BARRIERS TO DISPERSAL OF RAINFOREST BUTTERFLIES IN TROPICAL AGRICULTURAL LANDSCAPES

Sarah A. Scriven[1*]; Colin M. Beale[1]; Suzan Benedick[2] and Jane K. Hill[1]

[1] Department of Biology, University of York, York, YO10 5DD, UK

[2] Faculty of Sustainable Agriculture, Universiti Malaysia Sabah, Beg Berkunci No. 3, 90509,

Sandakan, Sabah, Malaysia

*Corresponding author; email: sas550@york.ac.uk; sarah_scriven@hotmail.co.uk

1   **ABSTRACT**

2   Fragmentation of natural habitats can be detrimental for species if individuals fail to cross habitat

3   boundaries to reach new locations, thereby reducing functional connectivity. Connectivity is

4   crucial for species shifting their ranges under climate change, making it important to understand

5   factors that might prevent movement through human-modified landscapes. In tropical regions,

6   rainforests are being fragmented by agricultural expansion, potentially isolating populations of

7   highly diverse forest-dependent species. The likelihood of crossing habitat boundaries is an

8   important determinant of species' dispersal through fragmented landscapes, and so we examined

9   movement across rainforest-oil palm plantation boundaries on Borneo by using relatively mobile

10 nymphalid butterflies as our model study taxon. We marked 1666 individuals from 65 species,

11 and 19 percent (100/527) of recaptured individuals crossed the boundary. Boundary crossing was

12 relatively frequent in some species, and net movement of individuals was from forest into

13 plantation. However, boundary crossing from forest into plantation was detected in less than 50

14 percent (12/28) of recaptured species, and was dominated by small-sized butterfly species whose

15 larval host plants occurred within plantations. Thus, whilst oil palm plantations may be relatively

16 permeable to some species, they may act as barriers to the movement of forest-dependent species

17 (*i.e.*, species that require rainforest habitat to breed), highlighting the importance of maintaining

18 forest connectivity for conserving rainforest species.

19

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 rainforests are global hotspots

for biodiversity but have already experienced extensive deforestation (Gibbs *et al.* 2010). For

example, in parts of SE 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 2004);

thus, an important component of dispersal involves species' behavior upon reaching the forest

edge. Responses to habitat boundaries affect emigration rates from suitable habitat (Ries &

Debinksi 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.

Whilst 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 rainforest fragmentation effects, but data quantifying movement of species across rainforest 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 rainforest-agricultural boundaries is important for understanding

1   species diversity and ecosystem functioning; for example, if forest pests move into plantations

2   and reduce crop yields, or if crop-dwelling predators move into forests and reduce biodiversity

3   (Rand *et al.* 2006).

4   Conversion of rainforest to oil palm agriculture reduces tropical biodiversity (Fitzherbert

5   *et al.* 2008) and remaining tracts of rainforest become isolated within agricultural landscapes

6   (Scriven *et al.* 2015). In order to develop effective conservation management there is a pressing

7   need to determine the permeability of forest-oil palm plantation boundaries to forest-dependent

8   species (*i.e.*, species that are dependent on forest habitat to breed). If forest species are unable to

9   cross forest boundaries, then plantations will form barriers to the movement of individuals

10   among forest patches thereby reducing habitat connectivity for these species. We investigated the

11   movement of species at forest-oil palm plantation boundaries, and tested the hypotheses that net

12   flow of individuals is from forest into plantations, and that plantations are barriers to movement

13   of many forest-dependent species, hence we predicted fewer overall movements of species from

14   forest into plantations compared with movements within forest. In addition, we predicted that

15   plantations will be less of a barrier to species whose larval host plants occur within the

16   plantation, and we also examined whether other species' traits (forewing length, larval host plant

17   specificity and geographical range size) affected boundary crossing. We selected these traits for

18   study because they have previously been shown to affect the sensitivity of tropical butterfly

19   species to forest fragmentation (Benedick *et al.* 2006). Our study taxon was nymphalid

20   butterflies, which are diverse (Benedick *et al.* 2006), relatively mobile (Marchant *et al.* 2015)

21   and many species are dependent on closed-canopy forest (Hill *et al.* 2001). Butterfly

22   distributions have also been shown to correlate well with observed patterns in other taxa

1 (Schulze *et al.* 2004, Thomas 2005, Gardner *et al.* 2008) and so butterflies are considered

2 sensitive ecological indicators of environmental changes (Cleary 2004).

3

4 **METHODS**

5

6 STUDY SITES.—Butterflies were sampled at four sites spanning forest-oil palm plantation

7 boundaries in Sabah (Malaysian Borneo) between June-September 2013 and April-July 2014

8 (Fig. 1A). Our sampling design comprised two groups of two sites; groups were ~115 km apart,

9 and sites within each group were more than 5 km apart (Fig. 1A). Sites were located at

10 boundaries between mature fruiting oil palm (cleared and planted between 1998-2000) and

11 production forest that had been selectively logged at least twice (Fig. S1), representing habitat

12 mosaics and boundaries typical of plantation landscapes (Tawatao *et al.* 2014). We selected four

13 forest sites that had experienced similar levels of disturbance (due to repeated commercial

14 selective logging) and that were adjacent to oil palm plantations of similar age (~13-16 yr since

15 planting). Thus, we minimized site-level differences in habitat structure, allowing us to focus on

16 general patterns of boundary crossing. Oil palm plantations at sites 3 and 4 (adjacent to Tabin

17 Wildlife Reserve; Nakashima *et al.* 2010) were members of the Roundtable for Sustainable Palm

18 Oil (RSPO), but sites 1 and 2 (adjacent to the Ulu Segama Forest Reserve; Hector *et al.* 2011,

19 Reynolds *et al.* 2011) were not (Fig. 1A). To characterize the structure of forest-oil palm

20 plantation boundaries at the four study sites we measured a number of variables in the two

21 habitat types (detailed descriptions of structural habitat and abiotic measurements taken at study

22 sites are given in Appendix S1). Differences in the means and standard errors of these variables

1   among the four sites were small, showing that boundary characteristics were broadly similar

2   (Table S1), thus minimizing any influence of site effects on our results.

3

4   SAMPLING TECHNIQUES.—At each of the four sites, 24 banana-baited traps (Dumbrell & Hill

5   2005, Benedick *et al.* 2006) were set up 50 m apart in a grid design spanning the boundary (Fig.

6   1B) and sampled for a total of 18 d per site (1728 trap-days in total). Traps were checked daily

7   and trapped individuals were identified (following Otsuka 1988, Corbet & Pendlebury 1992),

8   uniquely marked (Lucey & Hill 2012), and released. Some *Tanaecia* and *Euthalia* species cannot

9   be identified in the field and so were grouped for analysis as *Tanaecia/Euthalia* sp.

10

11   SPECIES TRAITS.—To investigate factors affecting the likelihood of species crossing the forest

12   boundary, we examined the importance of four species traits that are associated with dispersal

13   and with specialist-generalist characteristics. Traits examined were: (1) forewing length (mm),

14   computed as the mean of male and female values quoted in Otsuka (1988), who measured the

15   distance from the base of the forewing to the apex with a ruler; (2) larval host plant diet breadth

16   (subsequently termed 'specificity') computed as the ln-transformed number of larval host plant

17   genera each butterfly species has been recorded feeding on, based on information in Robinson *et*

18   *al*. (2001); (3) presence/absence of larval host plants in oil palm plantations (subsequently

19   termed 'availability') based on data from Lucey and Hill (2012), who recorded butterfly larval

20   host plants in oil palm plantations in Sabah and assigned butterflies according to the

21   presence/absence of host plant families occurring in plantations; and (4) geographical range size,

22   analyzed according to three categories: narrow (restricted to Sundaland – Borneo, Sumatra, Java

23   and West Malaysia), intermediate (restricted to the Oriental region) and widespread (all other

7

1 species), using species' distribution information in D'Abrera (1985) and Otsuka (1988), and

2 following Benedick *et al*. (2006). Rainforest is the main natural habitat on Borneo and

3 historically covered most of the island (Gaveau *et al.* 2014), and so we assumed that larval host

4 plants were present in forest habitats and that species with no larval host plants in plantations

5 could breed only in forest habitats. We refer to species without larval host plants in plantations as

6 'forest-dependent' species.

7 In our analysis of species traits (see below) we included only those species with ≥ two

8 individuals recaptured moving between traps. Of these species, larval host plant data were not

9 available for *Junonia atlites,* because this species was not recorded by Lucey and Hill (2012).

10 Larvae of this species feed on species of grasses (family Poaceae, formerly Gramineae; Robinson

11 *et al*. 2001), and grass is abundant in oil palm plantations, so we assumed that larval host plants

12 of *J. atlites* were present in plantations. There was also no host plant information for two species

13 of *Mycalesis* (*M. anapita* and *M. orseis*) in relation to the number of larval host plant genera

14 used, and so we assigned them a value based on the average number of host plant genera used by

15 other *Mycalesis* species (*M. horsfieldi* and *M. mineus*; Table 1). Larval host plants of *Bassarona*

16 *dunya* are not known and so we excluded this species from our trait analysis.

17

18 DATA ANALYSIS.—For our analyses, we combined species data from the four sites because there

19 were insufficient boundary crossing events from any single site to provide robust estimates of

20 species movements per site. However, to check for any site-level effects, we re-ran analyses with

21 species data split by site, and included site identity as a random factor (see Appendix S2 and

22 Table S2). This did not alter our main conclusions, although the local abundance of species

23 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%; 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. We used

chi-squared 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 < two

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

1   individuals, hence our GLMMs comprised two sets of proportion data for each of the 16 study

2   species: one set of data for the total number of within-forest recaptures and boundary crossing

3   events by forest individuals and another set of data for the total number of within-plantation

4   recaptures and boundary crossing events by plantation individuals. This statistical design, where

5   movement data per species from all four study sites are summed for forest and plantation

6   individuals before analysis, provides reliable species-specific estimates of boundary crossing, but

7   more detailed information such as the precise location on the study grid of original capture,

8   capture day or site were not included. To avoid over-fitting models, we could not include

9   multiple traits within a single model. Therefore, to determine which trait was most important for

10   boundary crossing, we fitted four separate GLMMs (examining the importance of forewing

11   length, host plant availability in plantations, diet specificity and geographical range size) and we

12   included only a single trait predictor variable in each model. In addition, we also fitted a separate

13   model that included a measure of species abundance (ln-transformed number of individuals

14   marked in each habitat) as a fixed effect to control for variation in local density and recapture

15   rates of species. Our predictor variables were weakly correlated, *i.e.*, the smallest species were

16   generally the most abundant, and had host plants present in plantations (see Fig. 2 for

17   relationships between species traits), but we ran separate models for all four traits in order to

18   explore the relative importance of traits on the probability of boundary crossing. In addition, we

19   also incorporated an obligate habitat (of first capture) covariate into each of the models,

20   interacting with each trait variable and species abundance, in order to control for the different

21   numbers of individuals marked in forest or plantation habitats. Butterfly Subfamily was included

22   as a random factor to control for phylogeny.

1   We compared the difference in the Akaike information criterion (ΔAICc) and models

2   where ΔAICc < 2 were considered to be no better than a 'habitat-only' model (*i.e.*, a model

3   including only habitat of first capture and butterfly Subfamily) (Burnham & Anderson 2004). We

4   compared models that included species traits and abundances to habitat-only models in order to

5   determine the influence of each trait on boundary crossing, whilst accounting for the effect of the

6   habitat individuals were marked in. For each of the four trait models where ΔAICc > 2 compared

7   to the habitat-only model, we calculated four movement probabilities: forest to plantation,

8   plantation to forest, forest to forest and plantation to plantation. To aid interpretation of model

9   outputs, we report the logit probabilities of movement between and within habitats for the

10   smallest and largest species (forewing lengths = 19 mm and 54.5 mm, respectively) and for

11   species with larval host plants present and absent in plantations. We also calculated 95% CIs for

12   all logit movement probabilities to assess the relative importance of the species traits. All

13   statistical analyses were carried out in R statistical software version 3.2.0 (R Core Team 2015).

14

15   **RESULTS**

16

17   Boundary crossing by species.—We marked a total of 1666 individuals from 65 species, of

18   which 527 individuals from 28 species were recaptured (recapture rate of individuals = 31.6%;

19   see Table S3 for summary data of butterfly recaptures). Of the 28 species recaptured, 11 species

20   had larval host plants present within oil palm plantations, whilst eight species did not, and so

21   were assumed to be forest-dependent; for nine species there was no host plant information (see

22   Table S4 for full species list). Boundary crossing was relatively common in some species, and

23   100 individuals from 13 species crossed the boundary (Table 1), corresponding to 19 percent

1 (100/527) of all individuals recaptured. Overall, individuals from a total of 12 species (42.9% of

2 the 28 species recaptured) crossed the boundary from forest into plantation (Table 1). Even

3 though more individuals and species were marked in plantation (1105 individuals, 51 species)

4 compared with forest (561 individuals, 42 species), individuals were 5.6 times (odds ratio test;

5 95% CIs: 3.4, 9.1) more likely to move across the boundary if they were originally marked in

6 forest (57/139 recaptured individuals) than if they were originally marked in plantation (43/388

7 recaptured individuals; χ^2 (1) = 59.6, P < 0.0001) (Fig. 3). Thus, net flow of movement of

8 individuals was from forest into plantation.

9   A higher proportion of individuals was recaptured in plantation compared with forest

10 (Fig. 3A), but only 18 percent (43/243) of plantation individuals that were recaptured in a

11 different trap crossed the boundary into forest. By contrast, forest individuals that were

12 recaptured in a different trap had an approximately equal chance of moving to plantation (52.8%;

13 57/108 recaptured individuals) as moving within forest (47.2%; 51/108 recaptured individuals).

14 This implies that most forest individuals did not perceive the boundary as a barrier. However,

15 there was considerable variation among species marked in forest in relation to boundary crossing

16 (Table 1), and larval host plant availability, forewing length and abundance were important

17 factors affecting these movements (Table 2). Crossing from forest into plantation was more than

18 twice as likely for species with larval host plants present in plantations (ten species crossed) than

19 for species without host plants present (only two species crossed) (Fig. 4A). Boundary crossing

20 from forest into plantation was also more than twice as likely by small species than large species

21 (Fig. 4B).

22

1   MOVEMENT WITHIN HABITATS.—Plantation individuals were less likely to move between traps

2   (243/388: number of individuals marked in plantations that moved traps/total number of

3   plantation individuals recaptured; 62.6%) than forest individuals (108/139 individuals moved

4   traps; 77.7%; χ^2 (1) = 10.45, P = 0.001; N = 20 species, including individuals that crossed the

5   boundary). Moreover, plantation individuals were 2.1 times (odds ratio test; 95% CIs: 1.3, 3.3)

6   more likely to be recaptured in the same trap compared with those marked in forest, and moved

7   shorter distances when they did move (plantation individuals: mean distance moved = 114 m;

8   forest individuals: mean = 121 m; Mann-Whitney U test: W = 14,813; P = 0.047). This finding

9   was qualitatively the same if we restricted our analyses to only those species with individuals

10   that were recaptured in both habitats (N = 12 species; plantation: 234/367 (63.8%) of recaptures

11   in a different trap, mean distance moved = 116 m; forest: 90/111 (81.1%) of recaptures in a

12   different trap, mean distance moved = 128 m; P < 0.02 for both analyses). Thus, we conclude

13   that butterflies were more sedentary in oil palm plantations compared with forest.

14

15   **DISCUSSION**

16

17   BOUNDARY PERMEABILITY AND FACTORS AFFECTING CROSSING.—We found that boundary

18   crossing was relatively frequent at our study sites for some species, although crossing from forest

19   into plantations occurred in only 12 (43%) of the 28 species that were recaptured. Small species

20   with larval host plants present in plantations were most likely to cross from forest into

21   plantations, whilst species dependent on rainforest habitat to breed were recorded crossing the

22   boundary less frequently. We deemed species to be rainforest-dependent if their larval host

23   plants were not found in plantation habitats and hence the species could not breed there (see

1   Lucey & Hill 2012), and we assumed that species whose larval host plants were found in the

2   plantation matrix did not solely rely on forest habitat to breed. Therefore, boundary crossing was

3   dominated by species that could potentially breed within both rainforest and plantation habitats.

4   These species included several in the genus *Mycalesis* (Satyrinae), whose larval host plants

5   include a variety of grasses (Robinson *et al.* 2001). *Mycalesis* species are often found in gap sites

6   within forest habitats (Hill *et al.* 2001), and these high-light conditions are typical of habitats

7   within oil palm plantations (Luskin & Potts 2011). In many insect groups, body size is a good

8   proxy for mobility (Nieminen *et al.* 1999, Greenleaf *et al.* 2007, Kuussaari *et al.* 2014), but this

9   relationship was not evident in our study, because boundary crossing was dominated by small

10 Satyrinae species. Whilst we included Subfamily as a random factor in our models to control for

11 phylogeny, it is likely that phylogenetic relatedness among species within the genus *Mycalesis*

12 was an important determinant of edge crossing, and edge crossing ability may also have been

13 influenced by common traits within this group that we did not consider (*e.g.,* thermal tolerances,

14 visual abilities suited to high light environments and ability to feed upon a diverse range of adult

15 food sources).

16   Boundary crossing into plantations occurred less often in forest-dependent species whose

17 larval host plants did not occur in plantations. Conversion of rainforest to oil palm plantations is

18 accompanied by considerable changes in habitat structure, vegetation and microclimatic

19 characteristics (Foster *et al*. 2011, Luskin & Potts 2011; see Appendix S1: Table S1; Fig. S2 for

20 habitat characteristics at forest boundaries at our study sites), which make plantations unsuitable

21 for the persistence of many forest species (*e.g.*, for ants: Fayle *et al*. 2010 and frogs: Gillespie *et*

22 *al*. 2012, Gallmetzer & Schulze 2015). Oil palm plantations have more extreme diurnal

23 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 to 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 rainforest 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 focussed on butterflies, but active avoidance of rainforest edges has been shown by other tropica taxa (*e.g.,* birds: Laurance 2004), and is likely to be particulary 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 arise if individuals use previous knowledge to avoid crossing habitat boundaries, or if individuals

1   perceive sensory cues of changing habitat structure (Rittenhouse & Semlitsch 2006), *e.g.*, light

2   hue and polarisation (Douglas *et al.* 2007) as they approach the boundary. Our study grid

3   sampled up to ~65 m from the boundary, and edge effects may have permeated even further into

4   the forest (Ewers & Didham 2008). Thus, the area of forest habitat sampled in our study may

5   have already been avoided by forest-dependent species, and this may explain the low diversity of

6   species recorded in forest traps, and why we only recaptured a relatively small number of forest

7   species during the study. In addition, butterflies show vertical stratification in forest habitats

8   (Fordyce & DeVries 2016) and canopy species may have been under-represented in our ground-

9   level forest traps (Dumbrell & Hill 2005).

10   There is little information on whether trap efficiency varies among habitat types for

11   tropical butterflies. We captured more species and individuals in plantations, even though

12   plantations have greatly reduced diversity compared with primary forest (Fitzherbert *et al*. 2008),

13   and this might reflect increased efficiency of traps within plantations if there are fewer adult food

14   sources in plantations. It is also possible that increased fermentation of the banana bait due to

15   higher temperatures in plantations (see Fig. S2) may have increased the attractance of plantation

16   traps, and this topic requires further study.

17   From of a total of 65 species captured during our study, there were only 17 species with

18   multiple individuals recaptured in a different trap (of which larval host plant information was

19   available for 16 species), and so our analyses of species traits were based on a relatively small

20   number of species. In addition, the small number of species meant we could not include multiple

21   species traits in models because of over-fitting, yet it is likely that there are interactions among

22   traits that may affect movement (*i.e.,* the smallest species are also the most abundant; Fig. 2).

23   Our experimental design allowed us to examine general patterns of boundary crossing, but future

1   work examining factors such as trap-location, distance from edge, 'hardness' of the edge, or time

2   of day on boundary crossing would be interesting new topic areas for study.

3

4   MOVEMENT IN FOREST VERSUS PLANTATION HABITATS.—Forest individuals were more mobile

5   than those in plantations. However, all our forest traps were relatively close to the forest edge,

6   and so these mobility levels may not be representative of movement within closed-canopy

7   interior forest. Over half of all species we marked were not subsequently recaptured, likely

8   reflecting high mobility, large home ranges and lack of territoriality in our study species

9   (Marchant *et al.* 2015), as well as short adult lifespans in some species potentially leading to low

10 survival rates between recapture events. Tropical forest taxa typically have high species richness

11 but occur at low density, and so high mobility detected in our study may reflect tracking of low

12 density resources (*e.g.*, host plants, mates). Species were apparently more sedentary in the

13 plantation and tended not to cross into forest, which may reflect high availability of certain

14 resources in oil palm plantations, leading to a few species achieving very high levels of

15 abundance (*e.g.*, *Amathusia phidippus* whose larvae feed on palms). Extremely high abundances

16 of some species in oil palm plantations are also evident in other taxa such as termites (Hassall *et*

17 *al.* 2006), birds (Senior *et al.* 2013) and rats (Wood & Fee 2003), where species presumably

18 exploit hyper-abundant resources, such as palm fronds and fruit, present in plantations. Thus,

19 species apparently modify their behavior within plantations, being more sedentary and less likely

20 to cross the boundary than when in forest.

21

22 CONSERVATION IMPLICATIONS.—Our results suggest that boundary crossing was more frequent

23 from forest into oil palm plantations and was dominated by species whose larval host plants

1   occurred within the plantation matrix, and thus may be capable of breeding within plantations.

2   Failure of forest-dependent species to cross plantation boundaries in high numbers may result in

3   limited dispersal of these species through fragmented tropical agricultural landscapes, and these

4   species are likely to become confined to increasingly isolated forest fragments. Future

5   conservation effort to improve habitat connectivity may help to reduce extinction risks of species

6   in isolated populations, and facilitate range shifting of species under climate change (Scriven *et*

7   *al.* 2015). Forest connectivity may also be improved by making non-forest areas more hospitable

8   (Azhar *et al.* 2013), and by improving quality of remaining forest areas (Mair *et al.* 2014),

9   thereby helping to reduce biodiversity losses in tropical agricultural landscapes.

10

11   **ACKNOWLEDGMENTS**

12

21

22   **DATA AVAILABILTY**

23

The data used in this study are archived at the Dryad Digital Repository

(doi:10.5061/dryad.2m19h).

SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

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.*

LITERATURE CITED

ALMEIDA-GOMES, M., M. V. VIEIRA, C. F. D. ROCHA, J. P. METZGER, AND G. DE COSTER. 2016.

Patch size matters for amphibians in tropical fragmented landscapes. Biol. Conserv.195:

89–96.

ARATRAKORN, S., S. THUNHIKORN, AND P. F. DONALD. 2006. Changes in bird communities

following conversion of lowland forest to oil palm and rubber plantations in southern

Thailand. Bird Conserv. Int. 16: 71–82.

AZHAR, B., D. B. LINDENMAYER, J. WOOD, J. FISCHER, A. MANNING, C. MCELHINNY, AND M. ZAKARIA. 2013. The influence of agricultural system, stand structural complexity and landscape context on foraging birds in oil palm landscapes. Ibis 155: 297–312.

BARCELOS, E., S. D. A. RIOS, R. N. V. CUNHA, R. LOPES, S. Y. MOTOIKE, E. BABIYCHUK, A. SKIRYCZ, AND S. KUSHNIR. 2015. Oil palm natural diversity and the potential for yield improvement. Front. Plant Sci. 6: 1–16.

BENEDICK, S., J. K. HILL, N. MUSTAFFA, V. K. CHEY, M. MARYATI, J. B. SEARLE, M. SCHILTHUIZEN, AND K. C. HAMER. 2006. Impacts of rain forest fragmentation on butterflies in northern Borneo: species richness, turnover and the value of small fragments. J. Appl. Ecol. 43: 967–977.

BERGGREN, Å., B. BIRATH, AND O. KINDVALL. 2002. Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). Conserv. Biol. 16: 1562–1569.

BONTE, D., H. VAN DYKE, J. M. BULLOCK, A. COULON, M. DELGADO, M. GIBBS, V. LEHOUCK, E. MATTHYSEN, K. MUSTIN, M. SAASTAMOINEN, N. SCHTICKZELLE, V. M. STEVENS, S. VANDEWOESTIJNE, M. BAGUETTE, K. BARTON, T.G. BENTON, A. CHAPUT-BARDY, J. CLOBERT, C. DYTHAM, T. HOVESTADT, C. M. MEIER, S. C. F. PALMER, C TURLURE, AND J. M. J. TRAVIS. 2012. Costs of dispersal. Biol. Rev. 87: 290–312.

BURNHAM, K. P., AND D. R. ANDERSON. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociol. Methods Res. 33: 261–304.

CANALE, G. R., C. A. PERES, C. E. GUIDORIZZI, C. A. F. GATTO, AND M. C. M. KIERULFF. 2012. Pervasive defaunation of forest remnants in a tropical biodiversity hotspot. PLoS ONE 7:

e41671.

CHEN, I.-C., J. K. HILL, R. OHLEMÜLLER, D. B. ROY, AND C. D. THOMAS. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024–1026.

CLEARY, D. F. R. 2004. Assessing the use of butterflies as indicators of logging in Borneo at three taxonomic levels. J. Econ. Entomol. 97: 429–435.

CONRADT, L., AND T. J. ROPER. 2006. Nonrandom movement behavior at habitat boundaries in two butterfly species: implications for dispersal. Ecology 87: 125–132.

CORBET, A. S., AND H. M. PENDLEBURY. 1992. The butterflies of the Malay Peninsula. Malayan Nature Society, Kuala Lumpur, Malaysia.

D'ABRERA, B. 1985. Butterflies of the Oriental Region Part II. Hill House Publishers, London, UK.

DOUGLAS, J. M., T. W. CRONIN, T. CHIOU, AND N. J. DOMINY. 2007. Light habitats and the role of polarized iridescence in the sensory ecology of neotropical nymphalid butterflies (Lepidoptera: Nymphalidae). J. Exp. Biol. 210: 788–799.

DUMBRELL, A. J., AND J. K. HILL. 2005. Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: Implications for sampling. Biol. Conserv. 125: 123–131.

EWERS, R. M., AND R. K. DIDHAM. 2008. Pervasive impact of large-scale edge effects on a beetle community. Proc. Natl. Acad. Sci. USA 105: 5426–5429.

FAYLE, T. M., E. C. TURNER, J. L. SNADDON, V. K. CHEY, A. Y. C. CHUNG, P. EGGLETON, AND W. A. FOSTER. 2010. Oil palm expansion into rain forest greatly reduces ant biodiversity in canopy, epiphytes and leaf-litter. Basic Appl. Ecol. 11: 337–345.

1 FITZHERBERT, E. B., M. J. STRUEBIG, A. MOREL, F. DANIELSEN, C. A. BRÜHL, P. F. DONALD,

2 AND B. PHALAN. 2008. How will oil palm expansion affect biodiversity? Trends Ecol.

3 Evol. 23: 538–545.

4 FORDYCE, J. A., AND P. J. DEVRIES. 2016. A tale of two communities: Neotropical butterfly

5 assemblages show higher beta diversity in the canopy compared to the understory.

6 Oecologia 181: 235–243.

7 FOSTER, W. A., J. L. SNADDON, E. C. TURNER, T. M. FAYLE, T. D. COCKERILL, M. D. F.

8 ELLWOOD, G. R. BROAD, A. Y. C. CHUNG, P. EGGLETON, C. V. KHEN, AND K. M. YUSAH.

9 2011. Establishing the evidence base for maintaining biodiversity and ecosystem function

10 in the oil palm landscapes of South East Asia. Philos. Trans. R. Soc. Lond. B Biol. Sci.

11 366: 3277–3291.

12 GALLMETZER, N., AND C. H. SCHULZE. 2015. Impact of oil palm agriculture on understory

13 amphibians and reptiles: A Mesoamerican perspective. Glob. Ecol. Conserv. 4: 95–109.

14 GARDNER, T. A., J. BARLOW, I. S. ARAUJO, T. C. ÁVILA-PIRES, A. B. BONALDO, J. E. COSTA , M.

15 C. ESPOSITO, L. V. FERREIRA, J. HAWES, M. I. M. HERNANDEZ, M. S. HOOGMOED, R. N.

16 LEITE, N. F. LO-MAN-HUNG, J. R. MALCOLM, M. B. MARTINS, L. A. M. MESTRE, R.

17 MIRANDA-SANTOS, W. L . OVERAL, L. PARRY, S. L. PETERS, M. A. RIBEIRO-JUNIOR, M.

18 N. F. DA SILVA, C. DA SILVA MOTTA, AND C. A. PERES. 2008. The cost-effectiveness of

19 biodiversity surveys in tropical forests. Ecol. Lett. 11: 139–150.

20 GAVEAU, D. L. A., S. SLOAN, E. MOLIDENA, H. YAEN, D. SHEIL, N. K. ABRAM, M. ANCRENAZ,

21 R. NASI, M. QUINONES, N. WIELAARD, AND E. MEIJAARD. 2014. Four decades of forest

22 persistence, clearance and logging on Borneo. PLoS ONE 9: e101654.

23 GIBBS, H. K., A. S. RUESCH, F. ACHARD, M. K. CLAYTON, P. HOLMGREN, N. RAMANKUTTY, AND

J. A. FOLEY. 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. USA 107: 16732–16737.

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.

GONZÁLEZ, E., A. SALVO, AND G. VALLADARES. 2015. Sharing enemies: evidence of forest contribution to natural enemy communities in crops, at different spatial scales. Insect Conserv. Divers. 8: 359–366.

GREENLEAF, S. S., N. M. WILLIAMS, R. WINFREE, AND C. KREMEN. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153: 589–596.

HADDAD, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. 153: 215–227.

HANSBAUER, M. M., I. STORCH, S. LEU, J. P. NIETO-HOLGUIN, R. G. PIMENTEL, F. KNAUER, AND J. P. W. METZGER. 2008. Movements of neotropical understory passerines affected by anthropogenic forest edges in the Brazilian Atlantic rainforest. Biol. Conserv. 141: 782–791.

HANSKI, I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

HASSALL, M., D. T. JONES, S. TAITI, Z. LATIPI, S. L. SUTTON, AND M. MOHAMMED. 2006. Biodiversity and abundance of terrestrial isopods along a gradient of disturbance in Sabah, East Malaysia. Eur. J. Soil Biol. 42: 197–207.

HECTOR, A., C. PHILIPSON, P. SANER, J. CHAMAGNE, D. DZULKIFLI, M. O'BRIEN, J. L. SNADDON, P. ULOK, M. WEILENMANN, G. REYNOLDS, AND H. C. J. GODFRAY. 2011. The Sabah

Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366: 3303–3315.

HILL, J. K., K. C. HAMER, J. TANGAH, AND M. DAWOOD. 2001. Ecology of tropical butterflies in rainforest gaps. Oecologia 128: 294–302.

HODGSON, J. A., C. D. THOMAS, S. CINDERBY, H. CAMBRIDGE, P. EVANS, AND J. K. HILL. 2011. Habitat re-creation strategies for promoting adaptation of species to climate change. Conserv. Lett. 4: 289–297.

KALLIONIEMI, E., A. ZANNESE, J. E. TINKER, AND A. M. A. FRANCO. 2014. Inter- and intra-specific differences in butterfly behaviour at boundaries. Insect Conserv. Divers. 7: 232–240.

KOH, L. 2008. Can oil palm plantations be made more hospitable for forest butterflies and birds? J. Appl. Ecol. 45: 1002–1009.

KUUSSAARI, M., M. SAARINEN, E.-L. KORPELA, J. PÖYRY, AND T. HYVÖNEN. 2014. Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. Ecol. Evol. 4: 3800–3811.

LAURANCE, S. G. W. 2004. Responses of understory rain forest birds to road edges in central Amazonia. Ecol. Appl. 14: 1344–1357.

LUCEY, J. M., AND J. K. HILL. 2012. Spillover of insects from rain forest into adjacent oil palm plantations. Biotropica 44: 368–377.

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

MAIR, L., J. K. HILL, R. FOX, M. BOTHAM, T. BRERETON, AND C. D. THOMAS. 2014. Abundance

changes and habitat availability drive species' responses to climate change. Nat. Clim. Chang. 4: 127–131.

MAIR, L., C. D. THOMAS, A. M. A. FRANCO, AND J. K. HILL. 2015. Quantifying the activity levels and behavioural responses of butterfly species to habitat boundaries. Ecol. Entomol. 40: 823–828.

MARCHANT, A., PURWANTO, A. HARSANTO, F, S. BOYD, N, E. HARRISON, M, AND R. HOULIHAN, P. 2015. "Random-flight" dispersal in tropical fruit-feeding butterflies? High mobility, long lifespans and no home ranges. Ecol. Entomol. 40: 696–706.

MARTENSEN, A. C., R. G. PIMENTEL, AND J. P. METZGER. 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: implications for conservation. Biol. Conserv. 141: 2184–2192.

MELO, F. P. L., V. ARROYO-RODRÍGUEZ, L. FAHRIG, M. MARTÍNEZ-RAMOS, AND M. TABARELLI. 2013. On the hope for biodiversity-friendly tropical landscapes. Trends Ecol. Evol. 28: 461–468.

MIETTINEN, J., C. SHI, W. J. TAN, AND S. C. LIEW. 2012. 2010 land cover map of insular Southeast Asia in 250-m spatial resolution. Remote Sens. Lett. 3: 11–20.

NAKASHIMA, Y., E. INOUE, M. INOUE-MURAYAMA, AND J. R. A. SUKOR. 2010. Functional uniqueness of a small carnivore as seed dispersal agents: a case study of the common palm civets in the Tabin Wildlife Reserve, Sabah, Malaysia. Oecologia 164: 721–730.

NIEMINEN, M., H. RITA, AND P. UUVANA. 1999. Body size and migration rate in moths. Ecography 22: 697–707.

OTSUKA, K. 1988. Butterflies of Borneo. Tobishima Corporation, Tokyo, Japan.

PERFECTO, I., AND J. VANDERMEER. 2002. Quality of agroecological matrix in a tropical montane

landscape: ants in coffee plantations in southern Mexico. Conserv. Biol. 16: 174–182.

PULLIAM, H. R. 1998. Sources, sinks, and population regulation. Am. Nat. 132: 652–661.

R CORE TEAM. 2015. R: A language and environment for statistical computing. R Foundation for
Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/.

RAND, T. A., J. M. TYLIANAKIS, AND T. TSCHARNTKE. 2006. Spillover edge effects: the dispersal
of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol.
Lett. 9: 603–614.

REYNOLDS, G., J. PAYNE, W. SINUN, G. MOSIGIL, AND R. P. D. WALSH. 2011. Changes in forest
land use and management in Sabah, Malaysian Borneo, 1990-2010, with a focus on the
Danum Valley region. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366: 3168–3176.

RIES, L., AND D. M. DEBINSKI. 2001. Butterfly responses to habitat edges in the highly
fragmented prairies of Central Iowa. J. Anim. Ecol. 70: 840–852.

RITTENHOUSE, T. A. G., AND R. D. SEMLITSCH. 2006. Grasslands as movement barriers for a
forest-associated salamander: migration behavior of adult and juvenile salamanders at a
distinct habitat edge. Biol. Conserv. 131: 14–22.

ROBINSON, G. S., P. R. ACKERY, I. J. KITCHING, W. G. BECCALONI, AND L. M. HERNÁNDEZ.
2001. Hostplants of the moth and butterfly caterpillars of the Oriental region. Natural
History Museum, London, UK.

RODRÍGUEZ, A., H. ANDRÉN, AND G. JANSSON. 2001. Habitat-mediated predation risk and
decision making of small birds at forest edges. Oikos 95: 383–396.

SCHULTZ, C. B., AND E. E. CRONE. 2001. Edge-mediated dispersal behavior in a prairie butterfly.
Ecology 82: 1879–1892.

SCHULTZ, C. B., A. M. A. FRANCO, AND E. E. CRONE. 2012. Response of butterflies to structural

and resource boundaries. J. Anim. Ecol. 81: 724–734.

SCHULZE, C. H., M. WALTERT, P. J. A. KESSLER, R. PITOPANG, SHAHABUDDIN, D. VEDDELER, M.

MÜHLENBERG, R. GRADSTEIN, C. LEUSCHNER, I. STEFFAN-DEWENTER, AND T.

TSCHARNTKE. 2004. Biodiversity Indicator Groups of Tropical Land-Use Systems:

Comparing Plants, Birds, and Insects. Ecol. Appl. 14: 1321–1333.

SCRIVEN, S. A., J. A. HODGSON, C. J. MCCLEAN, AND J. K. HILL. 2015. Protected areas in Borneo

may fail to conserve tropical forest biodiversity under climate change. Biol. Conserv.

184: 414–423.

SENIOR, M. J. M., K. C. HAMER, S. BOTTRELL, D. P. EDWARDS, T. M. FAYLE, J. M. LUCEY, P. J.

MAYHEW, R. NEWTON, K. S.-H. PEH, F. H. SHELDON, C. STEWART, A. R. STYRING, M. D.

F. THOM, P. WOODCOCK, AND J. K. HILL. 2013. Trait-dependent declines of species

following conversion of rain forest to oil palm plantations. Biodivers. Conserv. 22: 253–

268.

STEVENS, V. M., C. TURLURE, AND M. BAGUETTE. 2010. A meta-analysis of dispersal in

butterflies. Biol. Rev. 85: 625–642.

TAWATAO, N., J. M. LUCEY, M. SENIOR, S. BENEDICK, C. VUN KHEN, J. K. HILL, AND K. C.

HAMER. 2014. Biodiversity of leaf-litter ants in fragmented tropical rainforests of

Borneo: the value of publically and privately managed forest fragments. Biodivers.

Conserv. 23: 3113–3126.

THOMAS, J. A. 2005. Monitoring change in the abundance and distribution of insects using

butterflies and other indicator groups. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360: 339–

357.

TSCHARNTKE, T., T. A. RAND, AND F. J. J. A. BIANCHI. 2005. The landscape context of trophic

interactions: insect spillover across the crop-noncrop interface. Ann. Zool. Fenn. 42: 421–432.

WADE, T. G., K. H. RIITTERS, J. D. WICKHAM, AND K. B. JONES. 2003. Distribution and causes of global forest fragmentation. Conserv. Ecol. 7. Available at: http://www.consecol.org/vol7/iss2/art2 (accessed 30 May 2015).

WATSON, J. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. Biol. Conserv. 120: 311–327.

WOOD, B. J., AND C. G. FEE. 2003. A critical review of the development of rat control in Malaysian agriculture since the 1960s. Crop Prot. 22: 445–461.

11   *TABLE 1. Summary data and trait information for butterfly species sampled during the study for which individuals were originally*

12   *marked in either forest ('forest individuals') or plantation ('plantation individuals'); only species with ≥ two individuals recaptured*

13   *moving between traps were included.*

14

Species	Subfamily	# Individuals that moved between traps	# F to P movements[a]	# P to F movements[b]	# Forest individuals	# Plantation individuals	Forewing length (mm)	LHP specificity[c]	LHP availability[d]	Geographical 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*).

24   *TABLE 2. Model comparisons for binomial logistic regression models (GLMMs) determining the*

25   *effect of species traits (forewing length, larval host plant (LHP) specificity, larval host plant*

26   *availability and geographical range size) and abundance on probability of crossing the*

27   *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
Geographical range size * Habitat	NA	7	-61.15	140.96	8.02	0.007

28

29   [a] Positive (+) or negative (-) relationship between each trait and boundary crossing probability

30   from forest into plantation for each model that was better (Δ Akaike information criterion (AICc)

31   > 2) than the habitat-only model. NA = not computed.

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

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

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

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

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

37

38

39

FIGURE LEGENDS

41

42 FIGURE 1. (A) Map of Sabah (north Borneo), arrows show study sites. The landcover category

43 'forest' consists of peatswamp forest, lowland evergreen forest, and lower and upper montane

44 forest, and the category 'oil palm plantation' shows the extent of mature fruiting oil palm

45 plantations (see Miettinen *et al*. 2012 for details). (B) Sampling design comprising 24 fruit-

46 baited butterfly traps placed 50 m apart and sampled for a total of 18 d at each site.

47

48 FIGURE 2. Relationships between species traits for 16 species included in our trait analyses (see

49 Table 1). (A) Forewing length (mm) vs. larval host plant (LHP) availability (presence and

50 absence in oil palm plantations); (B) abundance vs. larval host plant availability; and (C) ln-

51 transformed abundance vs. forewing length (mm); trend line shows significant correlation

52 between ln-transformed abundance and forewing length (mm) (Pearson's correlation $r = -0.53$; P

53 $= 0.04$).

54

55 FIGURE 3. (A) Pie charts showing number of all individuals initially marked in forest or

56 plantations, and the number subsequently recaptured at least once in the same habitat (shaded

57 portion; *i.e.*, excluding individuals that crossed the boundary). (B) Stacked bar chart showing

58 percentage of all individuals marked in forest ($N = 139$ marked individuals) and plantations ($N = $

59 388 marked individuals) that were subsequently recaptured in the same habitat (medium shading;

60 either within the same trap, or a different trap), or crossed the boundary (dark shading). Forest

61 individuals were more likely to cross the boundary compared with plantation individuals ($\chi^2 (1) = $

62 59.6, $P < 0.0001$).

63

64   FIGURE 4. Probabilities (logit probability from binomial GLMMs) of individuals moving

65   within the same habitat (medium shading) or crossing the boundary (dark shading) for forest and

66   plantation individuals. Separate probabilities are calculated for species with (A) larval host plants

67   (LHP) present ($N = 12$ species) and absent ($N = 4$ species) in plantations, and (B) for the smallest

68   (19 mm forewing length) and largest (55 mm forewing length) species with $\geq$ two individuals

69   recaptured. Error bars show 95% CIs, and traits with bars that do not overlap are significant

70   factors affecting boundary crossing (*i.e.,* forest individuals with host plants present in plantations

71   (A) and small forest individuals (B).