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Title: Movement across woodland edges suggests plantations and farmland are barriers to dispersal

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ABSTRACT

Context. The behavioural response of animals to edges between habitat patches and the matrix can influence population dynamics and species persistence in fragmented landscapes.

Objectives. We aimed to answer two questions: (1) How do edge-effects between three land-cover types affect movement of adult male butterflies, and; (2) is response to edges influenced by perceptual range?

Methods. In south-eastern Australia, we visually tracked the flight behaviour of the butterfly *Heteronympha merope* at edges between three land-cover types: native eucalypt woodland, farmland and exotic pine plantation. Using six replicates of each edge type, we released animals on both sides of the edges, and at two distances from the edge (5 m and 30 m).

Results. Butterflies avoided pine edges, appeared to have low perceptual range in pines, and when released in pines, departed quickly. Butterflies often crossed from farmland into woodland and stayed, whereas none crossed from woodland into farmland or pines and stayed. Butterflies moved further away from pine edges when they were in woodland than when they were in farmland, suggesting edge-effects of one land-cover type depend on how animals respond to the alternative land-cover.

Conclusions. Avoidance, and low perceptual range in plantations suggests plantations reduce landscape connectivity. Limited use of farmland is consistent with global reports that intensification of agriculture contributes to insect declines. Resource requirements of butterflies overlap with many other insects, and so extensive forestry plantations and intensive agriculture likely have negative impacts on a range of taxa, with improved land-sharing a possible solution.

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39 **Keywords** Agriculture; edge-effects; fence effect; habitat fragmentation and loss; landscape
40 ecology; boundary behaviour.

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Introduction

In landscapes that are extensively cleared and fragmented for agriculture (Mony et al. 2018) or tree plantations (Liu et al. 2020), movement of individuals between subpopulations can have an important influence on population dynamics and species persistence (Crooks et al. 2017; Thomas 2000). Movement between remnant patches can reduce the risk of local extinction through rescue effects (Brown and Kodric-Brown 1977), by avoiding genetic deterioration (Lynch et al. 1995), and by enabling metapopulation dynamics (Hanski 1998). However, such movement depends substantially on the nature of the matrix which is defined as the predominantly human-modified non-habitat that surrounds remnants (Driscoll et al. 2013). Different matrix types can have a strong influence on how species respond to landscape connectivity (Kormann et al. 2019). How animals complete departure, transfer, and settlement from patch, through the matrix to a new habitat (Bonte et al. 2012; Clobert et al. 2009) is therefore critical for population dynamics in fragmented landscapes.

Successful movement through fragmented landscapes depends on the detection of edges between different land cover types and the subsequent behavioural response leading to edge avoidance or entry into a different cover type (boundary behaviour, Chapman et al. 2007; Kuefler et al. 2010). Movement is often modelled as a single parameter, however in reality, it is usually condition-dependent (Bowler and Benton 2005; Ricketts 2001). For example, in Spanish dune-scrub mosaics, the butterfly *Plebejus argus* would rapidly cross boundaries into high quality patches, but would spend time exploring edges of low quality areas and often did not cross into lower quality vegetation (Fernandez et al. 2016). As remnant patches are commonly embedded in landscapes with multiple land-cover types (e.g. Öckinger et al. 2012; Ricketts 2001),

comparisons of behavioural responses to edges of different types are needed to understand the boundary aspects of animal dispersal (Brown et al. 2017; Hansen et al. 2020).

Whether species depart through habitat edges will, in part, depend on their perceptual range (Fletcher et al. 2013). Species can choose to move towards or away from edges, only if they are close enough to sense them. For example, when rainforest patches were more than 80 m apart, separated by an agricultural matrix, the rainforest bird *Pyriglena leucoptera* used longer routes and had a higher risk of mortality because they could not detect distant patches (Awade et al. 2017). A limited perceptual range means that individuals cannot make informed decisions about habitat edges and this has flow on effects for connectivity (Pe'er and Kramer-Schadt 2008) and population structure (Grant et al. 2018).

Limited perceptual range may be a particularly important factor in butterfly dispersal because many butterfly species have perceptual ranges of just a few meters to tens of meters (Conradt et al. 2000; MacDonald et al. 2019; Schtickzelle et al. 2007; Schultz and Crone 2001), and this can make them vulnerable to effects of habitat fragmentation (Dover and Settele 2009). Moreover, butterflies and other insects have suffered major declines in some parts of the world, primarily as a result of land use change (Sanchez-Bayo and Wyckhuys 2019; Wagner et al. 2021; Warren et al. 2021). Understanding potential mechanisms affecting insect survival in fragmented landscapes may therefore contribute to broader knowledge about these concerning declines (Schultz et al. 2019).

In this study, we focus on movement responses to habitat edges of the Common Brown butterfly *Heteronympha merope* in a landscape of remnant woodland patches, cleared grazing land, and pine plantations in south-eastern Australia. *Heteronympha merope* is usually associated with

eucalypt woodlands (Braby 2005), but can occur in farmland and is generally absent from pine plantations (Sweaney 2014). Furthermore, *H. merope* reaches highest abundance in woodland patches partially or fully embedded in pine plantations compared to patches on farmland (Sweaney 2014). The mechanisms that drive these responses, however, have not yet been directly investigated, but could be related to 'fence effects' (Krebs et al. 1969; Ostfeld 1994) if pines are a barrier to movement out of patches.

In this study, we asked: How do edge-effects between the three land-cover types affect movement of adult male butterflies? We also investigated possible influences of perceptual range by releasing butterflies at 5 m and 30 m from boundaries. We hypothesised that: (i) individuals would move towards, or remain in, preferred woodland habitat (Delattre et al. 2010; Villemey et al. 2016), and (ii) responses to edges would be weakened if individuals were at the limit of their perceptual range.

Understanding movement within, and at the edges of, different habitats should lead to better generalisations and predictions concerning species conservation and successful land management (Driscoll et al. 2013; Ross et al. 2005). Our research is particularly relevant as plantations and planted forest occupy huge areas of land (294 M ha globally), and continue to expand (Crawford et al. 2016; FAO 2020; McEwan et al. 2020) while agriculture continues to intensify (Garcia et al. 2020). This study also has wider implications for other taxa associated with open woodland habitats or those faced with increasing land use change, as they may respond to landscape transformation in similar ways to our focal species (Scriven et al. 2017; van Halder et al. 2008; Villemey et al. 2016).

108 **Methods**

109 We address our research questions by releasing butterflies and monitoring subsequent flight
110 behaviour at two different distances on either side of three different edge types in a landscape
111 mosaic of pines, native eucalypt woodland and cleared grazing land.

112 Study area

113 Nanangroe, in SE Australia (Fig. 1, Lindenmayer et al. 2001), historically consisted of extensive
114 stands of open *Eucalyptus* woodlands, 85% of which have been cleared for agriculture over the
115 past 170 years (Lindenmayer et al. 2008). Beginning in 1998, extensive areas of land were
116 converted to pine plantations. The remaining *Eucalyptus* woodlands consist of relatively small
117 fragments (most <5ha), surrounded by a matrix of either agricultural pastures or dense pine
118 plantations (Fig. 1).

119 The agricultural land use at Nanangroe is predominantly grazing by livestock, with some
120 cropping, fertiliser and pesticide use. Pine plantations are thinned every 12-15 years and clear-
121 felled after 25 years (Lindenmayer et al. 2008). At the time of our study, the pine plantation was
122 mature (>12 years old) and densely stocked; the ground cover of all plantation sites was
123 comprised exclusively of fallen pine needles. The remnant grassy woodlands are a threatened
124 ecological community and were dominated by yellow box (*Eucalyptus melliodora*), white box
125 (*Eucalyptus albens*) and Blakely's red gum (*Eucalyptus blakelyi*). The understorey in remnant
126 sites was simple; mostly comprised of short native and exotic grasses. All woodland patches
127 used in our study were <5 ha in size, separated by areas of matrix, with distinct edges (Fig. 1).

128 Study species

129 *Heteronympha merope* is endemic to Australia, and occupies a wide range of habitats, preferring
130 open grassy *Eucalyptus* woodlands (Orr and Kitching 2010). At Nanangroe, *H. merope* is most
131 commonly found in woodland, also occurs on farmland, but not in pine plantations (Sweaney
132 2014). *Heteronympha merope* feeds on nectar, fermenting fruit, and gum from trees (Braby
133 2005). Sexual dimorphism is marked in this species (Braby 2005). Both sexes emerge in spring
134 to mate (Orr and Kitching 2010). Males are active over summer and die off with the cooler
135 Autumn weather (Edwards 1973). Females aestivate over summer, delaying egg production until
136 cooler weather and rainfall encourages grass growth, which provides resources for caterpillars
137 (Braby 2005). Females lay eggs on leaves of host plants, which include numerous species of
138 common native and exotic grasses on which the caterpillars feed (Orr and Kitching 2010).
139 Female *H. merope* die with the onset of winter.

140 Field experiment

141 We completed our experiment in February 2012 (Australian summer) using male butterflies. At
142 this time of year, *H. merope* individuals had completed mating and females were dormant (Braby
143 2005; Edwards 1973), meaning that male movement was driven by resource needs rather than
144 mate-finding (which may encourage more movement than usual, Kingsolver 1983). We
145 conducted our release experiments at 18 sites comprising three different edge combinations; 1)
146 six eucalypt woodland fragments adjacent to farmland, 2) six eucalypt woodland fragments
147 adjacent to pine plantation, and 3) six pine plantation sites adjacent to farmland (Fig. 1).

148 At each site, we completed four trials using a separate butterfly for each trial; releasing an
149 individual at either 5 m or 30 m from the edge on both sides of the boundary (i.e. two trials on

each side of the edge; Fig. 1). This gave us a total of 72 trials using 72 butterflies. We chose these distances because at 5 m into pines, the edges were easily visible, but at 30 m, the dense pines made it hard to see the edge.

Before any observations commenced at a site, the four butterflies needed for trials were captured using large hand nets (one net to a butterfly) to ensure the same butterfly was not used more than once. Butterflies were allowed to settle in their net for 10 minutes without an observer present before observations began. Trials in the matrix were usually performed with butterflies captured from the nearest woodland fragment, as individuals were scarce in pines and farmland.

Individuals were released from nets at ground level and followed by a single observer from a distance of at least five metres (to avoid disturbing the butterfly's natural movements) for 10 minutes or until the butterfly was lost from sight ($n = 16$). The butterfly's flight path was recorded; the distance of each flight (a single flight was recorded as the path between take off and when a butterfly came to rest), the direction of each flight, and how this related to the edge (Fig. 2). The distance travelled by a butterfly was estimated to the nearest meter for flights greater than 1 m or nearest 0.1 m for shorter flights, as the observer followed the flight path. Table 1 lists summary statistics derived from flight paths and environmental variables collected during the surveys.

We conducted surveys only during favourable weather conditions (i.e. not on days characterized by rain, low-lying cloud cover or high winds) and when the maximum temperature was forecast to be over 21°C (so we could be assured of having several hours in which the butterflies would be active). We began surveys after butterflies had sufficient time to warm and become active and ceased surveys for the particular day if weather conditions became unfavourable and before light levels dropped. This meant we conducted all trials between 9:30am and 4pm.

173 Statistical analyses

174 We combined release point and adjacent area to produce one explanatory variable, 'release
175 location' with six levels: Farm-Patch (i.e. butterfly released in the farmland matrix adjacent to a
176 woodland patch), Farm-Pine, Patch-Farm, Patch-Pine, Pine-Farm and Pine-Patch.

177 To get an overview of butterfly responses to edge type, we scored each flight as one of four
178 categories: never cross the edge; crossed the edge and did not return; crossed the edge then
179 returned, or; up and over, where butterflies flew straight up and out of the habitat soon after
180 observations began (known as 'up and over' behaviour, Walker 1985). This created a sparse
181 matrix when classified by release location, a dataset that could not be effectively modelled. We
182 therefore used pair-wise Fisher's exact tests to test for differences in flight behaviour among
183 release locations, with P values adjusted using the Benjamini-Hochburg method for controlling
184 the family-wise false-discovery rate, with R package fmsb (Nakazawa 2021).

185 We examined whether survey covariates were important to include in models, including date of
186 trial, time of trial, cloud cover, temperature and wind level. Date and cloud cover were strongly
187 correlated (Spearman's Rank Order correlation co-efficient - 0.76) and so date was excluded. We
188 fitted the remaining four survey covariates to the full model described below, but these variables
189 had P values > 0.18 and so had negligible influence on our results and were excluded from the
190 analyses.

191 We measured eight butterfly flight responses to release location and release distance (Table 1).
192 'Final distance from edge' and 'mean distance per flight ' were highly correlated with other
193 variables and were excluded from analysis (Online Resource 1). Therefore six response
194 variables were tested using linear models: number of flights; total distance; furthest from the

edge; closest approach to the edge; net displacement, and; furthest into the edge (Table 1). With the exception of 'furthest into the edge', these response variables were fitted against a full model that included explanatory variables of release location (combination of land cover released in and the adjacent land cover, six levels), release distance (5 m, 30 m), and their interaction. We also fitted an additive model without the interaction, and models with just one main effect. We identified the best fitting model using Akaike Information Criteria for small samples (AICc) and plotted effects that were significant ($P \leq 0.05$).

For all generalised linear models, we excluded butterflies released in the pine matrix 30 m from a boundary because 11 of 12 butterflies flew up and over. All GLMs included an 'offset variable' (McCullagh and Nelder 1989) to account for differing sampling durations, as six of the observations (excluding pine – 30m releases) were shorter than ten minutes due to the butterfly disappearing from sight.

The response variable 'furthest into the edge' only had positive values for animals that crossed the edge, thus all such values coincided with zeros for closest approach to edge and these variables were highly correlated (- 0.849). To analyse 'furthest into the edge' we excluded trials where the animals did not cross the edge (35 trials), reducing the dataset to 25 trials where it was possible to measure this response. We also excluded the only record from farm-pine (butterfly released in farm near a pine edge) because one record is inadequate for analysis. We could only fit main effects of release location and release distance as explanatory variables because only five trials were from 30 m releases, and four of these were from one release location (farm-patch). Release locations included were farm-patch ($n = 10$), patch-farm ($n = 4$), pine-farm ($n = 5$), pine-patch ($n = 5$).

Analyses were completed using R (R Core Team 2020), including packages lme4 (Bates et al. 2015), MuMIn (Barton 2020) and car (Fox and Weisberg 2019).

Results

Overall flight patterns

Total flight distances averaged 36.5 m (SD = 33.6 m, range 0.5 – 228 m, Online Resource 2) and overall flight patterns are summarised in Fig. 3. The number that never crossed the edge varied significantly with release location (Table 2), with only one of the 24 butterflies released adjacent to pines crossing into pines, and this individual returned to farmland before the end of the observation period (Fig. 3). Butterflies usually crossed from farmland into patches and stayed there, but never crossed from patches into farmland and stayed, nor did they cross into pine and stay (Table 2). A small proportion crossed out of pine into either farmland or patches and stayed (Table 2), but only when within 5 m of the edge (Fig. 3). Up and over behaviour was only observed when butterflies were released in pine (Table 2). Up and over behaviour occurred significantly more frequently at 30 m than at 5 m from the edge (Fig. 3, Fisher's exact test comparing number of up and over vs other responses at the two distances for pine-farm and pine-patch trials, $P = 0.0028$).

Release location and release distance analyses

We found a significant relationship between a butterfly's closest approach to the edge and the interaction between release location and release distance (Tables 3, 4). Butterflies released in

woodland patches 30 m from the edge flew significantly closer to edges of farmland compared to pine plantation, and butterflies released 30 m into farmland moved significantly closer to patches than to pines (Fig. 4a).

Butterflies that crossed the edge from pine plantation travelled further into woodland patches compared to any other boundary crossings, although they also moved significant distances away from the edge after crossing from pine to farm, and from farm to patch (Table 4, Fig. 4b).

Butterflies released in patches adjacent to pines had significant positive net-displacement indicating they moved further away from the edge, whereas those released in farms adjacent to patches were significantly displaced towards the patches (Table 4, Fig. 4c).

Butterflies released 30 m from edges travelled further than those released 5 m from the edge, but release location had no influence (Table 4, Fig. 4d). The furthest distance that butterflies moved away from the edge (on the release side) was also only affected by release distance, with larger distances when released 30 m from the edge (Table 4, Fig. 4e). The number of flights did not depend on release location or distance (Tables 3, 4).

Discussion

Faster, more directed movement is often reported when animals, including butterflies, are in non-habitat (Brown et al. 2017; Crone et al. 2019; Schultz et al. 2019), consistent with *H. merope*'s behaviour in pine plantations. *Heteronympha merope* had a strong aversion to exotic pine plantations, escaping as quickly as possible from pines if no edges were in sight, or if edges were perceived, crossing into woodland or pasture then moving away from the edge. Pine plantations had no understorey vegetation (including grasses), offering no food resources. Pine plantations

also had a closed canopy, blocking sunlight, which can limit activity and deter butterflies (Bennett et al. 2014). Many other studies have shown edge avoidance by a range of open-habitat species towards forests (Brown et al. 2017; French and McCauley 2019; Haddad 1999), suggesting that high-contrast vegetation types could commonly limit emigration for patch-associated species. Because resource requirements of butterflies (including *H. merope*) overlap with many other insects (New 1997; Thomas 2005), it is likely that dense pine plantations cannot support species from other animal groups. In our study system, this includes native bees nesting above ground, which were completely absent from pines, and flying beetles, with significantly fewer species in pines (Yong et al. 2020).

Tree plantations, by eliciting avoidance behaviours, may pose strong fence effects, preventing emigration and leading to increased abundance in enclosed patches (Krebs et al. 1969; Ostfeld 1994). Sweaney (2014) observed higher abundance of *H. merope* in woodland patches partially or fully surrounded by a pine matrix than in patches surrounded by farmland. Fence effects can increase population density in the short-term which could increase population persistence, but have a number of risks that could reduce population viability, particularly the risk of resource depletion (Krebs et al. 1969; Ostfeld 1994). We do not know how substantial these risks are in our study system. Further, fence effects may not be the only mechanism contributing to high abundance in remnant woodland with pine edges. Effects of changed bird, reptile and insect predator communities (Lindenmayer et al. 2019; Mortelliti et al. 2015; Sweaney et al. 2015), and possible resources or shelter at plantation edges (Koneri and Nangoy 2019; Toivonen et al. 2017) cannot be ruled out.

Although rarely reported in the literature, other butterfly species use up and over behaviour to move over areas of tall trees and forest (Kaye et al. 2011; Ross et al. 2005). However, unlike our

observations, the aforementioned studies noted this behaviour only from within habitat patches towards matrix edges. In our study, up and over behaviour was observed only when butterflies were released *within* the matrix, and not for butterflies in patches or farmland adjacent to pine plantations. This is an important difference as it implies that this behaviour is a way to avoid being in pine plantations, rather than a mechanism readily employed to cross over them. Further, the high abundance of *H. merope* in patches embedded in pine (Sweaney 2014) suggests that the up and over mechanism is not frequently used to escape from patches embedded in plantations.

Butterflies moved further away from a pine edge when they were in a woodland patch than when they were in farmland. This behaviour could arise if there is a higher predation risk at woodland-pine edges (Haddad and Tewksbury 2005) or if there is lower 'resistance' to movement in favoured woodland habitat (Villemey et al. 2016). An implication of our results is that shallower edge effects (e.g. negative rather than extended negative, Villaseñor et al. 2014) or even positive edge effects, with highest abundance near the edge, may arise when animals enter a low quality area from a lower-quality area because they do not disperse far from the edge.

Heteronympha merope individuals were able to orientate towards woodland patches at a range of at least 30 m in farmland, but smaller distances in pine plantations. A change in vegetation density or height in the matrix can therefore be expected to affect movement behaviour by altering perceptual range (Biz et al. 2017; Olden et al. 2004). Butterflies typically have relatively short perceptual ranges, often of only tens of meters (MacDonald et al. 2019; Schtickzelle et al. 2007), meaning that changes at the relatively large scale of plantation establishment are likely to affect many species. In landscapes where open habitats are being converted to tree plantations (Lindenmayer et al. 2019), a range of species likely face reduced perceptual range, which can increase risk of mortality in the matrix (Awade et al. 2017), and alter connectivity (Brown et al.

2017; Pe'er et al. 2011). In our study area, the plantation also reduced connectivity for one of two lizards (Mortelliti and Lindenmayer 2015) and four bird species (Mortelliti et al. 2014). Furthermore, others have reported barrier effects of plantations, such as for small mammals in Chile (Barcelo and Simonetti 2020) and Malaysia (Brunke et al. 2020), birds in Brazil (Giubbina et al. 2018) and spiders in Hungary (Galle et al. 2018). While there are several factors that can affect movement behaviour through fragmented landscapes (Doherty and Driscoll 2018), perceptual range could have a role in the response of animals to plantation establishment.

Like the pines, farmland may be a hostile matrix, but with spill-over at the ecotone (e.g. Pe'er et al. 2011). It is possible that *H. merope* cannot always distinguish between farmland and woodland without first 'sampling' the farmland (Fernandez et al. 2016; Ries and Debinski 2001). Our examination of overall flight patterns lends support to this idea, as individuals that crossed over into farmland from woodland patches never stayed, while those crossing from farmland into patches almost always stayed (Table 2, Fig. 3). Further, many individuals avoided approaching a nearby farmland edge if they were released 30 m in woodland (Fig. 4a) and other survey data (Sweaney 2014) showed very low abundance in farmland compared with woodland remnants. Farmland and woodland in our study area both have a range of host plants and food resources (Braby 2005; Orr and Kitching 2010), and scattered paddock trees can provide important structure in farmland (Prevedello et al. 2018). We suggest further research is likely to reveal a continuum of habitat suitability, related to the intensity of land use (e.g. Schwarz and Fartmann 2021) and density of woodland trees. More intensively used farmland, such as crops or areas without scattered trees, may offer few resources for insects and act as a matrix (Ng et al. 2021; Salek et al. 2018), while light grazing with substantial tree retention may offer low quality habitat rather than a matrix.

Butterflies released further from an edge moved further (Fig. 4d). This partly reflects the larger distance that butterflies had to travel when approaching an edge to interact with it. Butterflies released at 30 m also had larger individual flight distances (mean flight distance was highly correlated with total distance, spearman's correlation = 0.76, Online Resource 1). Fast, straight movements are typically observed in unfavourable habitat as animals attempt to move away (Brown et al. 2017; Schultz et al. 2016). However, this does not explain longer flight distances in *H. merope* released 30 m from the edge because long flights occurred in favoured woodland habitat and the farmland matrix. Perhaps *H. merope* prefers to use short flights near edges to gather information that informs their decision to stay or leave the patch, similar to finer grained flight patterns in other butterfly species when making a decision at a boundary (Fernandez et al. 2016). Flight patterns are also influenced by food availability (Evans et al. 2020), so more detailed behavioural observations are needed to understand reduced flight lengths near the edge.

In future research, it would be valuable to investigate movement patterns at other times and in both sexes. Butterfly movement across the pine matrix may increase during periods of clear-felling or thinning when the structure is more open. In addition, male *H. merope* butterflies may cross inhospitable boundaries during the mating season, as has been observed in other butterfly species (e.g. Kingsolver 1983; Schultz 1998). Female butterflies often have different dispersal behaviours than males (Turlure et al. 2011), sometimes moving further (Goff et al. 2019; Reim et al. 2019) or moving less (Ehl et al. 2018) than males. Further, butterfly flight capacity can be affected by local and landscape habitat characteristics (Crawford and Keyghobadi 2018), so there is potential for butterflies from different habitats to have different edge responses. Although it will be difficult to capture substantial numbers of butterflies in farmland, future research could

investigate whether the source of captured butterflies (woodland vs farmland) influences behavioural responses at edges.

Management implications

Tree plantations and planted forests cover 294 M ha worldwide, increased by 56% between 1990 and 2020, and continued expansion is expected (Crawford et al. 2016; FAO 2020; McEwan et al. 2020). Over half of plantations consist of native species (56%, FAO 2020), and these can have beneficial effects for some species when established on cleared land (Ashman and Watchorn 2019). However, where plantation structure is substantially denser and with a simple understory compared with native vegetation, perhaps the most effective management strategy to enable open woodland specialists to persist is one that increases permeability. By lowering tree density in plantations (Kleintjes et al. 2004; Waltz and Covington 2004), species associated with open land-cover types may cross edges in a similar way to which grassland butterflies can make use of clear-cuts or other forest clearings in Europe (van Halder et al. 2008; Viljur and Teder 2016). Further, establishing corridors of native vegetation or understorey vegetation would increase plantation similarity with open woodland patches, providing species, such as *H. merope*, with resources not available in densely stocked stands (Hartley 2002). Both of these management options are not expected to reduce fibre production (Hartley 2002), therefore protecting the economic investment and return of plantation agencies.

A wide range of taxa are disadvantaged by plantations, and intensive agriculture (Bohada-Murillo et al. 2020; Doherty et al. 2020; Giubbina et al. 2018). Our study highlights how behavioural mechanisms contribute to such effects. Butterflies preferred to stay in woodland

habitat rather than plantations or farmland, and they appeared to have reduced perceptual range in plantations, leading to complete avoidance of that land-cover type. Consequently, adopting a land-sharing approach (Phalan 2018) by improving landscape structure and permeability for wildlife has potential to increase movement and improve population persistence of many species in highly modified landscapes (Hendershot et al. 2020). Altering the matrix to increase the structural and compositional similarity to native vegetation patches should be part of a range of actions used to enhance successful biodiversity conservation in patchy networks (Arroyo-Rodriguez et al. 2020; Eycott et al. 2012). This is all the more urgent given the spectre of the mass loss of insect biodiversity in highly developed regions of the world associated with landscape transformation (Sanchez-Bayo and Wyckhuys 2019; Wagner et al. 2021; Warren et al. 2021).

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Declarations

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Conflicts of interest/Competing interests (include appropriate disclosures)

394 Not relevant

395 **Ethics approval (include appropriate approvals or waivers)**

396 Not relevant

397 **Consent to participate (include appropriate statements)**

398 Not relevant

399 **Consent for publication (include appropriate statements)**

400 Not relevant

401 **Availability of data and material (data transparency)**

402 We will deposit the data in a publically accessible data repository.

403 **Code availability (software application or custom code)**

404 Not relevant

405 **Authors' contributions**

406 All authors designed the research. NS collected the data and wrote the first draft with input from

407 DAD and DBL. DAD did the analysis, revised the final manuscript with input from DBL and

408 NS and completed revisions after review.

409

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679 **Table 1.** Response variables summarising flights after release. * excluded from analysis due to
680 high correlations with other variables (see Online resource 1).

Variable	Description
Number of flights	Total number of flights (a single flight defined as a butterfly taking off and then coming to rest) performed during observation period
Total distance	Sum of distance of all flights taken during observation time
Furthest from the edge	The furthest the butterfly flew away from the edge during observation period
Closest approach to the edge	The closest the butterfly approached to the edge during observation period (this would be 0 if it crossed over the edge)
Net displacement	Final distance from the edge minus release distance. Negative values where the butterfly was closer to the edge than the release point, positive values if they moved further from the edge.
Furthest into the edge	After crossing an edge, the maximum distance away from the edge that a butterfly flew into the bordering land-cover during observed flight (this would be 0 if they did not cross the edge)
*Final distance from edge	Distance from the edge at the end of the observed flight period (represented as a negative number if it crossed over and stayed in the edge habit)
*Mean distance per flight	The average distance between the sequence of take-offs and landings during the observation period.

681

Table 2. Frequency of occurrence of four butterfly flight patterns for six release locations. Never cross = never cross the edge; cross stay = cross the edge and stayed in the adjacent vegetation type; cross return = crossed the edge but then returned; up over = flew straight up and out of release vegetation. Other = number of butterflies with flight behaviour other than the behaviour being tested. Letters that are the same within each pairwise comparison row indicate responses were not significantly different at $P \leq 0.05$.

	Farm-Patch	Farm-Pine	Patch-Farm	Patch-Pine	Pine-Farm	Pine-Patch
Pairwise comparison	ab	c	ac	c	ab	b
Never cross	2	11	8	12	2	0
Other	10	1	4	0	10	12
Pairwise comparison	a	b	b	b	ab	ab
Cross stay	9	0	0	0	3	4
Other	3	12	12	12	9	8
Pairwise comparison	a	a	a	a	a	a
Cross return	1	1	4	0	1	0
Other	11	11	8	12	11	12
Pairwise comparison	a	a	a	a	b	b
Up over	0	0	0	0	6	8
Other	12	12	12	12	6	4

Table 3. Models fitted to each response variable and Akaike Information Criteria for small samples (AICc).

Response	Model fitted	DF	AICc
Closest approach to the edge	release-point * distance	11	433.4
	release-point + distance	8	435.4
	distance	3	440.3
	release-point	7	464.5
Furthest into the edge	release-point * distance	NA	NA
	release-point + distance	6	147.8
	distance	3	146.7
	release-point	5	144.4
Net displacement	release-point * distance	11	574.5
	release-point + distance	8	568.1
	distance	3	571
	release-point	7	566.3
Total distance	release-point * distance	11	609.8
	release-point + distance	8	603.3
	distance	3	591.7
	release-point	7	607
Furthest from the edge	release-point * distance	11	555.4
	release-point + distance	8	551.6
	distance	3	547.3
	release-point	7	566.4
Number of flights	release-point * distance	11	320.9
	release-point + distance	8	314.8
	distance	3	307.6
	release-point	7	312.2

694 Table 4. Anova tables for the best fitting linear models of flight behaviours.

Response	Fitted variable	Sum of		F	P value
		squares	DF		
Closest approach to the edge	release location	1214.7	5	4	0.004
	distance	2533.9	1	41.6	<0.0001
	release	596.5	3	3.3	0.0288
	location:distance				
	residuals	3043.4	50		
Furthest into the edge	release location	161.7	3	3.3	0.0429
	residuals	330.5	20		
Net displacement	release location	9157.7	5	2.9	0.0206
	residuals	33727.8	54		
Total distance	distance	10077.9	1	9.7	0.0029
	residuals	60532.4	58		
Furthest from the edge	distance	12497.9	1	25.1	<0.0001
	residuals	28871.9	58		
Number of flights	distance	0	1	0	0.9925
	residuals	531.4	58		

695

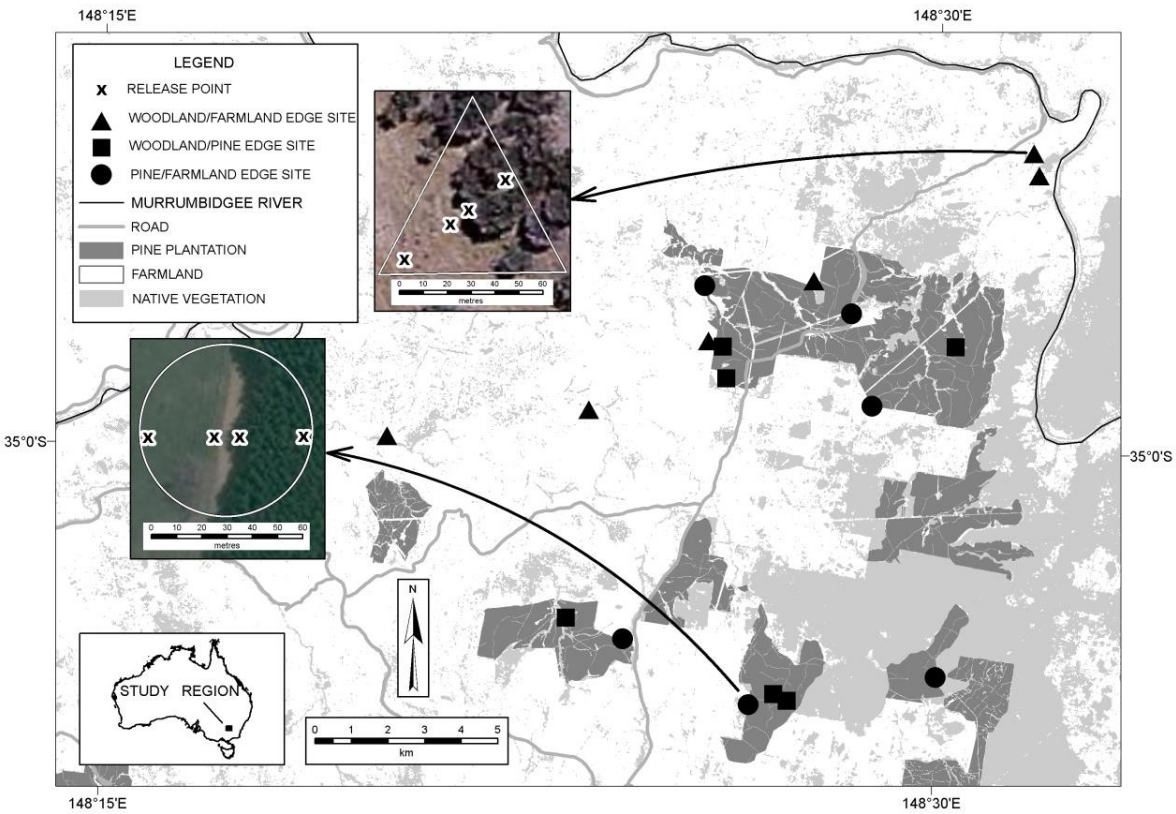


Fig. 1 Left panel: the Nanangroe landscape on the south-west slopes of NSW (SE Australia). Symbols show positions of the 18 study sites. Butterflies were released at either 5 m or 30 m from the edge on both sides of the edge (shown in insets). One butterfly was used per trial, resulting in four trials per site, giving 72 trials in total. Right panel: a woodland patch at the edge of a pine matrix.

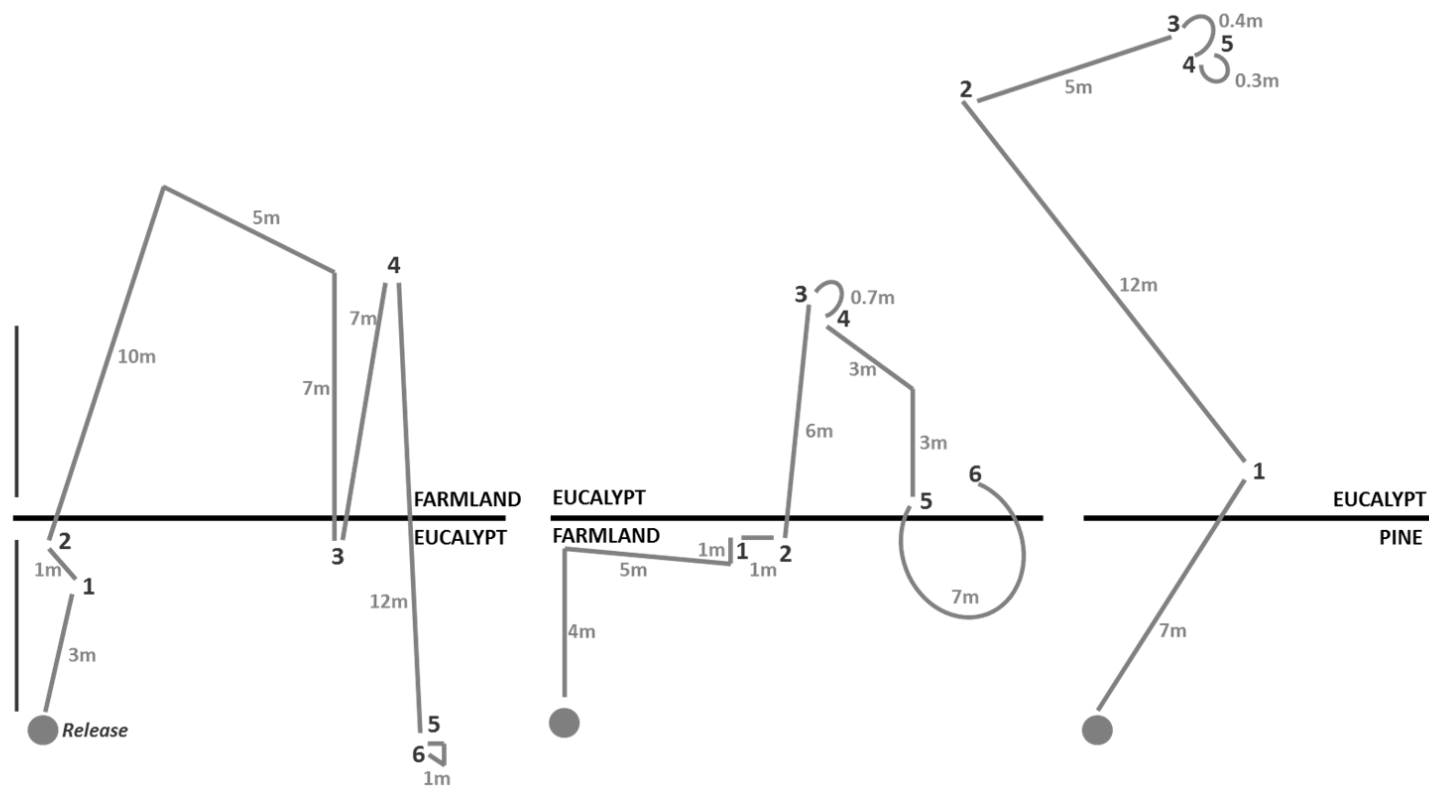


Fig. 2 Examples of flight paths for a butterfly released in; a) a woodland patch, 5 m from a farmland edge, b) in farmland, 5 m from a woodland patch edge and c) in pine plantation, 5 m from a woodland patch edge. Movement was recorded for 10 minutes. Flight path shows sequence of flights between stops (bold numbers), direction and distance of each flight (grey numbers)

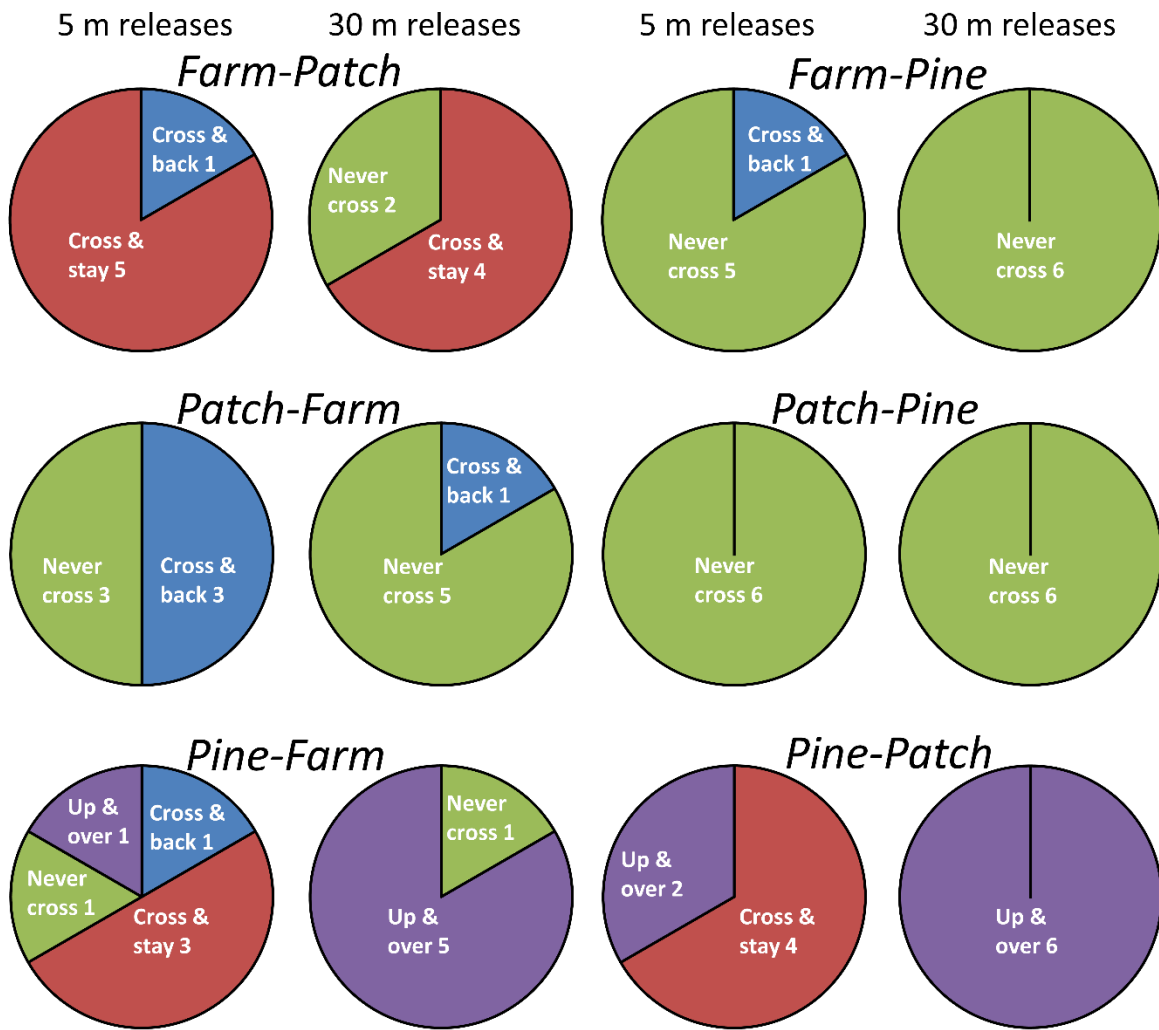


Fig. 3 The number of butterflies at each release location and distance that never crossed the edge, crossed over and stayed in adjacent habitat, crossed over and returned to release habitat, or flew up and over. The first named land cover type indicates the release location (e.g. Farm-Patch indicates released in a farm either 5 m or 30 m from the adjacent patch).

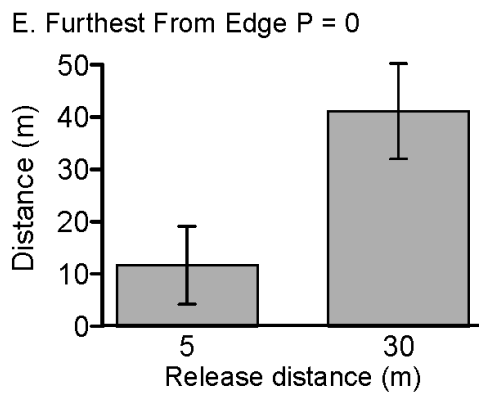
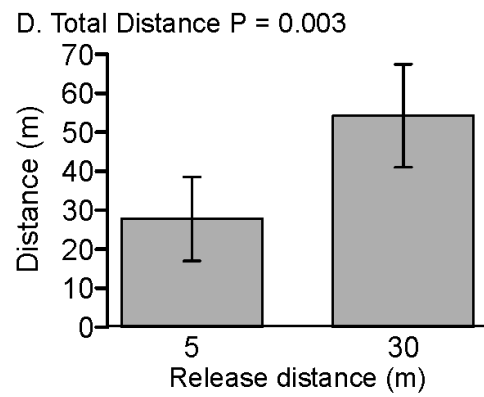
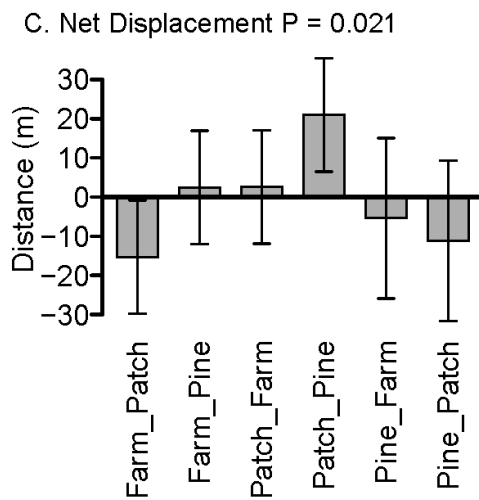
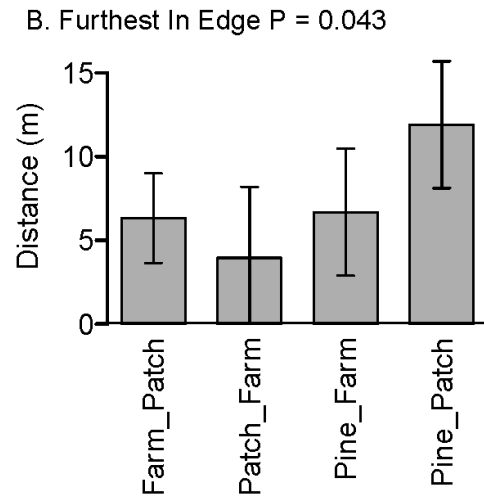
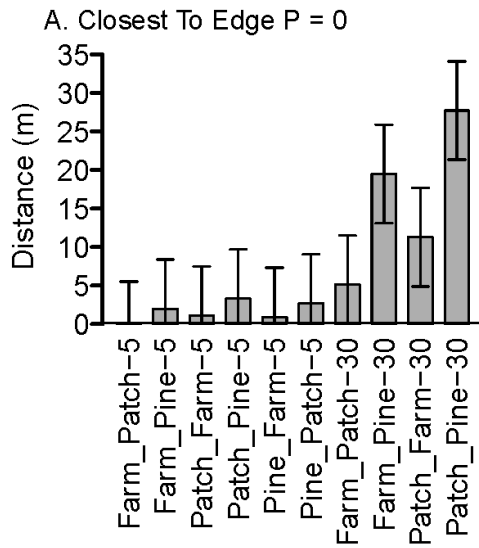


Fig. 4 (A) The closest *H. merope* individuals approached edges for the interaction of release location and distance; (B) the distance butterflies flew into the adjacent vegetation type after crossing the edge for the four release locations that could be evaluated, (C) net displacement at the end of the observation period (perpendicular to the edge) for each release location, (D) total distance travelled from the release point for each release distance, (E) the maximum distance moved away from the edge within the release vegetation type, for each release distance. P indicates the P value testing for the displayed effect, with P = 0 indicating $P < 0.0001$. Almost all butterflies released 30 m into pines flew up and over and so this treatment was excluded from analysis. Values are predicted mean distances (m) with 95% confidence intervals.

Movement across woodland edges suggests plantations and farmland are barriers to dispersal

Landscape Ecology

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Online Resource 1 Spearman correlation coefficients between response variables. Strong correlations (where correlation co-efficient $\geq |0.7|$) are shown in bold type. Furthest into edge only had positive values for animals that crossed the edge, thus all such values coincided with zeros for closest approach to edge and these variables were highly correlated (- 0.849). For response variable 'furthest into edge' we therefore excluded all trials where the animals did not cross the edge (35 trials), and calculated correlations with other variables using the reduced dataset (25 trials). Therefore no correlation is available for furthest into edge compared with closest approach to edge because all 25 values for the latter response in the reduced dataset are zero.

	No. flights	Total distance	Mean distance per flight	Closest approach to edge	Furthest from edge	Furthest into edge	Final distance
Total distance	0.541						
Mean distance per flight	-0.043	0.763					
Closest approach to edge	-0.255	-0.096	0.075				
Furthest from edge	0.005	0.454	0.506	0.631			
Furthest into edge	0.051	0.063	0.155	NA	-0.166		
Final distance	-0.114	0.178	0.278	0.792	0.794	-0.421	
Net displacement	-0.151	-0.095	0.007	0.496	0.375	-0.429	0.746

1 **Movement across woodland edges suggests plantations and farmland are barriers to**
2 **dispersal**

3 Landscape Ecology

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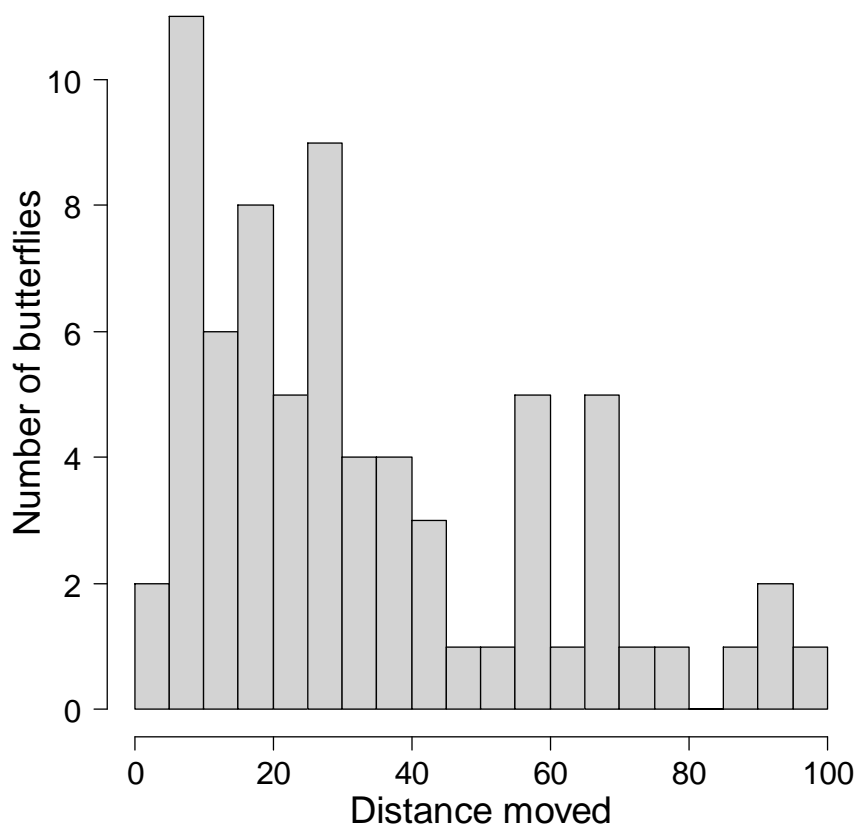
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11 **Online Resource 2.** Histogram of distances moved. Plot excludes one flight of 228m for
12 a butterfly released in woodland 30 m from a farm edge.



13