species), using species distribution information in D'Abrera (1985) and Otsuka (1988), and following Benedick *et al.* (2006). Rain forest is the main natural habitat on Borneo and historically covered most of the island (Gaveau *et al.* 2014), and so we assumed that larval host plants were present in forest habitats and that species with no larval host plants in plantations could breed only in forest habitats. We refer to species without larval host plants in plantations as 'forest-dependent' species.

In our analysis of species traits (see below), we included only those species with ≥2 individuals recaptured moving between traps. Of these species, larval host plant data were not available for *Junonia atlites,* because this species was not recorded by Lucey and Hill (2012). Larvae of this species feed on species of grasses (family Poaceae, formerly Gramineae; Robinson *et al.* 2001), and grass is abundant in oil palm plantations, so we assumed that larval host plants of *J. atlites* were present in plantations. There was also no host plant information for two species of *Mycalesis* (*M. anapita* and *M. orseis*) in relation to the number of larval host plant genera used, and so we assigned them a value based on the average number of host plant genera used by other *Mycalesis* species (*M. horsfieldi* and *M. mineus*; Table 1). Larval host plants of *Bassarona dunya* are not known, and so we excluded this species from our trait analysis.

DATA ANALYSIS.—For our analyses, we combined species data from the four sites because there were insufficient boundary-crossing events from any single site to provide robust estimates of species movements per site. However, to check for any site-level effects, we re-ran analyses with species data split by site and included site identity as a random factor (Appendix S2 and Table S2). This did not alter our main conclusions, although the local abundance of species became more important in the trait analyses (see below) because of low sample sizes per species per site, and so we only report findings from analyses based on combined data from all four sites. We report the number of individuals marked, the habitat they were marked in (forest or plantation; subsequently termed 'forest individuals' and 'plantation individuals'), if they were subsequently recaptured, and whether the recapture was in the same habitat or if the butterfly had crossed the boundary. Only a small number of individuals (14/100) were recaptured crossing the boundary more than once, and only two individuals crossed more than twice. Thus, the vast majority of individuals that crossed the boundary did so on only one occasion, and so for consistency, we only analyzed the first recapture, which corresponded to the direction moved after the individual was initially marked. Repeating our analysis using the last direction of recapture did not affect our results, and so, we only present results for the first recapture.

TABLE 1. *Summary data and trait information for butterfly species sampled during the study for which individuals were originally marked in either forest ('forest individuals') or plantation ('plantation individuals'); only species with ≥2 individuals recaptured moving between traps were included.*

Species	Subfamily	No. of individuals that moved between traps	No. of F to P movements[a]	No. of P to F movements[b]	No. of forest individuals	No. of plantation individuals	Forewing length (mm)	LHP specificity[c]	LHP availability[d]	Geographic range size
Agatasa calydonia	Charaxinae	2	0	0	6	6	54.5	1	Absent	Intermediate
Charaxes bernardus	Charaxinae	6	1	0	22	30	44.3	13	Absent	Intermediate
Prothoe franck	Charaxinae	7	0	1	19	3	40.3	2	Absent	Intermediate
Amathusia phidippus	Morphinae	20	2	3	46	110	53	10	Present	Intermediate
Discophora necho	Morphinae	7	1	1	22	32	46	1	Present	Narrow
Bassarona dunya	Nymphalinae	9	0	0	19	2	45.3	—	—	Intermediate
Dophla evelina	Nymphalinae	17	4	5	42	37	49	4	Absent	Intermediate
Hypolimnas bolina	Nymphalinae	4	0	0	0	29	36	28	Present	Wide
Junonia atlites	Nymphalinae	3	0	0	0	20	36.5	13	Present	Intermediate
Neorina lowii	Nymphalinae	7	1	1	19	5	48.5	1	Present	Narrow
Elymnias nesaea	Satyrinae	16	3	4	13	62	39	4	Present	Intermediate
Elymnias panthera	Satyrinae	13	2	2	23	58	31.5	3	Present	Narrow
Melanitis leda	Satyrinae	43	11	8	78	139	34.5	25	Present	Wide
Mycalesis anapita	Satyrinae	65	15	11	66	137	19	—[e]	Present	Intermediate
Mycalesis horsfieldi	Satyrinae	70	9	6	40	207	23	3	Present	Intermediate
Mycalesis mineus	Satyrinae	47	6	0	7	127	23.5	8	Present	Intermediate
Mycalesis orseis	Satyrinae	11	2	1	50	13	24.5	—[e]	Present	Intermediate

[a]Number of movements by forest individuals moving into plantation (F to P movements)

[b]Number of movements by plantation individuals moving into forest (P to F movements)

[c]Larval host plant (LHP) diet breadth

[d]Presence/absence of larval host plants in oil palm plantations. We classified species that were unable to breed in plantation habitat as forest dependent.

[e]There was no information on the number of larval host plant genera used by these species, and so they were assigned a value based on the average number of host plant genera for other species within the same genus that were included in our analyses (*Mycalesis horsfieldi* and *M. mineus*).

We used chi-square tests to examine whether the habitat (forest or plantation) an individual was marked in affected its likelihood of crossing the boundary and of moving between traps. For forest individuals, we compared the number of individuals marked in forest that crossed the boundary into plantation with the number that only moved within forest. We also used a Mann–Whitney U test to compare distances moved by forest and plantation individuals.

We used generalized linear mixed models (GLMMs) with a logit link and binomial errors to examine whether the proportion of individuals per species crossing the habitat boundary was influenced by species traits and habitat of first capture (excluding species with <2 individuals recaptured moving between traps, and excluding species without larval host plant data; 16 species analyzed). The dependent variable in these GLMMs comprised proportion data for each of the 16 study species, computed as the total number of individuals of a species crossing the boundary as a proportion of all recaptured individuals of that species that moved to a different trap. Data for each species comprised separate information for forest and plantation individuals, and hence, our GLMMs comprised two sets of proportion data for each of the 16 study species: one set of data for the total number of within-forest recaptures and boundary-crossing events by forest individuals and another set of data for the total number of within-plantation recaptures and boundary-crossing events by plantation individuals. This statistical design, where movement data per species from all four study sites are summed for forest and plantation individuals before analysis, provides reliable species-specific estimates of boundary crossing, but more detailed information such as the precise location on the study grid of original capture, capture day, or site was not included. To avoid overfitting models, we could not include multiple traits within a single model. Therefore, to determine which trait was most important for boundary crossing, we fitted four separate GLMMs

(examining the importance of forewing length, host plant availability in plantations, diet specificity, and geographic range size), and we included only a single trait predictor variable in each model. In addition, we also fitted a separate model that included a measure of species abundance (ln-transformed number of individuals marked in each habitat) as a fixed effect to control for variation in local density and recapture rates of species. Our predictor variables were weakly correlated, i.e., the smallest species were generally the most abundant, and had host plants present in plantations (see Fig. 2 for relationships between species traits), but we ran separate models for all four traits in order to explore the relative importance of traits on the probability of boundary crossing. In addition, we also incorporated an obligate habitat (of first capture) covariate into each of the models, interacting with each trait variable and species abundance, in order to control for the different numbers of individuals marked in forest or plantation habitats. Butterfly subfamily was included as a random factor to control for phylogeny.

We compared the difference in the corrected Akaike information criterion (ΔAICc) and models where ΔAICc < 2 were considered to be no better than a 'habitat-only' model (i.e., a model including only habitat of first capture and butterfly Subfamily) (Burnham & Anderson 2004). We compared models that included species traits and abundances to habitat-only models in order to determine the influence of each trait on boundary crossing, while accounting for the effect of the habitat individuals were
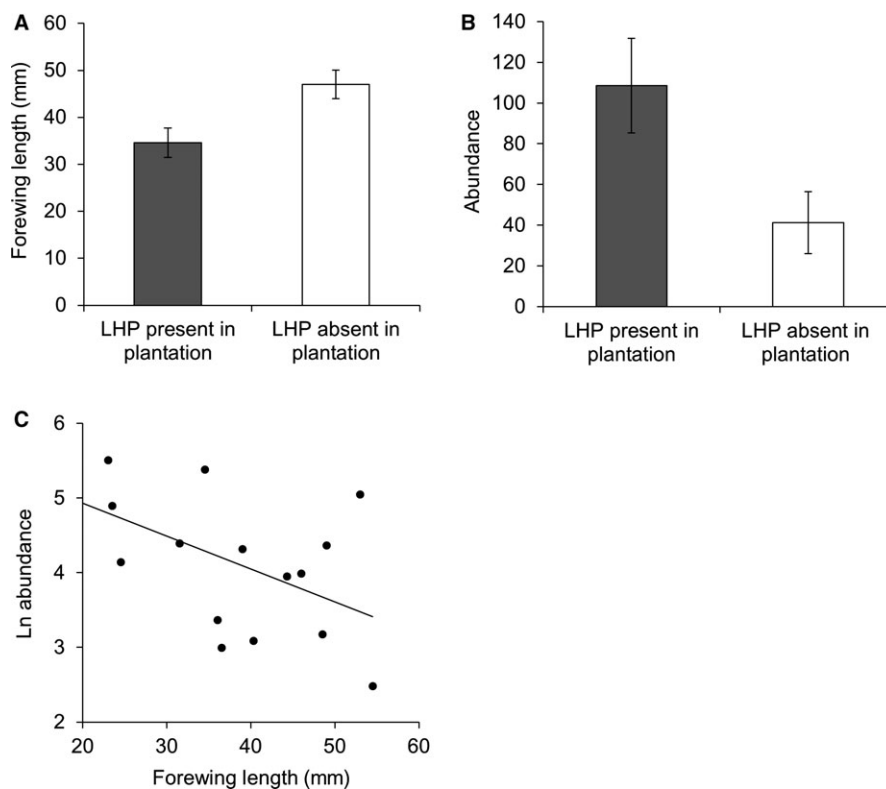

FIGURE 2. Relationships between species traits for 16 species included in our trait analyses (Table 1). (A) Forewing length (mm) versus larval host plant (LHP) availability (presence and absence in oil palm plantations); (B) abundance versus larval host plant availability; and (C) ln-transformed abundance versus forewing length (mm); trend line shows significant correlation between ln-transformed abundance and forewing length (mm) (Pearson correlation $r = -0.53$; $P = 0.04$).

marked in. For each of the four trait models where $\Delta AICc > 2$ compared to the habitat-only model, we calculated four movement probabilities: forest to plantation, plantation to forest, forest to forest, and plantation to plantation. To aid interpretation of model outputs, we report the logit probabilities of movement between and within habitats for the smallest and largest species (forewing lengths = 19 mm and 54.5 mm, respectively) and for species with larval host plants present and absent in plantations. We also calculated 95% CIs for all logit movement probabilities to assess the relative importance of the species traits. All statistical analyses were carried out in R statistical software version 3.2.0 (R Core Team 2015).

RESULTS

BOUNDARY CROSSING BY SPECIES.—We marked a total of 1666 individuals from 65 species, of which 527 individuals from 28 species were recaptured (recapture rate of individuals = 31.6%; see Table S3 for summary data of butterfly recaptures). Of the 28 species recaptured, 11 species had larval host plants present within oil palm plantations, while eight species did not, and so were assumed to be forest dependent; for nine species, there was no host plant information (see Table S4 for full species list). Boundary crossing was relatively common in some species, and 100 individuals from 13 species crossed the boundary (Table 1), corresponding to 19 percent (100/527) of all individuals recaptured. Overall, individuals from a total of 12 species (42.9% of the 28 species recaptured) crossed the boundary from forest into plantation (Table 1). Even though more individuals and species were marked in plantation (1105 individuals, 51 species) compared with forest (561 individuals, 42 species), individuals were 5.6 times (odds ratio test; 95% CIs: 3.4, 9.1) more likely to move across the boundary if they were originally marked in forest (57/139 recaptured individuals) than if they were originally marked in plantation (43/388 recaptured individuals; χ^2 (1) = 59.6, $P < 0.0001$) (Fig. 3). Thus, net flow of movement of individuals was from forest into plantation.

A higher proportion of individuals were recaptured in plantation compared with forest (Fig. 3A), but only 18 percent (43/243) of plantation individuals that were recaptured in a different trap crossed the boundary into forest. By contrast, forest individuals that were recaptured in a different trap had an approximately equal chance of moving to plantation (52.8%; 57/108 recaptured individuals) as moving within forest (47.2%; 51/108 recaptured individuals). This implies that most forest individuals did not perceive the boundary as a barrier. However, there was considerable variation among species marked in forest in relation to boundary crossing (Table 1), and larval host plant availability, forewing length, and abundance were important factors affecting these movements (Table 2). Crossing from forest into plantation was more than twice as likely for species with larval host plants present in plantations (ten species crossed) than for species without host plants present (only two species crossed) (Fig. 4A). Boundary crossing from forest into plantation was also more than twice as likely by small species than large species (Fig. 4B).
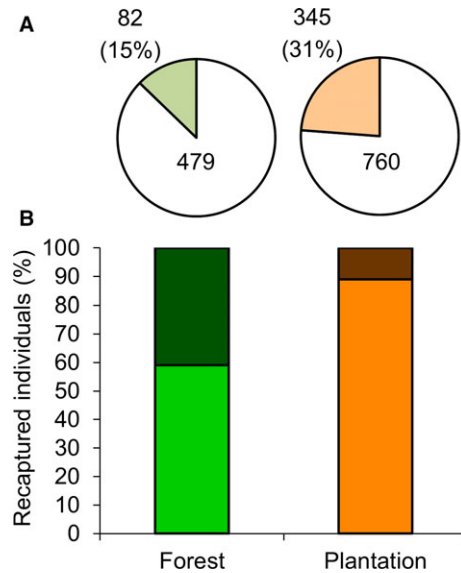

FIGURE 3. (A) Pie charts showing number of all individuals initially marked in forest or plantations, and the number subsequently recaptured at least once in the same habitat (shaded portion; *i.e.*, excluding individuals that crossed the boundary). (B) Stacked bar chart showing percentage of all individuals marked in forest (*N* = 139 marked individuals) and plantations (*N* = 388 marked individuals) that were subsequently recaptured in the same habitat (medium shading; either within the same trap, or a different trap), or crossed the boundary (dark shading). Forest individuals were more likely to cross the boundary compared with plantation individuals (χ^2 (1) = 59.6, $P < 0.0001$).

MOVEMENT WITHIN HABITATS.—Plantation individuals were less likely to move between traps (243/388: number of individuals marked in plantations that moved traps/total number of plantation individuals recaptured; 62.6%) than forest individuals (108/139 individuals moved traps; 77.7%; χ^2 (1) = 10.45, $P = 0.001$; $N = 20$ species, including individuals that crossed the boundary). Moreover, plantation individuals were 2.1 times (odds ratio test; 95% CIs: 1.3, 3.3) more likely to be recaptured in the same trap compared with those marked in forest, and moved shorter distances when they did move (plantation individuals: mean distance moved = 114 m; forest individuals: mean = 121 m; Mann–Whitney U test: $W = 14,813$; $P = 0.047$). This finding was qualitatively the same if we restricted our analyses to only those species with individuals that were recaptured in both habitats ($N = 12$ species; plantation: 234/367 (63.8%) of recaptures in a different trap, mean distance moved = 116 m; forest: 90/111 (81.1%) of recaptures in a different trap, mean distance moved = 128 m; $P < 0.02$ for both analyses). Thus, we conclude that butterflies were more sedentary in oil palm plantations compared with forest.

DISCUSSION

BOUNDARY PERMEABILITY AND FACTORS AFFECTING CROSSING.—We found that boundary crossing was relatively frequent at our study sites for some species, although crossing from forest into plantations occurred in only 12 (43%) of the 28 species that were

TABLE 2. *Model comparisons for binomial logistic regression models (GLMMs) determining the effect of species traits (forewing length, larval host plant (LHP) specificity, larval host plant availability, and geographic range size) and abundance on probability of crossing the boundary for forest and plantation individuals.*

Model	Direction[a]	K[b]	LL[c]	AICc[d]	ΔAICc[e]	w_i[f]
LHP availability * Habitat	+	5	−60.32	132.94	−	0.372
Forewing length * Habitat	−	5	−60.51	133.32	0.38	0.307
Ln habitat abundance * Habitat	+	5	−61.03	134.37	1.43	0.182
Ln LHP specificity * Habitat	NA	5	−61.68	135.67	2.73	0.095
Habitat-only model	NA	3	−65.34	137.53	4.59	0.037
Geographic range size * Habitat	NA	7	−61.15	140.96	8.02	0.007

[a]Positive (+) or negative (−) relationship between each trait and boundary-crossing probability from forest into plantation for each model that was better (Δ corrected Akaike information criterion (AICc) > 2) than the habitat-only model. NA = not computed.

[b]Number of estimated parameters in the fitted model.

[c]Log likelihood (LL): overall model fit.

[d]A measure of model fit corrected for sample size.

[e]Change in AICc from that of the best model.

[f]Akaike weight, representing the model's relative strength compared to other best models.

recaptured. Small species with larval host plants present in plantations were most likely to cross from forest into plantations, while species dependent on rain forest habitat to breed were recorded crossing the boundary less frequently. We deemed species to be rain-forest dependent if their larval host plants were not found in plantation habitats and hence the species could not breed there (see Lucey & Hill 2012), and we assumed that species whose larval host plants were found in the plantation matrix did not solely rely on forest habitat to breed. Therefore, boundary crossing was dominated by species that could potentially breed within both rain forest and plantation habitats. These species included several in the genus *Mycalesis* (Satyrinae), whose larval host plants include a variety of grasses (Robinson *et al.* 2001). *Mycalesis* species are often found in gap sites within-forest habitats (Hill *et al.* 2001), and these high light conditions are typical of habitats within oil palm plantations (Luskin & Potts 2011). In many insect groups, body size is a good proxy for mobility (Nieminen *et al.* 1999, Greenleaf *et al.* 2007, Kuussaari *et al.* 2014), but this relationship was not evident in our study, because boundary crossing was dominated by small Satyrinae species. While we included subfamily as a random factor in our models to control for phylogeny, it is likely that phylogenetic relatedness among species within the genus *Mycalesis* was an important determinant of edge crossing, and edge-crossing ability may also have been influenced by common traits within this group that we did not consider (*e.g.,* thermal tolerances, visual abilities suited to high light environments, and ability to feed upon a diverse range of adult food sources).

Boundary crossing into plantations occurred less often in forest-dependent species whose larval host plants did not occur in plantations. Conversion of rain forest to oil palm plantations is accompanied by considerable changes in habitat structure, vegetation, and microclimatic characteristics (Foster *et al.* 2011, Luskin & Potts 2011, see Appendix S1; Table S1; Fig. S2 for habitat characteristics at forest boundaries at our study sites), which make plantations unsuitable for the persistence of many forest species (*e.g.,* for ants: Fayle *et al.* 2010 and frogs: Gillespie *et al.*

2012, Gallmetzer & Schulze 2015). Oil palm plantations have more extreme diurnal temperature variation, higher light levels, increased evaporation rates, and lower humidity compared with forest (Luskin & Potts 2011), and so forest-dependent species that prefer shaded, cooler conditions may actively avoid crossing boundaries. However, compared with other types of habitat boundaries (*e.g.,* forest-grassland: see Ries & Debinski 2001, Rittenhouse & Semlitsch 2006, Schultz *et al.* 2012), structural differences between selectively logged rain forest and oil palm plantations may be less severe. For example, mature oil palm plantations (>10 yr) provide some shade cover (Table S1; Fig. S2), an understory shrub/herb layer (Aratrakorn *et al.* 2006), and support epiphyte species that are important for some forest species (*e.g.,* birds: Koh 2008). In our study, some species with larval host plants restricted to forest were nonetheless captured in plantation in relatively high abundance, despite being recorded crossing the boundary less frequently than some species that could breed within the plantation matrix (Table 1). This implies that some forest-dependent species (*e.g., Charaxes bernardus* and *Dophla evelina;* Table 1) are more capable of crossing the boundary than we recorded, and hence may be able to move through the oil palm matrix, particularly strong fliers such as *C. bernardus* (S.A.S. pers. obs.).

Boundary crossing from forest to plantations is likely influenced by both internal (*e.g.,* genetic dispersal cues and behavior) and external factors (*e.g.,* vegetation structure, abiotic conditions, and habitat quality). Certain butterfly species have been shown to actively avoid habitat edges and may respond by modifying their movement behavior when within close proximity to the boundary, likely due to 'edge effects' penetrating the forest habitat (Haddad 1999, Ries & Debinski 2001). Our study focused on butterflies, but active avoidance of rain forest edges has been shown by other tropica taxa (*e.g.,* birds: Laurance 2004), and is likely to be particularly pronounced for forest species that are sensitive to changes in abiotic conditions (*e.g.,* amphibians: Gillespie *et al.* 2012). Such behavioral avoidance of boundaries may
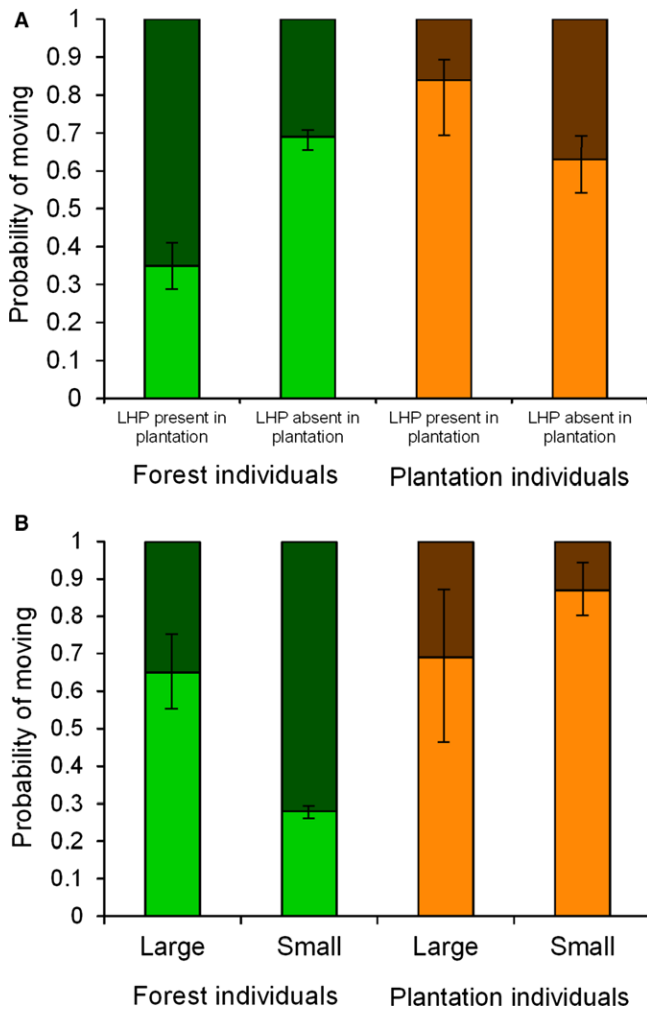
FIGURE 4. Probabilities (logit probability from binomial GLMMs) of individuals moving within the same habitat (medium shading) or crossing the boundary (dark shading) for forest and plantation individuals. Separate probabilities are calculated for species with (A) larval host plants (LHP) present ($N = 12$ species) and absent ($N = 4$ species) in plantations, and (B) for the smallest (19 mm forewing length) and largest (55 mm forewing length) species with ≥ 2 individuals recaptured. Error bars show 95% CIs, and traits with bars that do not overlap are significant factors affecting boundary crossing, *i.e.,* forest individuals with host plants present in plantations (A) and small forest individuals (B).

arise if individuals use previous knowledge to avoid crossing habitat boundaries, or if individuals perceive sensory cues of changing habitat structure (Rittenhouse & Semlitsch 2006), *e.g.,* light hue and polarization (Douglas *et al.* 2007) as they approach the boundary. Our study grid sampled up to ~65 m from the boundary, and edge effects may have permeated even further into the forest (Ewers & Didham 2008). Thus, the area of forest habitat sampled in our study may have already been avoided by forest-dependent species, and this may explain the low diversity of species recorded in forest traps, and why we only recaptured a relatively small number of forest species during the study. In

addition, butterflies show vertical stratification in forest habitats (Fordyce & DeVries 2016), and canopy species may have been underrepresented in our ground-level forest traps (Dumbrell & Hill 2005).

There is little information on whether trap efficiency varies among habitat types for tropical butterflies. We captured more species and individuals in plantations, even though plantations have greatly reduced diversity compared with primary forest (Fitzherbert *et al.* 2008), and this might reflect increased efficiency of traps within plantations if there are fewer adult food sources in plantations. It is also possible that increased fermentation of the banana bait due to higher temperatures in plantations (Fig. S2) may have increased the attractance of plantation traps, and this topic requires further study.

From of a total of 65 species captured during our study, there were only 17 species with multiple individuals recaptured in a different trap (of which larval host plant information was available for 16 species), and so our analyses of species traits were based on a relatively small number of species. In addition, the small number of species meant we could not include multiple species traits in models because of overfitting, yet it is likely that there are interactions among traits that may affect movement (*i.e.,* the smallest species are also the most abundant; Fig. 2). Our experimental design allowed us to examine general patterns of boundary crossing, but future work examining factors such as trap location, distance from edge, 'hardness' of the edge, or time of day on boundary crossing would be interesting new topic areas for study.

MOVEMENT IN FOREST VERSUS PLANTATION HABITATS.—Forest individuals were more mobile than those in plantations. However, all our forest traps were relatively close to the forest edge, and so these mobility levels may not be representative of movement within closed-canopy interior forest. Over half of all species we marked were not subsequently recaptured, likely reflecting high mobility, large home ranges, and lack of territoriality in our study species (Marchant *et al.* 2015), as well as short adult lifespans in some species potentially leading to low survival rates between recapture events. Tropical forest taxa typically have high species richness but occur at low density, and so high mobility detected in our study may reflect tracking of low-density resources (*e.g.,* host plants, mates). Species were apparently more sedentary in the plantation and tended not to cross into forest, which may reflect high availability of certain resources in oil palm plantations, leading to a few species achieving very high levels of abundance (*e.g.,* *Amathusia phidippus* whose larvae feed on palms). Extremely high abundances of some species in oil palm plantations are also evident in other taxa, such as termites (Hassall *et al.* 2006), birds (Senior *et al.* 2013), and rats (Wood & Fee 2003), where species presumably exploit hyperabundant resources, such as palm fronds and fruit, present in plantations. Thus, species apparently modify their behavior within plantations, being more sedentary and less likely to cross the boundary than when in forest.

CONSERVATION IMPLICATIONS.—Our results suggest that boundary crossing was more frequent from forest into oil palm plantations

and was dominated by species whose larval host plants occurred within the plantation matrix, and thus may be capable of breeding within plantations. Failure of forest-dependent species to cross plantation boundaries in high numbers may result in limited dispersal of these species through fragmented tropical agricultural landscapes, and these species are likely to become confined to increasingly isolated forest fragments. Future conservation effort to improve habitat connectivity may help to reduce extinction risks of species in isolated populations and facilitate range shifting of species under climate change (Scriven *et al.* 2015). Forest connectivity may also be improved by making non-forest areas more hospitable (Azhar *et al.* 2013) and by improving quality of remaining forest areas (Mair *et al.* 2014), thereby helping to reduce biodiversity losses in tropical agricultural landscapes.

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DATA AVAILABILITY

Data deposited in the Dryad Repository: http://doi.org/10.5061/dryad.2m19h (Scriven *et al.* 2016)

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

APPENDIX S1. Measuring vegetation structure at study sites.
APPENDIX S2. Additional statistical analyses with species data split by site.
FIGURE S1. Photographs of forest-oil palm plantation boundaries at study sites.
FIGURE S2. Temperature, shade cover, and ground cover summarized across lateral section of study site.
TABLE S1. Habitat variables summarized across study sites.
TABLE S2. Model comparisons for GLMMs with species data split by site.
TABLE S3. Summary data of butterfly recaptures across study sites.
TABLE S4. Butterfly species list with trait and abundance information.

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