Dispersal of butterflies in a New Guinea rainforest: using mark–recapture methods in a large, homogeneous habitat

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Abstract. 1. In an intensive mark-release-recapture study of all butterfly species in a tropical rainforest understory, 5903 individuals from 90 butterfly species (from the estimated total of 104 ± 9 species present in understory habitat) were marked, and 1308 recaptured at least once.

2. The study proved that mark-recapture methods are feasible in tropical rainforests, but also showed its limitations, as after 232 person-days of sampling we could only characterise dispersal for one-third of the species present.

3. The mean dispersal distance was 184 ± 46.1 m per species, while for six of the 14 species studied >1% of individuals were estimated to disperse 1 km or more. These parameters are, however, strongly dependent on the size and spatial configuration of the study plots, particularly in large homogeneous habitats. A new method proposed here to correct this bias revised the mean distance between two captures from 135 ± 33.6 to 325 ± 87.0 m per species.

4. These results, in combination with data from large permanent rainforest plots, suggest that most woody plant species in tropical forests are sufficiently abundant to serve as host plant species even to monophagous Lepidoptera species.

Key words. Lepidoptera, lowland rainforest, mark–release–recapture, Melanesia, Papilionoidea.

Introduction

Mark–release–recapture (MRR) is a well-established method for the study of animal dispersal, as well as for population size and dynamics (Lebreton *et al.*, 1992; Hanski *et al.*, 2000; Hagler & Jackson, 2001). First used for the study of fishes and waterfowl (Petersen, 1894; Dahl, 1918; Lincoln, 1930), it continues to be used mostly for the study of vertebrate species (Schaub *et al.*, 2001; Trolle & Kery, 2003; Calambokidis & Barlow, 2004). The only other group where MRR techniques have been widely used is insect, mostly dragonflies (Beirinckx *et al.*, 2006) and butterflies (Dowdeswell *et al.*, 1949; Ehrlich, 1965; Ehrlich *et al.*, 1975; Hanski *et al.*, 1994) where they

have led to a better understanding of the structure of butterfly metapopulations, including the frequency and distance of their dispersal (Baguette, 2003; Zimmermann *et al.*, 2011a). MRR is also an important tool for butterfly conservation, as it is used to estimate population size and mortality of endangered butterfly species (Nowicki *et al.*, 2005; Vlasanek *et al.*, 2009).

There is a marked contrast between the frequent use of MRR techniques in temperate zone ecosystems, particularly meadows and other open habitats (Bonebrake *et al.*, 2010), and the near absence of such studies of tropical, particularly rainforest, habitats. This bias, caused by technical difficulties faced by MRR studies in tropical rainforests, is unfortunately responsible for the lack of data on the dispersal and demography of butterfly, as well as other insect, species in tropical forests. This in turn seriously hinders our understanding of plant–insect interactions in highly diverse rainforest ecosystems. In particular, it has been suggested that many

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plant species are too rare in tropical forests for them to be used by specialised herbivores (Dixon *et al.*, 1987). Such a hypothesis cannot be tested using plant density only, as we also need to quantify dispersal ability of their herbivores.

One of the first tropical MRR studies focused on the population structure and dispersal of *Heliconius* butterflies (Ehrlich & Gilbert, 1973; Cook *et al.*, 1976; Ramos & Freitas, 1999; de-Andrade & Freitas, 2005), followed by population structure studies by Francini *et al.* (2005) and Beirao *et al.* (2012). Several MRR studies evaluated the impacts of habitat fragmentation (Uehara-Prado *et al.*, 2005; Benedick *et al.*, 2006; Marin *et al.*, 2009) or selective logging (Lewis, 2001) on butterfly diversity. All these studies except those focused on population structure used fruit traps (Corbet, 1942) to capture butterflies. Some of them, such as Molleman *et al.* (2007), achieved a large sample size, thus proving the feasibility of MRR in tropical forests. However, while fruit traps are useful for comparing communities from different habitats (Pinheiro & Ortiz, 1992) or different forest strata (Tangah *et al.*, 2004), they limit sampling to a single guild, fruit eating butterflies mostly from the family Nymphalidae. Further, traps actively attract butterflies to baits, possibly biasing their dispersal patterns (Fermon *et al.*, 2003; Marini-Filho & Martins, 2010) and distorting the relative abundance of different species, as some are attracted or caught more efficiently than others (Hughes *et al.*, 1998). In contrast, hand collecting by butterfly net is the standard method for MRR studies in simple habitats, such as meadows, as it enables sampling of all butterfly species equally (Pradel, 1996). In theory, collecting by net should be equally suitable for the understory butterfly species in tropical rainforests, but as far as we are aware, it has not been used in this habitat. This is probably because the low density of butterflies in understory make large sampling effort necessary and because lower levels of tropical forest are very tangled and it is tricky to chase butterflies inside such habitat. There is thus a dichotomy between MRR studies using butterfly nets in mostly temperate zone grasslands and MRR studies using fruit traps mostly in tropical forests.

The dispersal parameters obtained from MRR studies depend both on the behaviour of studied species and the size and spatial configuration of study plots (Schneider, 2003). Some studies monitor all locally available habitat patches suitable for the studied species so that their dispersal parameters reflect real constraints of habitat distribution (Hill *et al.*, 1996; Konvicka *et al.*, 2005) while in the studies within large, homogeneous habitats, where the study plots have to be arbitrarily delimited, the dispersal parameters may reflect predominately the design of the study. In both cases, differences in spatial configuration of study plots make comparisons between studies difficult (Fric *et al.*, 2010).

The present study: (i) tests the feasibility of MRR by netting in tropical forests; (ii) measures dispersal ability of all common understory butterfly species in a New Guinea lowland rainforest; (iii) explores relationships between dispersal ability and other ecological traits of species; and (iv) develops a correction for dispersal parameters reflecting spatial configuration of study plots, particularly important in the study of large, homogeneous habitats.

Material and methods

Study system

This MRR study took place in 10 000 ha of primary tropical rainforest in the Wanang Conservation Area (Madang Province, Papua New Guinea; 5.23°S 145.08°E; altitude 100 m). The study area consisted of four plots, 3.15–3.99 ha in size (Table 1), situated 45–682 m from each other (Fig. 1). Each plot was divided into 25×25 m grid marked by flagging tape and mapped in ArcGIS 9.3 (©ESRI, Inc.). The plots were representative of the vegetation and topography of the forest except that we avoided steep slopes where we could not mark and recapture butterflies efficiently.

Butterfly recording

Two teams of three people (rarely four or two people) each worked in the field daily from 09.00 to 16.00 hours (butterfly activity was minimal outside of these times), except when it was raining, from 25 April to 26 June 2009. Each team surveyed (zigzagged, no trails or paths were available) two plots every day. The pairs of plots were alternating daily between teams to limit collector effects. The collectors always surveyed the entire plot and tried to record and capture all the butterflies found there. They were marked, their sex, habitat (gap or understory) and position within the plot recorded, then released. Altogether, 232 person-days were spent in the field (Table 1).

Statistical analyses

The dispersal distance (D) was measured as the total distance travelled between individual captures for each butterfly captured at least twice. Butterfly species with D values available for at least three individuals were characterised by the mean dispersal distance (D_{avg}). Regression-based models were used to estimate the probability density (d) of a butterfly dispersing a given distance D (Baguette, 2003; Fric & Konvicka, 2007): inverse power function (IPF), $d = c \times D^z$ and negative exponential function (NEF), $d = c \times e^{zD}$. The constants c and z quantify species' dispersal over shorter and longer distances respectively. Further, recapture rates (R) were estimated as the proportion of recaptures to captures for butterfly species with ≥ 15 captures.

The mean dispersal distance between two captures was corrected for the proportion of dispersal events that could not be recorded because of the size and spatial configuration of the study plots. One million points were generated using random coordinates for a rectangle comprising four study plots. The points inside plots, representing butterfly captures (almost 100 000 points), were given random angle (direction) and distance from 20 to 1680 m (i.e. longest distance between any two points from the four sampling plots) in 20 m increments (i.e. 20, 40, 60 m, etc.). The random direction and distance simulated a dispersal event. The proportion of points that had their the new location within a sampling plot was used as an

Table 1. Description of study plots and mark-recapture sampling effort.

Plot	Area (ha)	Gaps (%)	No. of gaps	No. of visits	No. of person-visits	No. of captures	No. of species
A	3.15	6.5	13	36	112	2296	61
B	3.99	2.1	7	43	132	2428	54
C	3.99	3.9	11	42	113	1203	53
D	3.45	4.6	6	38	109	1719	51
X	–	–	–	–	–	905	54
Sum	14.58	–	37	159	466	8551	90

No. of person-visits denotes the total number of times a particular person visits on a particular day in each plot. A, B, C and D are individual plots (see Fig. 1); X denotes captures outside the plots. No. of visits indicates the number of times we worked in each plot (for variable lengths of time).
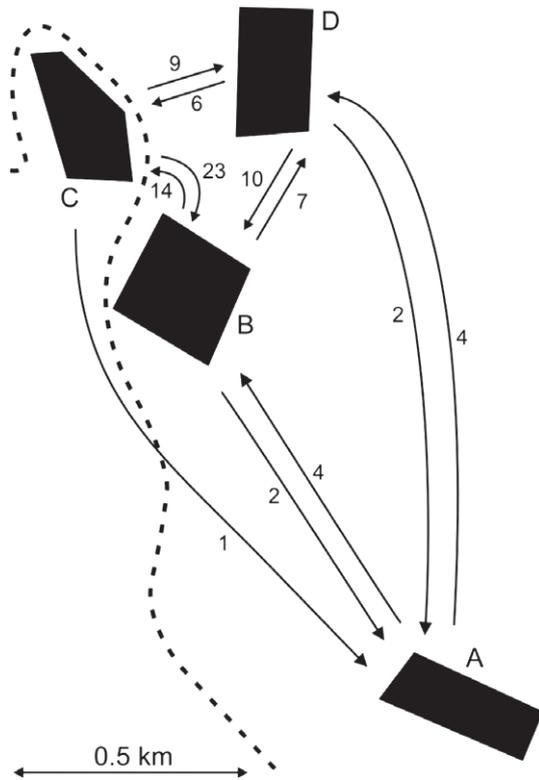

Fig. 1. Map of the study plots. Dashed line is the Digitam stream. The number of individuals moving from one plot to another (summed across all species) is shown by arrows. The entire area comprised continuous lowland primary forest.

Fig. 2. Recapture probability of a butterfly captured within the four plots and flying a given distance in a random direction. Note slight peaks at about 900 and 1300 m.

estimate of the probability (P_C) that dispersal at a particular distance will be recorded in four sampling plots (Fig. 2). The mean dispersal distance between two captures (D_{obs}) was calculated for each species, using observed dispersal distances (D) rounded up to 20, 40, 60 m, etc., and then corrected for the effect of plot size and position. The corrected mean dispersal distance (D_{cor}) was calculated as the sum of D/P_C values for each dispersal distance from 20 m to maximal dispersal distance of each species.

The D_{avg}, D_{cor}, z and R parameters were correlated with other characteristics of butterfly species, including gap preference, succession preference, altitudinal and geographic range, and body size. T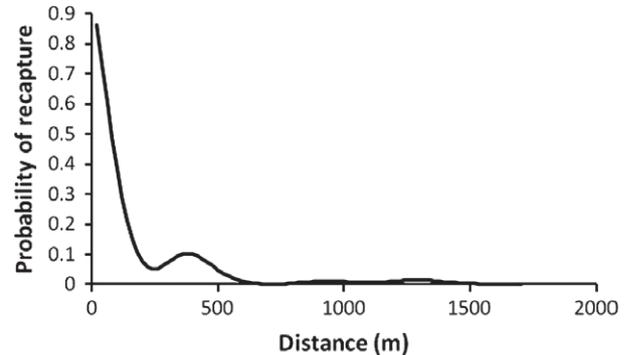he gap preference (*Gap*) was measured on a scale 0–1 of frequency of being captured in a gap (as opposed to forest understory). Succession preference (*Succession*) was estimated as the species score on the constrained axis in an ordination analysis (CCA) of butterfly distribution on a gradient from secondary (lower CCA values) to primary (higher CCA values) forest (from Sam, 2009). Altitudinal range (*Altitude*) was the difference between maximum and minimum altitude recorded for New Guinea. Geographical range (*Geography*) was classified as either endemic for New Guinea, or extending to the Australasian tropics (there were no species with even wider distributions). Body size (*Size*) was measured as the average wingspan for males and females. The last three variables were obtained from Parsons (1999).

The program ESTIMATES 8.2.0 (Colwell, 2006) was used to calculate rarefaction curves (Colwell *et al.*, 2004) and Chao's species richness (Chao, 1984).

Results

A total of 5903 individual butterflies were marked from 90 species, including 1308 individuals, which were then recaptured at least once. The total number of recaptures was 2648 so that the total number of butterfly captures was 8551. The most abundant butterfly was *Danis danis* with 5916 captures, i.e. approximately two-thirds of the total (Supplementary Table S1). The second most frequently captured butterfly 'species', *Taenaris* sp., was in fact a mix
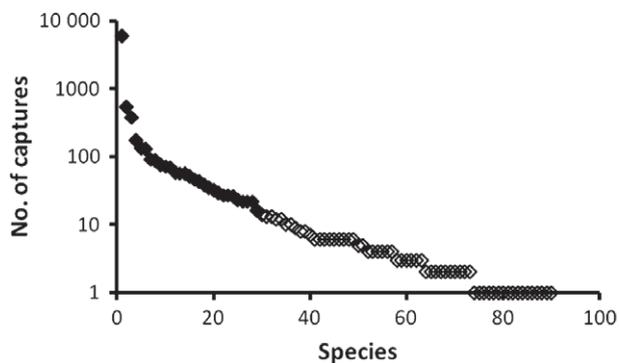
Fig. 3. Abundance distribution of butterfly species, as reflected by the number of captures, in our study plots. Only 29 species were caught at least 15 times (black diamonds). Three of the most captured butterflies *Danis danis, Taenaris* sp. and *Parthenos aspila* had 5916, 537 and 379 captures respectively.

of two species (*T. catops* and *T. myops*). They could not be distinguished by external morphology and are analysed here as a single unit. In contrast, 61 species were captured fewer than 15 times each (Fig. 3, Supplementary Table S2).

The probability density of dispersal (*d*) over a particular distance (*D*, from 0.2 to 10.0 km) was estimated for 14 species. The NEF and IPF regressions were significant for respectively 12 and 11 species (Supplementary Table S3). The NEF provided a better fit for nine species while IPF fitted better for four species. We have therefore used NEF for the overall analysis and interspecific comparisons of dispersal parameters. Butterfly species were ranked from the most sedentary species (*Parthenos aspila*) to species with the highest dispersal (*Papilio ambrax*, Fig. 4, Supplementary Table S3). There were significant differences in dispersal, based on *z* values from

NEF, between sexes in the four species from five that could be tested: *Danis danis* ($t_{1,22} = 4.389$, $P < 0.001$), *Taenaris* sp. ($t_{1,23} = -2.672$, $P < 0.01$), *Tellervo nedusia* ($t_{1,7} = -5.952$, $P < 0.001$), *Parthenos aspila* ($t_{1,5} = 1.064$, $P > 0.05$) and *Cethosia cydippe* ($t_{1,4} = -4.585$, $P < 0.01$). In all cases except *Danis danis*, females are more mobile. Both primary forest habitats, gaps and understory, included relatively sedentary as well as mobile species. For example, based on NEF results, in the understory, *Danis danis* was extremely sedentary as only 3% of individuals were likely to disperse over 500 m, while in *Taenaris* sp. it was 29% of individuals. In gaps also, individuals of *Parthenos aspila* were confined mostly to a single gap while for *Papilio ambrax* we documented dispersal over 1 km.

The recapture rate ranged from 0 to 0.5 (mean 0.15 ± 0.02) in the 29 species with ≥ 15 captures (Supplementary Table S2). The mean dispersal distance was $D_{avg} = 184 \pm 46.1$ m for the 17 species with at least three *D* values available, including extreme values of 648 and 649 m respectively for *Neptis nausicaa* and *Papilio ambrax*. Nevertheless, D_{avg} is underestimated because position of four plots underestimated long movements. The probability that recorded flight of a given distance initiated in one of four plots decreased rapidly from almost 90% for 20 m flight to 5% for 240 m flight, followed by increase to 10% for 380 m, drop to 0.01% at 720 m, and finally by two minor peaks of 1.1% and 1.4% at 940 and 1300 m, respectively (Fig. 2). This probability distribution was used to correct the observed mean distance between two captures from $D_{obs} = 135 \pm 33.6$ m ($n = 17$ species) to $D_{cor} = 326 \pm 87.0$ m (Supplementary Table S3).

The relationships between measures of dispersal and other species characteristics are summarised in Table 2. NEF parameter *z* (slope) was positively correlated with mean dispersal distance D_{avg} and D_{cor} (Fig. 5a) but not with
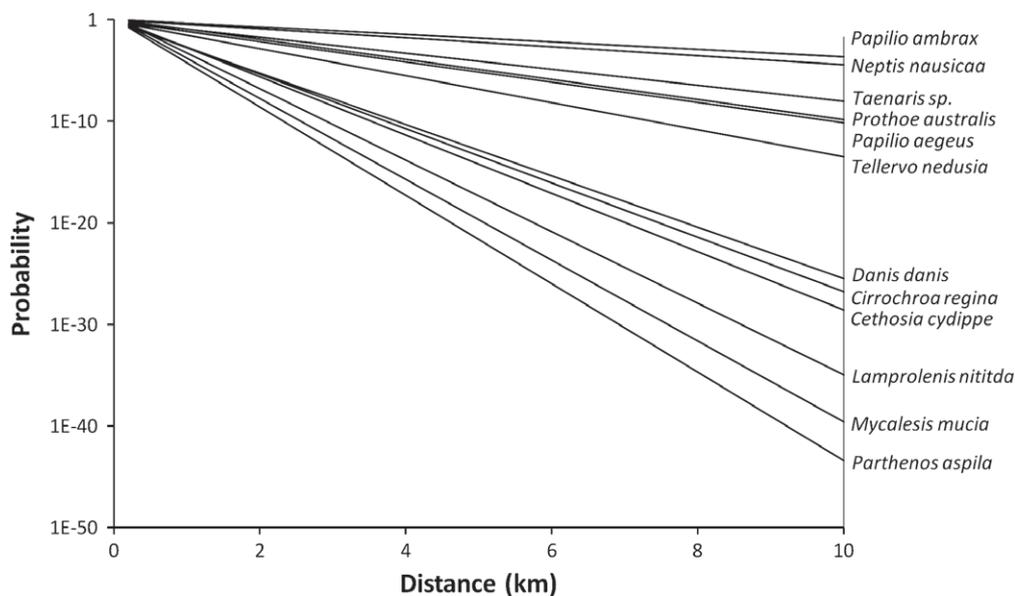

Fig. 4. Probability of dispersal with distance for individual butterfly species. The fitted negative exponential function shows decreasing dispersal ability from *Papilio ambrax* to *Parthenos aspila*. See Supplementary Table S3 for parameters of individual functions.

Table 2. Relationships of recapture rate (R), mean dispersal distance (D_{avg}), adjusted mean dispersal distance between two captures (D_{cor}) and NEF parameter (z) with gap and succession preference, geographical and altitudinal range and body size.

		R	D_{avg}	D_{cor}	z (NEF)	Gap
R	n		17	17	12	
	r		−0.07	−0.22	0.39	
	P		0.80	0.41	0.21	
D_{avg}	n				12	
	r				0.75	
	P				0.005**	
D_{cor}	n				12	
	r				0.86	
	P				< 0.001***	
Gap	n	29	17	17	12	
	r	−0.16	−0.04	−0.06	0.41	
	P	0.40	0.86	0.82	0.18	
Succession	n	28	17	17	12	28
	r	0.41	−0.26	−0.23	0.08	−0.46
	P	0.03*	0.30	0.37	0.80	0.01*
Geography	n	16, 13	10, 7	10, 7	6, 6	16, 13
	t	0.78	−0.90	−1.19	−0.89	−0.12
	P	0.44	0.38	0.25	0.39	0.91
Altitude	n	29	17	17	12	
	r	0.02	−0.1	−0.02	0.06	
	P	0.90	0.68	0.94	0.85	
Size	n	29	17	17	12	
	r	0.11	0.28	0.47	0.17	
	P	0.56	0.27	0.06	0.58	

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. P values from t-test for geographical range, Pearson correlation for the rest.

recapture rate R. There was also no correlation between R and D_{avg} (D_{cor}).

Higher recapture rates, R, were found for species in the understory as well as in those strongly preferring gaps (Fig. 5b). Butterfly species that preferred secondary forests had significantly lower recapture rates than the species preferring primary forests (Fig. 6a). Additionally, those that preferred early succession vegetation also preferred gaps within primary forest (Fig. 6b). The gap preference ranged from 0 to 0.81 among butterfly species. Only *Lamprolenis nitida*, *Danis danis*, *Tellervo nedusia*, *Taenaris dimona* and *Taenaris* sp. preferred forest understory, while 24 species exhibited various degrees of preference for gaps (Fig. 7, Supplementary Table S2).

There was no difference in R, D_{avg} (D_{cor}), z and *gap* preference between butterfly species endemic to New Guinea and those with wider distribution (Table 2). Likewise, these three parameters were not correlated with the species' altitudinal range or body size.

The number of species living in the forest understory in our study area was estimated at 104 ± 9 species, based on the species accumulation curve (Fig. 8). The number of well sampled species, defined here as those with ≥15 captures or ≥5 recaptures, increased slowly with sampling effort (Fig. 9). Two hundred and thirty two person-days of sampling were needed to obtain such data for 29 and 17 butterfly species, respectively. Based on the amount of daily captures and
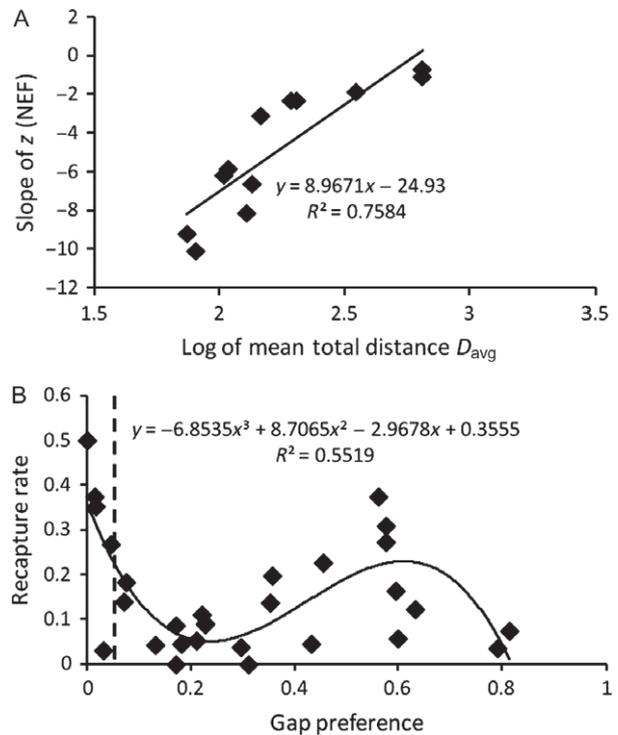
Fig. 5. (a) Correlation between mean dispersal distance D_{avg} and the slope of regression-based model z (NEF); (b) Relationship between recapture rate (R) and gap preference (peaking for understory species and species strongly preferring gaps; 4.3% of our study area were gaps, which is displayed as dashed line). This model performed significantly better than a second-order polynom in a test of deviance ($F_{25} = 25.43$, $P < 0.001$) and had a lower AIC ($\Delta AIC = 18.35$). NEF, negative exponential function.

recaptures for the 90 species sampled, 500 person-days would result in 20 species with ≥5 recaptures and 40 species with ≥15 captures, i.e. respectively 19% and 38% of the total.

Discussion

In this study the feasibility of the standard MRR protocol, used widely in temperate zone grasslands (Baguette & Neve, 1994; Hanski *et al.*, 1994; Kuussaari *et al.*, 1996; Zimmermann *et al.*, 2011b; Konvicka *et al.*, 2012) was tested on butterfly species from the understory of a lowland tropical rainforest in Papua New Guinea. With the help of numerous field assistants, 90 species were sampled from the estimated total pool of 104 ± 9 understory species in an MRR study. A comprehensive transect-based study in the same forest area, 10 km from our study plots, recorded a total of 176 butterfly species (of which 72 belonged to the family Nymphalidae, possible fruit feeders), including 100 species (46 species of Nymphalidae) from primary forest transects similar to this survey (Sam, 2009). It suggests that the present study captured most of the local species richness, whereas studies relying on fruit-baited traps are limited to fruit feeders, representing approximately half of all primary forest species.
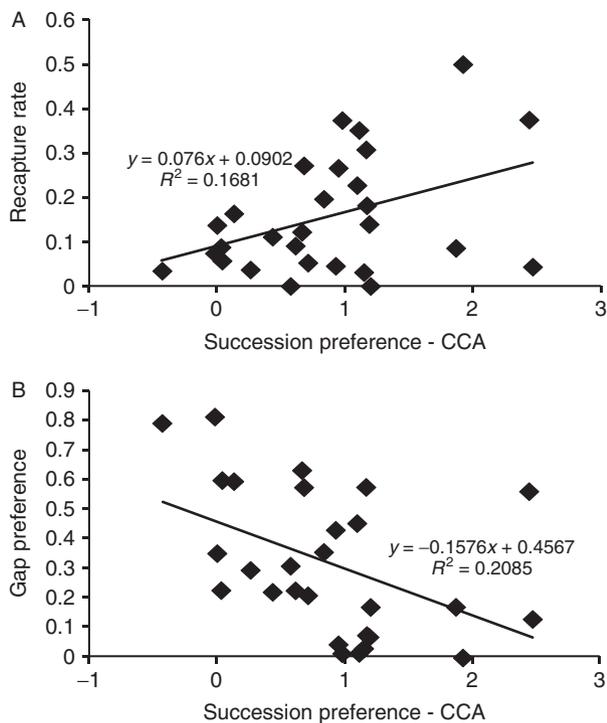
Fig. 6. (a) Correlation between the succession optimum of species and its recapture rate (recapture rate increased from secondary to primary forest); (b) Correlation between the succession optimum and gap preference (species preferring gaps to understory prefer also secondary to primary forest).
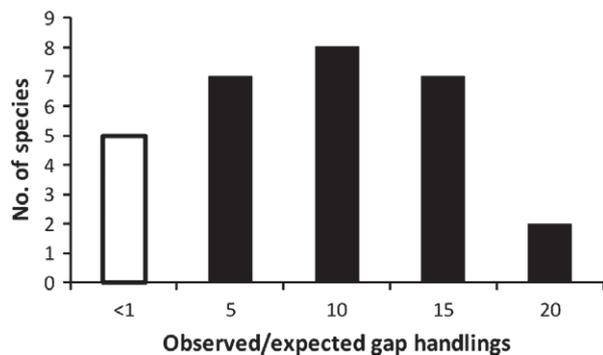

Fig. 7. Gap preference of primary forest butterfly species. The proportion of captures in gaps was compared to the expected proportion of 4.3%, corresponding to the area occupied by gaps in our study plots. The values <1 indicate preference for forest understory, while higher values indicate preference for gaps.

It should be noted that this study site might have been highly suitable for MRR methods as it has a higher butterfly density than some other lowland rainforests, including Barro Colorado Island in Panama and Khao Chong in Thailand (Basset *et al.*, 2011). The forest understory vegetation was also sparse, permitting relatively free movement. Further, the study relied on numerous paraecologists (Basset *et al.*, 2004) who may not be readily available to other tropical research teams.
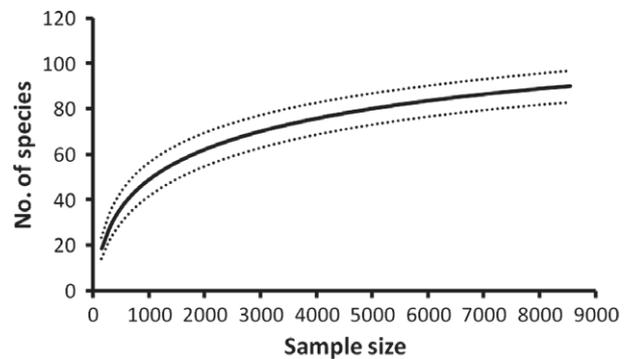

Fig. 8. Species accumulation curve (with 95% confidence interval) with increasing number of butterfly captures during the mark–release–recapture study.
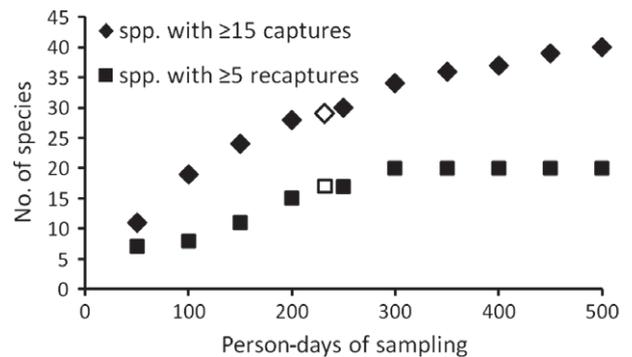

Fig. 9. The number of well sampled butterfly species (i.e. those with ≥15 captures or ≥5 recaptures) with increasing sampling effort, estimated from average captures and recaptures for one person-day and the relative abundance of butterfly species in our captures. White symbols denote our complete data set of 232 person-days.

This study has demonstrated the feasibility of using MRR in rainforest understories as at least some dispersal data were obtained for 29, i.e. 32% of all recorded species, which represented 97% of all individuals. Further, there were three species, which could be analysed in detail for population size, survival and other demographic parameters (Vlasanek & Novotny, unpublished). Even a considerable additional sampling effort would add analysable data for only a small number of new species. MRR thus remains feasible only for the most abundant species, which, however, often represent a large proportion of all individuals in the community. This is not unusual as tropical insect communities are renowned for a large number of rare species (Novotny & Basset, 2000), many of them 'tourists' from other habitats. Other ecological studies of insect communities are facing similar constraints. For instance, Novotny *et al.* (2002) documented host specificity for only 14–22% of folivorous species in New Guinea rainforest communities, but they represented 87–93% of all individuals.

This study, which sampled both nectar and fruit feeding species indiscriminately, found that approximately 50% of species were fruit feeding Nymphalidae. This is not surprising as fruit feeders are mostly concentrated in the understory

(DeVries *et al.*, 1997; Molleman *et al.*, 2006) while nectar feeders are mostly concentrated in the canopy (Schulze *et al.*, 2001).

Sam (2009) quantified habitat preferences of butterfly species along a rainforest succession gradient from deforested habitats, through secondary, to primary forests in our study area. In the present study, butterfly distribution was examined within primary forest, among gaps and shaded understory. Gaps represented 4.3% of the forest area in our plots, a share similar to other tropical forests (Brokaw, 1982; Lang & Knight, 1983; Chandrashekara & Ramakrishnan, 1994; Hubbell *et al.*, 1999). As expected, early succession species preferred gaps within the primary forest. More surprisingly, the majority of all butterfly species in the primary forest understory exhibited some degree of preference for gaps, despite them representing only 4.3% of the entire area. This illustrates the importance of gaps for butterfly species richness in tropical forests (Spitzer *et al.*, 1997; Hill *et al.*, 2001) or at least importance for observed butterfly diversity (butterfly may visit gaps frequently but only for nectaring, basking, etc. while its host plants may be in the understory).

All plot-based measurements of dispersal are biased by default (Wilson & Thomas, 2002). Schneider (2003) found a linear relationship between mean dispersal distance and size of study area. The size, shape and position of plots have a profound effect on the distribution of observable dispersal distances, as illustrated by the presented results. The mean dispersal distance between two captures rose almost 2.5 times when corrected for sampling bias, but remains underestimated, as our plot design could not easily measure dispersal distances from 620 to 880 m and from 1020 to 1180 m, over which only <1% dispersal events would have been recorded. Further, we could not record any dispersal longer than 1680 m. These results suggest that uncorrected comparisons of dispersal parameters between studies may be highly problematic (Fric *et al.*, 2010). We suggest that the MRR studies in large homogeneous habitats design their plots with reference to the recapture probability function (Fig. 2). This function should avoid zero probability of recapture for as wide a range of dispersal distances as possible.

Butterfly dispersal data could be fitted comparably well with different regression-based models, which give very different results for the same data set (Hill *et al.*, 1996; Baguette *et al.*, 2000; Baguette, 2003; Kuras *et al.*, 2003; Konvicka *et al.*, 2005), as was the case here. IPF fitted better (and with significant support) four species while NEF fitted better nine species. One difference between two used regression-based models is estimation of long distance movement probabilities. For instance in *Taenaris* sp., 2% of individuals disperse over 5 km distance based on IPF regression, but only eight individuals per 100 000 do so according to the NEF model. Although we do not have measurements for such long distance dispersal, we consider NEF values unlikely and IPF a better choice for such analyses.

The mean dispersal distance of 184 ± 46.1 m was similar to values from other studies in selectively logged tropical forests. With fruit-baited traps, Fermon *et al.* (2003) recorded 174 m and Lewis (2001) recorded that 88% of recaptured individuals travelled 20–141 m, 9% 200–412 m and 3% reached distances longer than 1 km. In areas with fragmented forest, where dispersal distances are expected to be biased, Marini-Filho and Martins (2010) recorded 369 m, but Marin *et al.* (2009) recorded only 57 m. Single species studies from South America recorded 232.3 and 136.7 m for males and females of *Actinote zikani* (studied along 2.5 km long road; Francini *et al.*, 2005), 283.3 and 198.7 m for males and females of *Parides burchellanus* (specialised species living inside canopy closed river basin; Beirao *et al.*, 2012), 270.6 and 236.3 m for males and females of *Heliconius erato* (Ramos & Freitas, 1999) or 65.2 m for males of *Heliconius erato*, again, and 84 m for males of *Heliconius ethilla* (de-Andrade & Freitas, 2005). Rather surprisingly, given the popularity of MRR techniques for the study of temperate zone butterflies, there are very few MRR studies from temperate forests (Freese *et al.*, 2006; Konvicka *et al.*, 2008). Most temperate zone studies focus on grasslands and other open habitats. Further, most of these studies examine fragmented habitats and the butterfly metapopulations colonizing them, rather than dispersal in a large continuous habitat. The mean dispersal distance in these grasslands varied from 322 m for *Maniola jurtina* and 272 m for *Lycaena virgaure* (Schneider *et al.*, 2003) through 253 m for *Parnassius mnemosyne* (Valimaki & Itamies, 2003), 231 m for *Euphydryas aurinia* (Zimmermann *et al.*, 2011b), 170 m for *Brenthis ino* (Zimmermann *et al.*, 2005) to 85 m for *Proclossiana eunomia* (Baguette & Neve, 1994) and 28 m for males and 8 m of females of *Plebejus argus* (median; Lewis *et al.*, 1997). Most of the temperate MRR studies focused on a single, often endangered, species, and therefore possibly having atypical biology, rather than the entire butterfly community.

The dispersal distances estimated here, even though they undoubtedly underestimate the life-time dispersal distances of butterflies, suggest that the presence of a single suitable host plant individual per hectare should be sufficient for most butterfly species to locate it. In the Center for Tropical Forest Science's (CTFS) network of 50 ha tropical forest plots, where all stems with DBH >1 cm are mapped, a large proportion of plant species had >1 individual plant per hectare: 65% of species in Lambir (Malaysia), 65% in Pasoh (Malaysia), 55% in Korup (Cameroon) or 65% in Barro Colorado Island (Panama) (data from http://www.ctfs.si.edu). Not all individual plants from a particular host species represent a suitable resource for herbivores all the time, though, because most herbivorous insects require young leaves for feeding (Coley, 1983; Cizek, 2005). It is, however, probable that dispersal ability does not limit most butterfly species from exploiting most shrub and tree species in tropical rainforests as their sole host plant species. Even rarer plant species may be available, as suggested by the NEF estimate that in six of 14 species, at least 1% of individuals dispersed 1 km or more.

Species from primary forest had a higher recapture rate than those from early succession vegetation. This could be a response to the transient nature of secondary forests, making higher dispersal advantageous. However, secondary forests are

a sufficiently long-living habitat compared to the generation time of tropical insects (Leps *et al.*, 2001) so it could also be argued that primary forest butterfly species are under greater selection pressure to disperse further than their secondary forest counterparts because they need to search for their host plants in more diverse vegetation. Hill *et al.* (2001) suggested that lower recapture rates indicated better dispersal. No such correlation was found between mean dispersal distance and recapture rate, which may have been caused by differences in butterfly mortality and behaviour, as, for instance, the canopy was not accessible for sampling.

Fermon *et al.* (2003) observed that females were more mobile in 10 of 13 species. Results from the temperate zone are similar (e.g. Baguette & Neve, 1994; Kuussaari *et al.*, 1996). Males tend to be more sedentary around the most hospitable mating sites while females have to search for a suitable location for oviposition (Scott, 1975). Our results are similar, as three species had females that were more mobile and only one species had males that were more mobile. This issue deserves further study on a larger number of rainforest species.

The geographical range of butterflies decreases along a succession gradient from secondary to primary rainforest (Spitzer *et al.*, 1993, 1997; Hamer *et al.*, 1997; Fermon *et al.*, 2000). This trend was not detected here, possibly because this study was limited to species, which were sufficiently common in primary forest. Additionally, there was no positive relationship between body size and mean dispersal distance (Sekar, 2012).

In conclusion, the study demonstrated the feasibility of the MRR method for tropical communities of butterflies in the forest understory but also showed that it requires large sampling effort and, even then, remains limited to common species. Further, it demonstrated that dispersal parameters are highly dependent on the spatial configuration of study plots, which has to be taken into account in comparisons between studies. Finally, the data on butterfly dispersal obtained by MRR suggest that most woody plant species in tropical rainforests are probably sufficiently abundant to be host plants even for specialised butterfly species.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12051

Table S1. Butterfly species caught in and around the study plots. A, B, C, D—captures from inside the plot; A^1, B^1, C^1, D^1—within 25 m from the plot; A^2, B^2, C^2, D^2—on paths connecting different plots, farther than 25 m from any plot. *Taenaris* sp. is a mixture of at least two species—*T. catops* and *T. myops*.

Table S2. Butterfly species with ≥ 15 captures. Count of total captures, marked and recaptured individuals. R, recapture rate (recaptures/captures); D_{avg}, mean dispersal distance in metres; D_{obs}, mean dispersal distance between two captures in meters; D_{cor}, mean dispersal distance between two captures adjusted for plots positions; Gap%, gap preference (proportion of captures in gaps); CCA, distribution optimum along succession gradient from secondary forests (low CCA values) to primary forests (high CCA values); Geo, geographical range (1, endemic for New Guinea and associated islands; 2, also in Australian tropics); Altitude, altitudinal range in PNG in metres; Size, wing span in mm.

Table S3. Probability of an individual butterfly dispersing a particular distance estimated for well-sampled butterfly species from regression-based models (IPF and NEF) with c and z as fitted parameters and coefficient of determination (R^2). Values in bold style show better fit of IPF or NEF. Probability (P): $*** < 0.001 < ** < 0.01 < * < 0.05 < NS$

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