Wood ants on the edge: how do the characteristics of linear edges affect the population dynamics of an edge specialist?

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Abstract

Landscape structure may facilitate or inhibit the dispersal of species by presenting barriers or opportunities. Slow dispersing edge specialists are likely to be most affected by local topography and land management practices because they require two different adjacent habitats within their limited dispersal range. The northern hairy wood ant, *Formica lugubris,* requires adjacent forest and open habitats to access aphid honeydew, invertebrate prey, and direct sunlight for thermoregulation. In plantation forest, canopy gaps that provide this combination are often linear and anthropogenic, such as paths, firebreaks, and roads (collectively termed 'rides'), and their orientation determines shade distribution. Using population data spanning 10 years, we ask how properties of rides, such as bearing and width, affect the distribution and dispersal of wood ant populations in the North York Moors. Regardless of orientation, nests were more abundant on the north side of rides, where they receive more sunlight, and nests were generally larger on narrower rides. Furthermore, we found that *F. lugubris* dispersed approximately 3 times quicker along rides that were oriented north-south or east-west compared to NE-SW or NW-SE. Because wood ants can suppress defoliating pests, these findings have potential forest management implications and may apply to other forest dwelling edge specialists.

Introduction

The ability of species to move through a landscape can have major implications for the conservation of biodiversity, and for preventing species loss in a changing climate (Mendenhall *et al.*, 2014; Lenoir and Svenning, 2015). How porous a landscape is to species movement will also affect the dispersal of

species, and this porosity may be determined by the contrast between one habitat and the next. Low contrast edges between forest patches and agricultural land in Costa Rican countryside ecosystems are more porous to bats than high contrast edges between forest patches and open water in Gutan Lake, Panama, and forest patches in the agricultural ecosystem harbour higher bat species richness as a result (Mendenhall *et al.*, 2014). The permeability of habitats to species may become more important as climate change induced range shifts along latitudinal or altitudinal gradients become more apparent (Lenoir and Svenning, 2015). The critical role that species movement can play in the conservation of biodiversity is in contrast to the well documented negative economic (Cuthbert *et al.*, 2022) and environmental (Pyšek *et al.*, 2020) effects of species invasions.

Natural linear features such as rivers, coasts, habitat edges, and mountain ranges, or anthropogenic ones such as roads, railways and canals can be major facilitators of species movement and invasion, providing corridors of suitable habitat for certain species through otherwise inhospitable areas. For example, wind-dispersed seeds travelled nearly four times the distance along linear forest disturbances than in undispersed forest (Roberts *et al.*, 2018) while, in a meta-analysis, 70% of studies indicated that either plant abundance or diversity was higher along linear gaps and verges than habitat interiors (Suárez-Esteban *et al.*, 2016). By facilitating the dispersal of food plants, linear features can indirectly promote the dispersal of invertebrate herbivores. Ragworts (genus: *Senecio*) disperse along anthropogenic linear features (e.g., oxford ragwort dispersal along railways; Harris, n. d.), while the cinnabar moth (*Tyria jacobaeae*) is more successful at dispersing and laying eggs on their host, *Senecio jacobaeae*, in alpine areas with roads and valleys than in areas where no linear features exist (Brunzel et al., 2004), suggesting that invertebrates may derive similar benefits from linear features as their plant hosts.

The creation of linear features can be used for conservation purposes, as in the use of habitat corridors to connect smaller areas of protected land and reserves (Bennett, 1990; Brito *et al.*, 2017). However, benefits of habitat corridors to some species have been questioned because they can affect generalist and specialist species differently: landscape corridors connecting areas of fragmented forest in south-eastern Estonia facilitated the dispersal of generalist plant species more than forest specialist species, (Liira and Paal, 2013). Positive or negative, the presence and structure of edges can have implications for species movement and survival in certain contexts.

The edges of forests are important for understanding the population dynamics of forest-dwelling species. Edges can be low quality or inhospitable forest to forest interior specialists, favouring generalists, but can serve as favourable habitat for certain edge specialist organisms (Lövei et al., 2006; Ruete et al., 2017; Taylor et al., 2008). On the other hand, larger forest patches with a shorter relative

edge length give interior specialists a competitive edge over generalists tolerant of both forest non-forest habitat because larger patches have more interior habitat which specialists are better adapted to; species richness of generalist ground beetles is lower in larger areas of forest than smaller ones (Lövei et al., 2006). Even comparatively distant forest patch edges can be directly detrimental to forest specialists; in black spruce forests in eastern Canada, the effects of edges on ground dwelling spiders extended 30-50m into the patch, meaning only patches more than 100m wide could support interior specialists (Larrivée et al., 2008). Overall, small patches are detrimental to forest dwellers and more permeable to non-forest specialists, but patches larger than 100m wide would have the capacity to support both interior specialist ground dwelling spiders and, at the fringes, generalists and edge specialists too.

The widespread anthropogenic changes in natural forests, and the creation of large areas of plantation forests, mean that human activities determine the present distribution and fragmentation of most forests. This makes the study of how fragmentation and edge habitats impact species dispersal important for conserving species in increasingly anthropogenic habitats. The structure of forest fragments and distribution of edges is especially important in the context of anthropogenic forests because the history of the edges themselves can cause differential effects on different species and their movement. Anthropogenic edges, which are maintained by recent human disturbance, are less permeable to forest specialist carabids (Magura *et al*., 2017) and fungi (Ruete *et al.*, 2017) than edges maintained by natural processes. In the context of plantation forest or managed woodland, this highlights the degree of influence that edge creation in forests can have of on species, including edge specialists.

Plantation forests represent a significant portion of forested area in the UK (Defra, 2021) and the management of these forests for timber necessitates canopy gaps to provide access for industrial activity, in addition to firebreaks, geographical features and land ownership boundaries constrain where trees can be planted. Many of the resulting canopy gaps will be linear. These gaps can harbour a distinct fauna (Oxbrough *et al.,* 2006) and flora (Smith *et al.,* 2007) from the interior of stands, providing refuges for species that might otherwise be unable to tolerate the planation environment. Some spider species found in rides greater than 15m wide in plantations forests in Ireland are absent from the forest interiors (Oxbrough *et al.,* 2006). Sunlight would seem to be an important factor in the differences in species richness and composition between canopy gaps and the interior of stands; the species richness of vascular plants is lower in more shaded rides (Sparks *et al.,* 1996), while shaded areas are richer in bryophyte species (Smith *et al.,* 2007). The presence of different species compositions in rides indicates that these features play an important role in maintaining biodiversity in the plantation environment.

The ability of the rides to harbour distinct communities is dependent on ride characteristics dependent on management practices, such as width. Rides greater than 15m in width support a distinct spider fauna absent from narrower rides (Oxbrough *et al.*, 2006), while similar results have been found for vascular plants (Smith *et al.*, 2007). Ride orientation also influences the suitability on rides for certain species and locations; in southern England ground spiders (Lycosidae) are more abundant on south facing edges, while ground beetle (Carabidae) abundance is unaffected by ride orientation (Carter *et al.*, 1991), but no effect of edge orientation was found on any invertebrate group studied in northern Finland (Jokimäki *et al.*, 1998). While these studies have focused on taxonomic groups, some individual species may be edge specialists and may respond differently ride characteristics.

Some species are more abundant in edge and transitional habitats between forest and open area because edges allow species to benefit from two habitats at once. In Australia, the noisy miner (*Manorina melanocephala*) is considered an 'aggressive edge specialist', strongly favouring the edges of forests (Major *et al*., 2001; Taylor *et al*., 2008) because it allows them better visibility to defend their territory and exclude other birds (Loyn, 1987). White-tailed deer (*Odocoileus virginianus*) are thought to spend more time foraging at forest edges because it allows them to benefit from the greater food resources in open habitats whilst remaining close to cover and a potential refuge from predators (Williamson and Hirth, 1985). Similarly, plants may benefit from improved seed dispersal or pollination opportunities provided by the edge habitat (Lamb and Mallik, 2003) while maintaining the benefits of shelter and nutrient availability (Weathers *et al*., 2001) from nearby forest. Highly mobile species commonly found on edges may merely be 'edge-tolerant' generalists exploiting their relative advantage over specialists of the bordering habitats (Ries and Sisk, 2010), rather than having any particular adaptive preference for edges. On the other hand, poor dispersers or sessile species that are more abundant in edge habitats are likely to be dependent on the edge habitat; they will spend multiple generations under its influence and would therefore locally die out if the edge habitat was unfavourable for them. These species may be properly called edge specialists.

Because of the importance of edges to some species, some study has been directed at the question of which qualities of edges are important for determining population dynamics. The geometry of the edge can be a consideration; the presence of complexities in the forests edge, such as corners, projections, and peninsulas of vegetation, are good predictors of noisy miner (*M. melanocephala*) occupation (Taylor *et al*., 2008). Both edge geographical orientation (henceforth: bearing) and corridor width affect the diversity and composition of butterfly communities, with a greater diversity of forest dwelling butterflies found on shadier south-facing edges (southern hemisphere). Additionally, transient butterflies were less strongly affected by edge bearing than less mobile ones (van Schalkwyk

et al., 2022). On the other hand, communities of leaf miners, parasitoids and plants seen to be relatively unaffected by differences in light availability due to bearing (Bernaschini *et al*., 2020). The evidence shows that edges affect population distributions, but some comparatively understudied edge characteristics, such as width and especially bearing, could affect the dispersal of organisms.

Formica lugubris is one of three species of wood ant in the *Formica rufa* group found in the UK and the only one that is common on the North York Moors. UK populations of *F. lugubris* establish new nests exclusively by budding: a mated queen and some workers leave the maternal nest on foot to establish new nests (Maeder *et al.*, 2016). As a result, they are very poor dispersers and previous data suggest that the North York Moors *F. lugubris* population margins grow by less than 50m per year, despite suitable habitat for colonisation (Procter, 2016). In this population, 78.5% of *F. lugubris* nests are found within 10m of canopy gaps (Procter *et al.*, 2015) and they are more likely to be encountered on the north side of gaps (Sudd et al., 1977). The preference for canopy gaps (especially those facing south) corresponds well with what we know about the habitat requirements of *Formica lugubris*: whilst they require honeydew from arboreal aphids as the ants' main source of carbohydrate, they also require sunlight to regulate the temperature of their nest (Domisch *et al*., 2016). Because these wood ants require direct sunlight from canopy gaps, their potential for dispersal and population expansion will be dependent on the distribution of shade. In managed forestry land where canopy gaps in the form of fire breaks, access roads, footpaths and felled areas are abundant, the distribution of shade will be determined by management decisions made during planting and ongoing management practices, and this raises the question of how characteristics of rides affect the population dynamics of *F. lugubris*.

The orientation of linear canopy openings has the potential to affect both the abundance and dispersal ability of wood ants. Along canopy gaps that run approximately east-west, the shadier (south) side of the ride will receive little insolation, so we would predict that wood ants would be less able to utilise nesting sites on the south side of these rides, while canopy gaps that run north-south would be occupied equally on either side, but to a lesser degree, due to the reduced hours in direct sunlight. Finally, we would predict that the width of a ride could affect wood ant abundance: narrow rides where the canopy nearly closes would be shadier, so we would expect fewer, larger nests on narrow rides and more, smaller nests on wider rides.

Because *F. lugubris* establish new colonies by budding, the suitability of potential nest sites and the health and size of the parent colony will be determining factors in the rate of new nest founding (Ellis and Robinson, 2014). We predict that, because the orientation and width of rides will affect the abundance of ants and ant nests, the rate of new nest establishment will also be affected, and this will

correspond to a faster rate of population margin expansion on rides where the orientation and width favour greater abundance. We conducted a survey of canopy gaps and edge characteristics in plantation forest of the North York Moors, and combined pre-existing long-term monitoring data with new data on wood ant populations at the study sites to answer the question: how do characteristics of rides affect the population dynamics of *F. lugubris*? We tested the following hypotheses:

H1 - The orientation of anthropogenic canopy gaps (degrees from N; 0-90°) affects wood ant nest a) abundance and b) total volume along those canopy gaps.

H2 - The orientation of anthropogenic canopy gaps (degrees from N; 0-90°) affects wood ant dispersal rate along those canopy gaps.

Methods

Ride selection: abundance and volume measures

Rides suitable for testing the hypothesis that canopy gap orientation will affect wood ant nest abundance and volume (H1) were identified prior to the field survey using pre-existing long-term data on wood ant population in the North York Moors (Procter *et al.*, 2015) to conduct a desk survey. A ride was defined as a linear feature causing a break in the canopy at least 5m wide, starting and ending where they intersected other rides or reached the end of the forest. Examples of rides included linear canopy gaps due to roads and footpaths, as well as gaps caused by forest management such as areas of row thinning (strips of trees harvested at intervals, leaving most of the crop standing) or fire breaks. We measured the length of the wood ant-occupied portion of the ride from the oldest nest on it to the nest furthest from the source population. The population margins and the source were identified using long-term data on the wood ant populations in the North York Moors (Procter, 2016; Holgate, 2021). For rides with nests along their entire length, this measurement equalled the total length of the ride. When mapping the margins, the survey attempt was stopped if no nest was encountered for 200m, as this is far greater than typical dispersal distance for this species, consistent with the long-term data on these populations that we used (Procter *et al.*, 2015). Rides were considered to have ended if the ride entered a stand of different tree species, a stand of different age/tree height, or rounded a corner (ride bearing changes by more than 15 degrees). We measured the length and bearing of the ride using the *Measure tool* in ArcGIS Pro version 2.3.3, connecting the first and last nest on the ride.

Selecting rides for calculating rate of expansion

In order to determine whether ride bearing affects wood ant dispersal, we required a subset of rides at the population margins, where population margin expansion could have occurred during our study

period, allowing us to use long-term wood ant monitoring on the North York Moors (since 2011) to calculate the average yearly population margins expansion along rides. In addition to the selection criteria in the previous section, margin rides were also required to meet the following criteria:

1. Have had potential for population expansion between 2011 and 2022 i.e., must have uncolonized length that does not extend into unsuitable habitat like open farmland.
2. Expansion has been unidirectional, from a single point of origin, to exclude situations where sections of the ride has been colonised from two origins (due to intersecting two rides with ant presence), as this might inflate the measures of margins expansion on this ride.
3. Expansion has not been interrupted by factors such as areas of forest on the ride being harvested during the period for which we have data, causing the ride to become unsuitable for wood ants. In cases where the expansion had been interrupted, we used the data up to the interruption. For example, a ride that was surveyed from 2011-21, but that was clear-felled in 2019, can provide us with an eight-year average expansion rate rather than ten.

An initial 13 suitable rides were identified from long-term data at Cropton and Broxa forests (Procter *et al.*, 2015) to assess the feasibility of this study. A power analysis on these data (power = 0.8, alpha = 0.05) suggested that a final sample size of 37 rides would be suitable to test H1 and 16 would be adequate for H2. Based on our desk survey using the long-term data for Cropton and Broxa (Procter *et al.*, 2015), this exceeded the number of rides suitable for each hypothesis at these sites. As a result, additional rides from East Moor Wood in the North York Moors were included. The final number of rides selected for the study was 50, including all 29 of margins rides that were suitable for H2 (site = number of rides/number of rides on the margin; Cropton = 11/11; Broxa = 14/9; East Moor Wood = 25/9). The 21 non-margins rides were selected randomly from Broxa and East Moor Wood.

Nest abundance and volume measurements

For each ride, the surveyor walked down one side of the ride and up the other, recording nest presence and volume. Nests more than 5m from the edge were excluded to ensure all surveyed nests were directly utilising the ride canopy gap. In practice, light from a gap may penetrate deeper than 5m, but this is highly tree species dependant. For example, many pines have very little light-blocking foliage low down on the trunk, whereas spruce can present a dense wall of needles that lets very little light through at any height. As a result, dominant tree species on each side of the ride was also recorded. In areas where the understory was relatively open, spotting nests up to 5m from the edge did not present a challenge but in areas where the understory was more dense, some nests were difficult to spot. At each ride, a judgement of the condition of the understory was made, and if the understory was too thick to confidently spot nests up to 5m from the edge, a second transect was walked parallel

to the first 2.5m from the edge (behind obscuring vegetation) to minimise the risk of missing nests. At each nest, we recorded the location (latitude and longitude) and on which side of the ride (east or west/north or south) the nest was, giving each nest a unique ID code to prevent recounting. Additionally, nest width, length and height were measured to calculate nest volume as a proxy for number of ants (Chen and Robinson, 2013).

Ride details were also be recorded: ride width (between opposite points where the canopy is directly overhead), canopy height (measured using *Toolbox* android app calibrated against a gun clinometer) of both sides of the ride and ride bearing (expressed as degrees east or west of north). We measured each of these ride variables at the beginning, midpoint and end of each ride and averaged them across the three to provide ride characteristics. Latitude and longitude were recorded at the start and end of each ride so that the length of the ride could be measured retrospectively using ArcGIS Pro version 2.3.3.

Calculating rate of margins expansion along rides

From the long-term data, we calculated two measures of margins change a) distance change and b) number of nests. The distance the margin changed along a ride was the distance in metres between the location of the last nest along a ride recorded in the oldest long-term data and the location of the last nest on the same ride surveyed in 2022. The change in the number of nests was defined as the number of nests between the last nest at the date of the earliest survey in the long-term data and the last nest along the ride in the 2022 survey. Although both rate of distance change and the rate of nest abundance change can be calculated from this data, rate of nest abundance change is a less reliable measure of expansion than the rate of distance change for two reasons. Firstly, there is a five-year gap in the long-term data and the entire population was not revisited on each survey (Procter *et al.*, 2015). This means that, in many cases, we have no evidence of continuous occupation, nor of the number of nests that may have been established and subsequently abandoned in the intervening period. Secondly, in areas where the wood ants have recently colonised, a period of consolidation may follow later in the year. Some small nests may be abandoned, and the occupying ants absorbed into neighbouring nests in the polydomous network (Burns *et al.*, 2020) and the numbers of nests may fluctuate. On the other hand, the predicted rate of distance change was low, owing to the slow dispersal of this species (Procter *et al.*, 2015) whereas we anticipated that the change in the number of nests would be large and more easily detectable. As a result, we collected both distance change and nest number change of wood ants along ride margins to afford us the benefits of both measures.

Statistical methods

Modelling the relationship between ride characteristics and population measures

The resulting data set included 50 rides, of which 29 were on the margins, each with record of the bearing of the ride, length, mean width, the number of nests on each side of the ride. For the 29 rides on the margins, we also had two measures of the rate of margin change calculated from long-term population data: abundance change (nests/year) and distance change (m/year). To test H1 (i.e., the effect of ride characteristics (bearing, width, and side) on the abundance and relative volume of nests) we fitted generalised additive models using the mgcv package version 1.8-41 (Wood, 2011) in R (version 4.2.1). Because our orientation data were circular and we could not make assumptions about the shape of the relationship between orientation and our wood ant population measures, the additional flexibility of a GAM was preferred over a GLM. We fitted models including all combinations of the three ride characteristics above, as well as site and ride ID as random effects and used the minimum AIC to select the most parsimonious model for each response variable. Because of the circular nature of ride bearing (-90° and 90° relative to north are equivalent), we included ride bearing smoothing term as a cyclic p-spline, whereas mean width was included as a p-spline only. We plotted response vs. fitted values, fitted vs. observed and histograms of the residuals to inspect the model fit and predicted from the models for visualisation. The GAMs provided estimations of degrees of freedom.

Pooling bearing into categories for margins growth analysis

Our initial power analysis used data gathered from the known nest locations along rides where the population margins were expanding and were close to E-W or N-S. This indicated that 30 rides would be adequate for an alpha of 0.1. However, this power analysis cut the data such that:

1. Bearing was categorical.
2. The difference between N-S and E-W rides was tested.

The data that we finally collected gave us sufficient resolution to treat bearing as continuous, and this was used to fit the GAM model for margins growth as described above. Inspection of the data, however, suggested a bigger difference between rides bearing near the cardinal points (N, S, E, W) and rides bearing near the intercardinals (NE, SW etc.) than between N-S and E-W rides. This suggests that, to test pooled bearing, bins should be E-W +/- 22.5°, N-S +/- 22.5°, and intercardinal +/- 22.5°, in order to appropriately capture the variability in the data. This variability has sound ecological justification: assuming that there is a minimum threshold of daily sunlight exposure for nesting sites to be viable for the wood ant nests to persist, we can be sure that this threshold lies some below 50%

of summer day lengths, as both sides of N-S rides are often utilised by ants. This threshold is also greater than 0% of the daily hours of sunlight because wood ants were often entirely absent from the south side of E-W rides. As such, going around the compass from north, the hours of available light on the north side will gradually increase from 50% up to c100% after 90°. Meanwhile, the south side will decrease from 50% to nearly 0%, passing below the threshold for wood ants to utilise potential nesting sites somewhere between. This reduction in potential nesting sites and the total availability of sunlight on the ride will have negative effects on wood ant populations and result in slower population growth leading to slower margins expansion.

Results

Ride bearing distribution

A total of 371 nests were recorded along 50 rides, including 29 rides on the population margins. One of the rides on the margins was also at the true edge of a forest stand and therefore the ride had no measurable width and only one side on which nests could occur. This ride was dropped from analyses that incorporated side or ride width as variables. The distribution of the rides we were able to collect data for represented bearings at most points of the compass and no orientation was much underrepresented. Regardless, there are orientations that we have more data for: rides approximately 15-30° west of north and 70-80° east of north were more abundant than other orientations (Figure 1A).

Nest aspect distribution

The aspect (direction of the long face/lower edge) of nests was overwhelmingly south facing (Figure 1B) with a circular mean of 191.47° (circular mean, $r = 197.47$, $var = 0.46$, $p < 0.0001$). This is in line with expectations, based on the assumption that the nests are constructed to present a large surface area to the sun and maximise insolation.

Does the orientation of canopy gaps affect wood ant nest abundance and volume?

The most parsimonious model, based on the comparison of AIC values for different combinations of explanatory variables in the model, included only side, bearing and width (Figure 2; Table 1). The model explained 31% of deviance and ride bearing was a significant smoothing term for both sides. Deviance explained is favoured over R^2 for non-Gaussian models as a more robust measure of explanatory power (Wood, 2006). The smooths for each side of the ride are also significantly different from one another (Table 1) and plots of the model predictions for values of ride bearing show that the number of nests per side is compensated by the other (Figure 2). When the east side has few nests (at bearings that cause the east side to be shaded), the west side has more: overall, the total sum of nests

on each side varies little with bearing. Generally, nest density is lower on a given side at ride bearings where that side would be shaded, i.e., lower at west of north bearings for the east side of the ride and the reverse for the west side of the ride. Ride width was not significant as a smoothing term in this model.

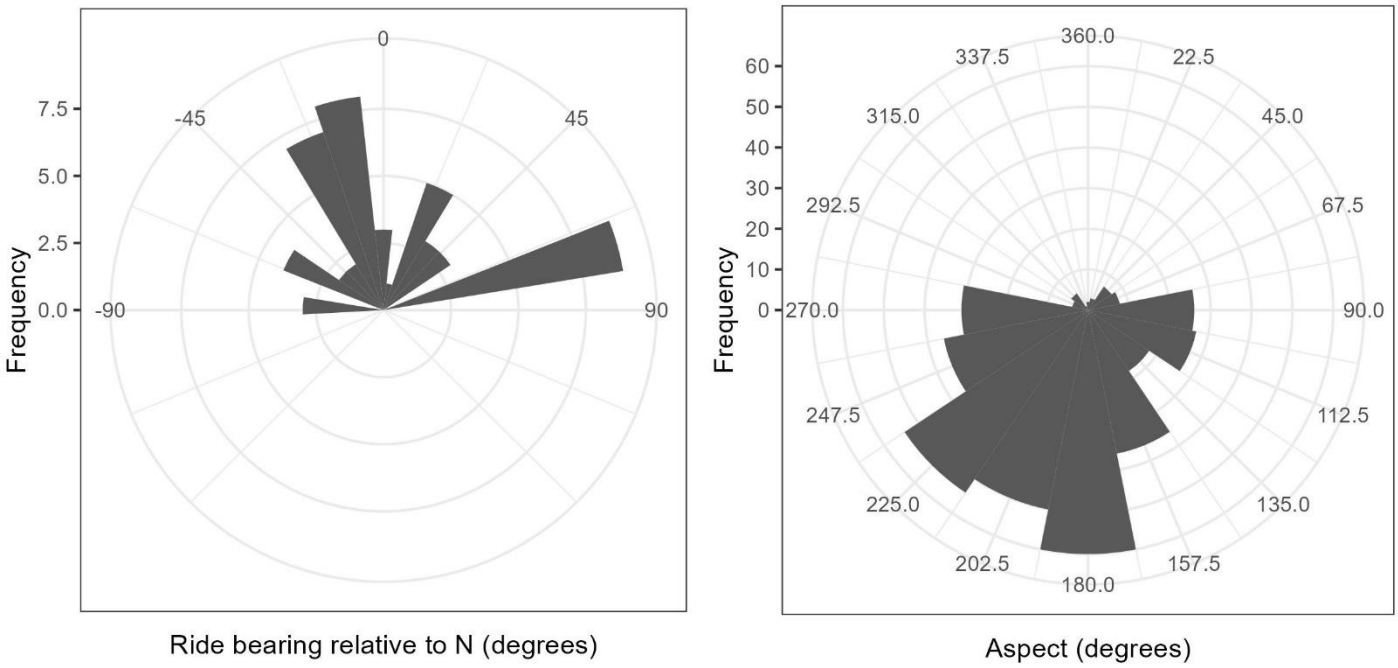

Figure 1. A. The frequency of rides at different bearings was determined by the availability of suitable rides at the field sites. Despite this, the data contains rides bearing along most possible directions without excessively favouring one direction. B. The aspect (direction of lower slope) of nests was far more often SSW, with a circular mean of 191.04 ($r = 197.47$, var = 0.46, $p < 0.0001$).

Table 1. Generalised additive models to predict several wood ant population measures using ride characteristics. Models 1-3 included the side of the ride that nests were on as a 'by' term (effectively fitting the two sides as separate splines) so that we can test the significance of each side (East and West) smooths (difference from line with gradient of 0) and test the smooths against one another (East:West).

Model	Dependant variable	'By' interaction	Smoothing term		Effective degrees of freedom	Test statistic (F unless specified)	P-Value	N	R^2 (Deviance explained)	Notes
1	Nest abundance	Side	Ride Bearing:	East	4	17.741 (X^2)	**0.001**	98	0.054 (31%)	Nest abundance offset by ride length (Figure 2)
				West	4	16.883 (X^2)	**0.002**			
				East:West	4	17.75 (X^2)	**0.001**			
			Ride Width		1.142	0.407 (X^2)	0.557			
2	Mean nest volume	Side	Ride Bearing:	East	5	3.476	**0.008**	69	0.267 (40.5%)	AIC = 82.64 (Figure 4)
				West	5	1.059	0.393			
				East:West	5	0.877	0.502			
			Ride Width		1.823	5.487	**0.006**			
3	Mean nest volume	Side	Ride Bearing:	East	5	3.775	**0.005**	69	0.299 (44.2%)	AIC = 80.36 (Figure 3)
				West	5	1.157	0.342			
				East:West	5	0.877	0.502			
			Ride Width		1.921	6.258	**0.003**			
			Site		0.98	1.11	0.107			
4	Mean nest volume	None	Ride Bearing		4	1.187	0.332	46	0.18 (28.7%)	(Figure 5)
			Ride Width		2.164	5.053	**0.009**			
5	Margins nest change per year	None	Ride Bearing		4	4.443	0.082	28	0.163 (41.1%)	(Figure 6)
			Ride Width		4	2.061	0.126			
6	Margins distance change per year	None	Ride Bearing		4	1.934	0.148	28	0.256 (50.8%)	
			Ride Width		4	1.011	0.428			
			Site		1.154	1.53	0.098			

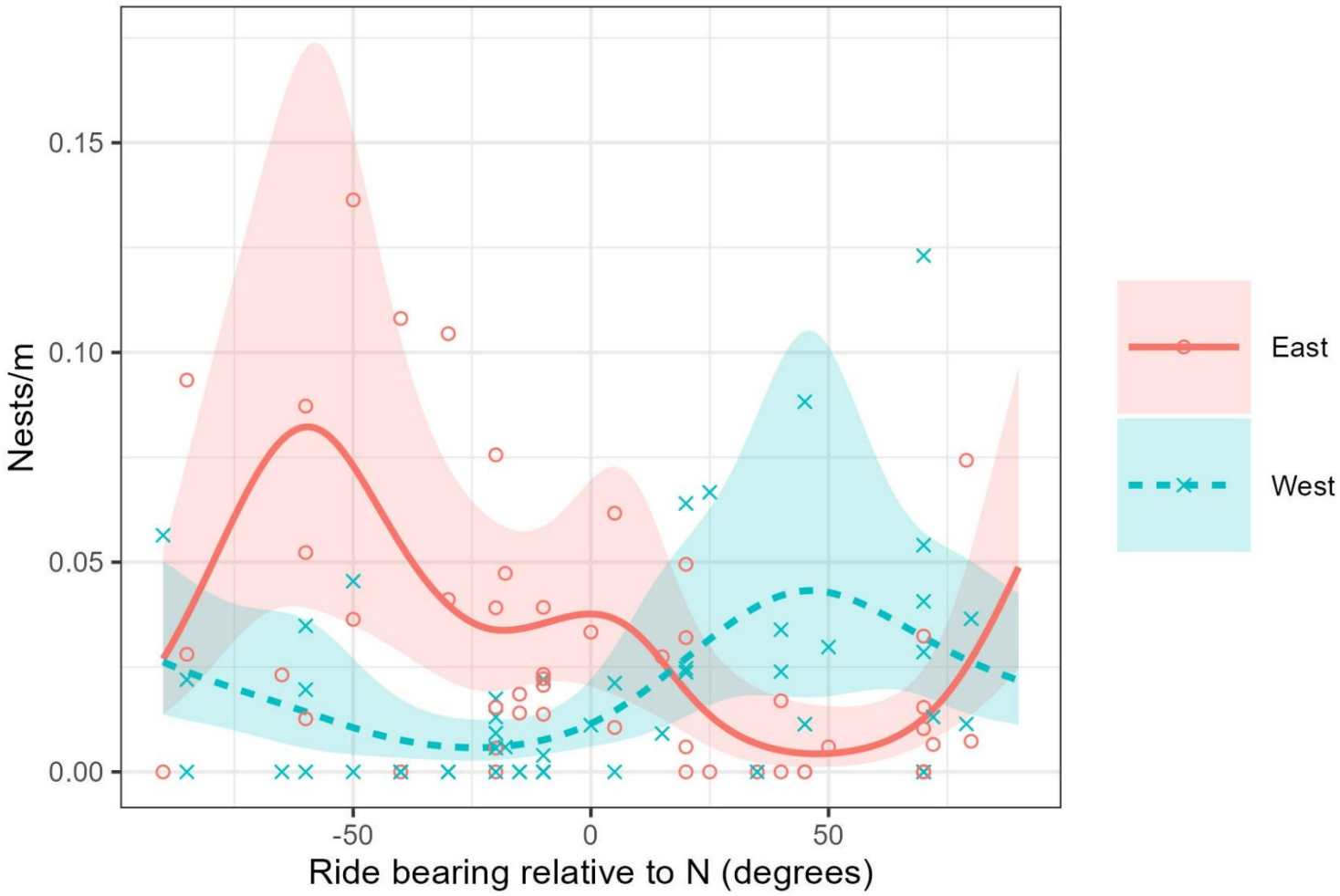

Figure 2. The number of nests per side of a ride (E or W) for rides of different bearings. Lines (by side) fitted from predicted values for ride bearing of a point count generalised additive model offset by ride length with the formula nest abundance ≈ side + s(bearing) + s(width) of the negative binomial family; Link function = log, offset = log(length), $R^2 = 0.0538$, deviance explained = 31%. Though the offset was included in the model for statistical testing, the offset is ignored when predicting. The points represent the real data, the lines are predicted values and the shaded areas are 95%CIs. Both east and west smooths were significant ($p < 0.005$) and significantly different from each other, width was not significant as a smoothing term in this model. Note that deviance explained is favoured for non-Gaussian models rather than variance based R^2 (Wood, 2006).

Additional GAMs were fit for the mean nest volume per ride by side with the explanatory variables of site, ride bearing and ride width. Based on AIC values, the most parsimonious model included site, bearing and width as smoothing terms (Figure 3; Table 1), however the ΔAIC between models with and without site (Figure 4; Table 1) as a term is 2.278 and only just outside of the widely used cut-off 2 for supporting a more complex model. Furthermore, site was not significant as a (random effect) smoothing term and, despite the slight difference in the mean nest volume of the three sites; its inclusion is unhelpful to the interpretation of the overall pattern and results in a very small increase in R^2 (0.267 without site; 0.299 with). In both models, the ride bearing was significant only for the east side smooth and the smooths of the two sides were not significantly different from one another. The asymmetry of this result, and the lack of difference between the two sides, suggests that ride bearing is a poor predictor of mean nest volume for these data. Additionally, the bearings where a horizontal line could not sit entirely within the 95% confidence intervals of the east smooth (i.e., the bearings that are responsible for the significance of the smooth) correspond to two extreme values for mean nest volume.

Mean ride width was significant as a smoothing term in both models ($p < 0.01$; Table 1) and a plot of model predictions (Figure 5) shows that the mean volume of nests is lower on wider rides but does not continue to change for rides wider than 8m. It is important to note, however, that a relatively small number of large nests on rides narrower 6m may be major contributors to this effect. This small number of nests (6 with volume above upper 95% confidence interval and ride width less than 6m) were, however, distributed across all three sites.

Does the orientation of canopy gaps affect wood ant dispersal rate?

We used two measures of population margins growth: the change in the number of nests at the margin and the distance that the margins moved per year over the study period. The GAM that best explained (lowest AIC) the change in nest number per year included ride bearing and width (Figure 6; Table 1). Neither term was below our chosen significance threshold of 0.05 (ride bearing $p = 0.082$, width $p = 0.126$) and the model explained only approximately 15% of the variation. A plot of the model predictions for values of ride bearing, and ride width fixed at the mean (7.118m), suggested a similar shaped pattern in the rate of nest number change as we saw for total nest abundance, with minima for rides bearing approximately NW-SE and NE-SW (intercardinal), though without statistical significance. The inclusion of width as a smoothing term results in the predictions being consistently

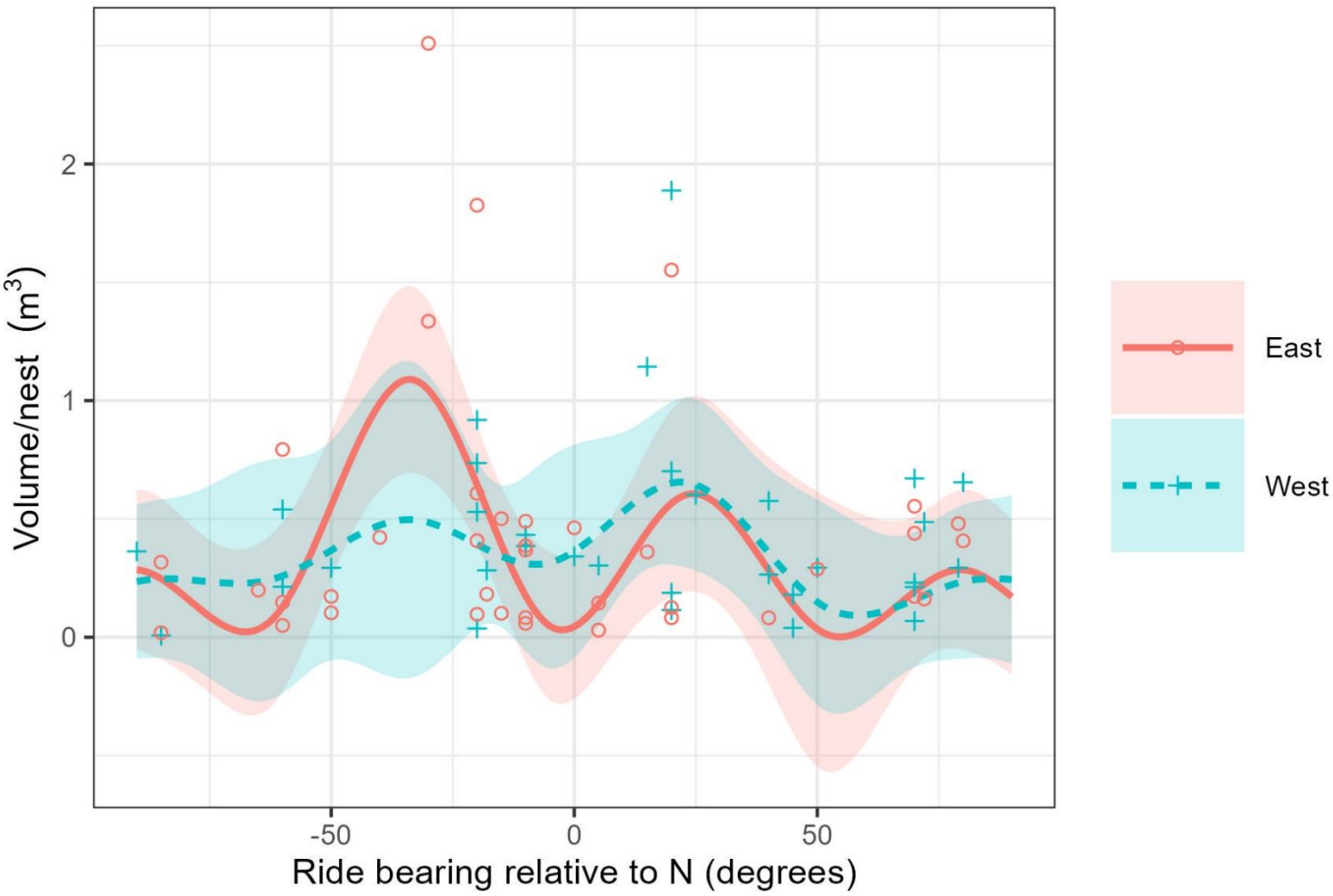

Figure 4. The total volume of all nests on each side of rides of different bearings. The lines are predicted values from a generalised additive model (GAM) with the formula volume per nest ≈ side + s(bearing) + s(width), $R^2 = 0.267$, deviance explained = 40.5% were plotted for values of ride bearing (lines) alongside the original data (points) and 95%CIs (shaded areas). Although the east side smooth was significantly different from a line at the intercept of gradient = 0 ($p < 0.01$), there was no significant difference between the east and west smooths and no clear pattern is discernible from the plot. Mean width was also significant as a smoothing term (Figure 5; Table 1, models 2-4).

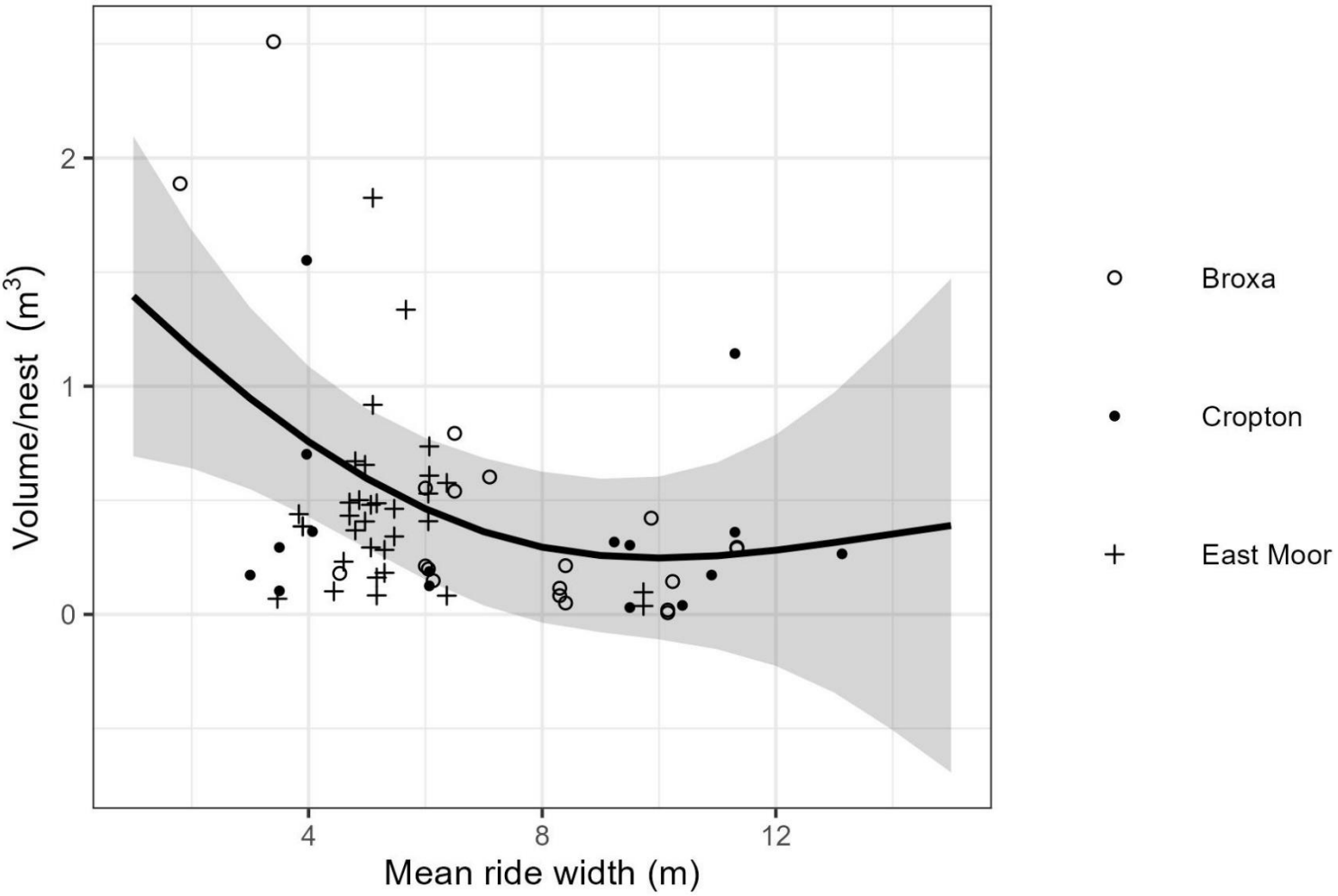

Figure 5. Prediction curve from a generalised additive model (GAM) with the formula volume per nest ≈ s(bearing) + s(width), $R^2 = 0.18$, deviance explained = 28.7% were plotted for values of width (line) alongside the original data (points) and 95%CIs (shaded area). The smooth of mean width was significantly different from the intercept ($p < 0.01$), whereas ride bearing alone (i.e. not split by side) was not.

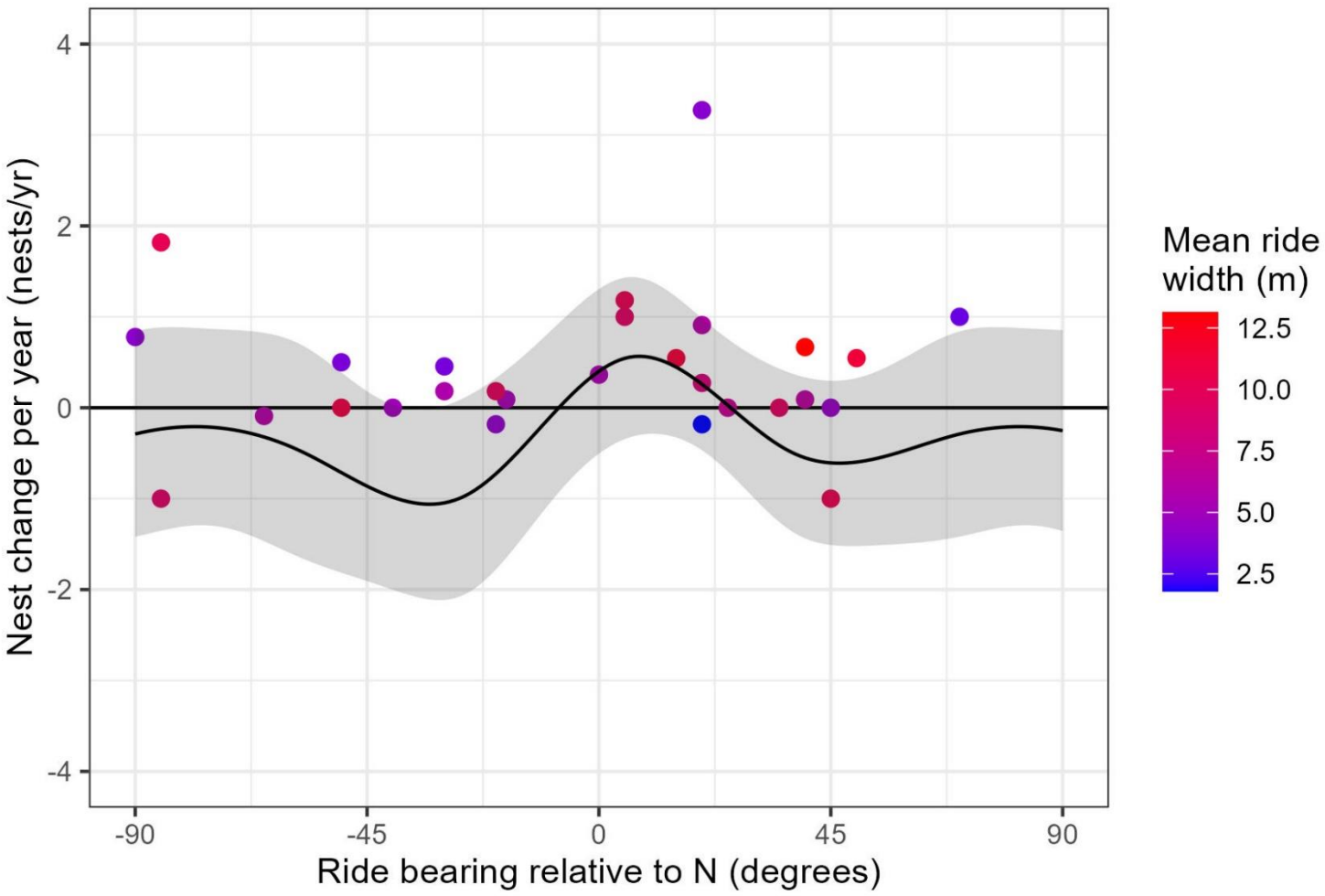

Figure 6. A generalised additive model (GAM) was fit for the change in the number of nests on rides on the margin with the formula nest change per year ≈ s(bearing) + s(width), R^2 = 0.163, deviance explained = 41.1% and the predictions for values of ride bearing were plotted (solid line) with 95%CIs (shaded areas). Ride bearing was significant as a smoothing term only to an alpha of 0.1, and the model has little explanatory power. Ride width is not correlated with bearing.

lower than the observed values (Figure 6) due to the fixing of ride width at the mean value, which may predict lower than observed values if ride with is highly skewed or non-Gaussian. The ride width distribution appears similar to a bimodal distribution, lending weight to this, but the high antimode relative to the maximum frequencies means that interpreting it as a Gaussian distribution is equally plausible. Regardless, this model has poor predictive power, but does suggest that bearing may play some role in the rate of change in nest number.

The median rate of nest change was greater on cardinal rides than intercardinal ones (approximately 0.5 nests/year; Figure 7), but we found that the difference between groups was just above our threshold for statistical significance (Welch's *t*-test, $t = 2.021$, df = 21.368, $p = 0.056$).

The distance that the margins moved per year over the study period was also included as a response variable in a GAM and the best model based on minimum AIC includes site, ride bearing and ride as smoothing terms (Figure 8; Table 1). This model performs better than the nest number change model ($R^2 = 0.256$) and the overall pattern was the same (minima on rides near intercardinal directions), but none of the smoothing terms were significant except for the random effect 'site', and that only to an alpha of 0.1 ($p = 0.098$; Table 1). Model predictions showed that rides in Cropton Forest experienced more wood ant population growth than either of the other two sites.

Pooling the data revealed the same pattern for ride bearing that we have seen for other variables and in the GAMs; that the rides running in intercardinal directions are less favourable to wood ants and result in lower population margins growth (Figure 9). We found that the rides that bear in cardinal directions experience significantly more margins expansion than intercardinal ones (Welch's *t*-test, $t = 2.122$, df = 22.497, $p = 0.045$; Figure 9; Table 2) and the effect size was medium, based on the recommended interpretation of Cohen's *d* (0.74).

Table 2. We tested the difference in the rate of change in the margins along rides from 2011 to 2022 between rides of varied orientation relative to north, with orientation binned into two groups: cardinal (N-S and E-W +/- 22.5°) and intercardinal (NW-SE and NE-SW+/- 22.5°).

Measure	Bins	Tests	Degrees of freedom	Test statistic	P-value
Rate of change in nest number at margins	2	Welch's *t*-test	21.368	t = 2.021	0.056
Rate of distance change at margins	2	Welch's *t*-test	22.497	t = 2.122	**0.045**

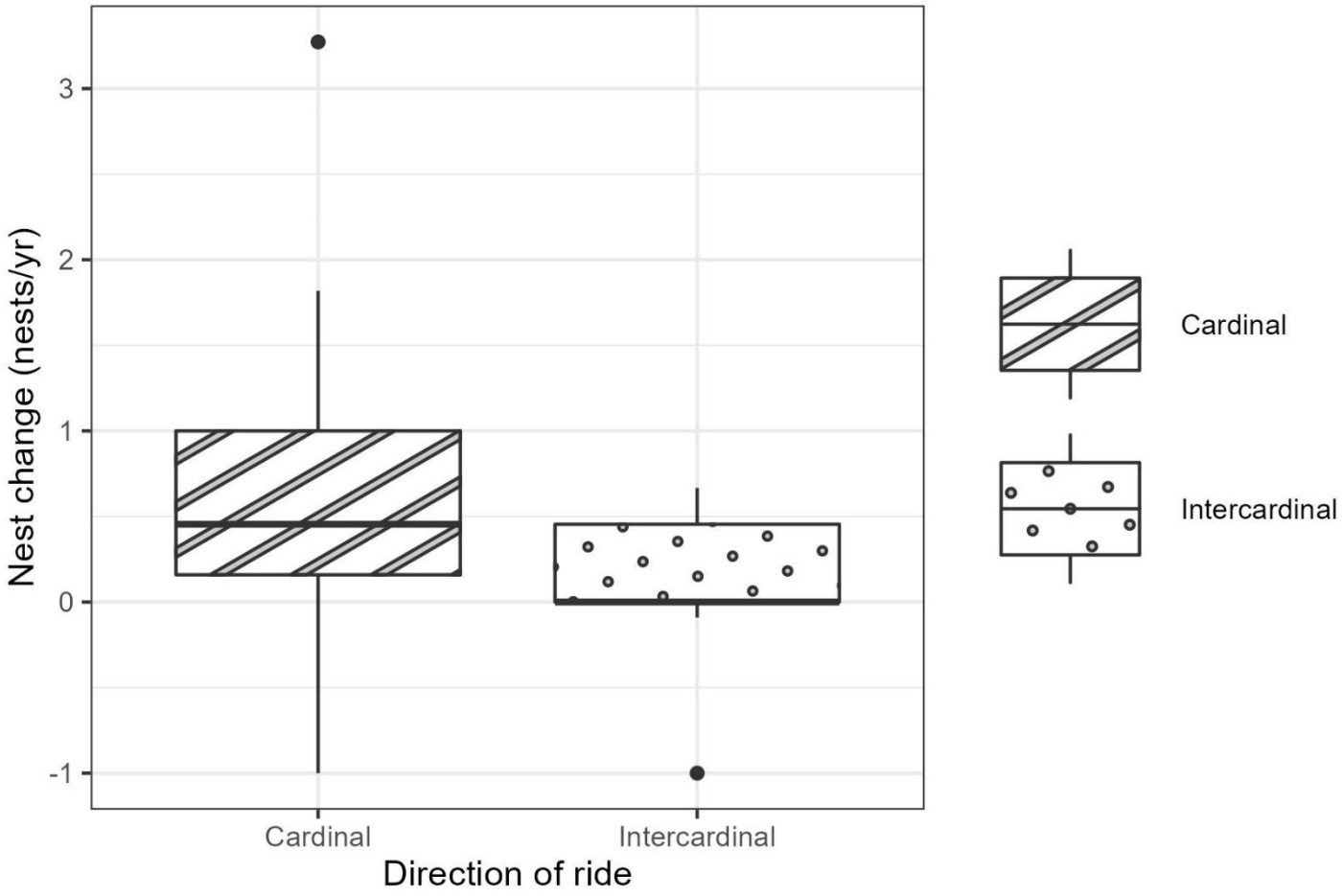

Figure 7. Ride data for change in nest number pooled into two categories: cardinal (22.5° +/- N, S, E or W) and intercardinal (22.5° +/- NE, NW, SE or SW). This was based on initial observations of the data and ecological reasons predicting differences between these groups (see methods).

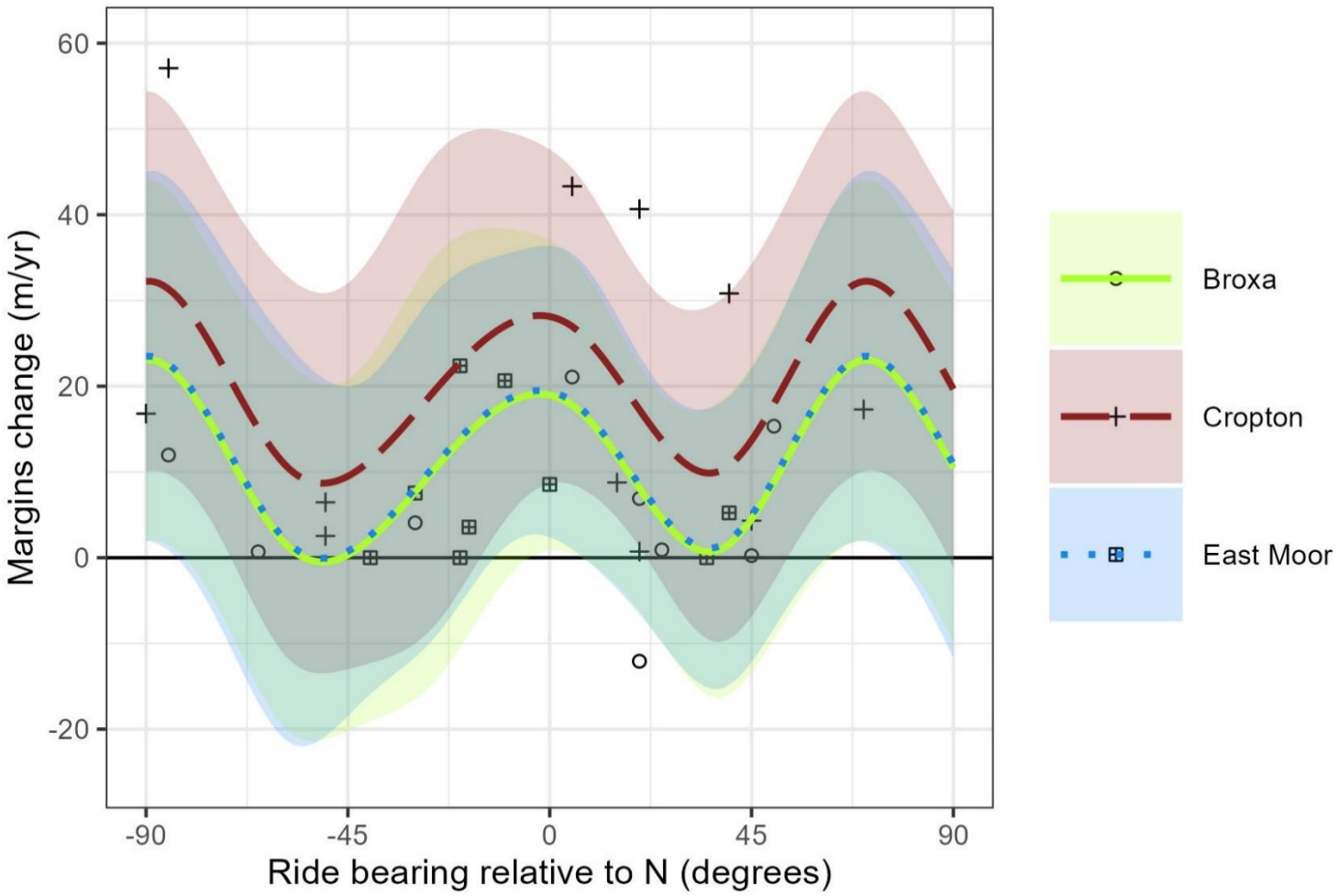

Figure 8. A generalised additive model was fit to predict the distance change along rides on wood ant population margins on the North York Moors with the formula margins change ≈ s(bearing) + s(width) + s(site), R^2 = 0.256, deviance explained = 50.8%. Empirical data (points), model predictions (lines) and 95%CIs (shaded areas) are shown. None of the smoothing terms were significant to an alpha of 0.05, but site was a significant random effect and its inclusion resulted in the most parsimonious model (ΔAIC < 2).

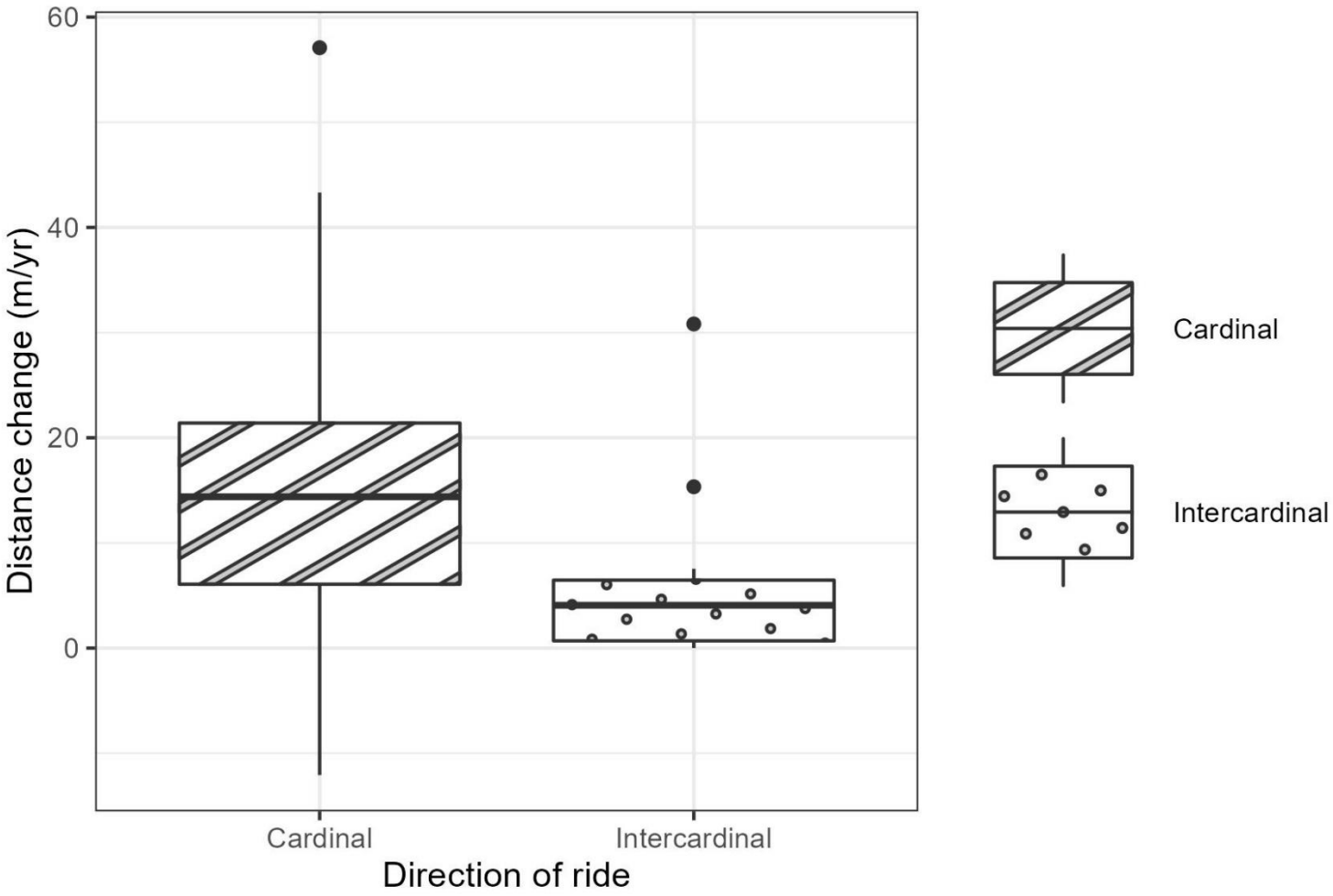

Figure 9. Distance margin change pooled into two categories: cardinal (22.5° +/- N, S, E or W) and intercardinal (22.5° +/- NE, NW, SE or SW).

Discussion

Summary of results

We aimed to determine the effect of anthropogenic canopy gap characteristics on populations of an edge specialist, the northern hairy wood ant *Formica lugubris*. Our results clearly show that the orientation and width of linear canopy gaps can affect *F. lugubris* populations. Nests were more abundant on the northern side of rides at in any orientation, as predicted, but orientation did not affect nest size in a consistent way. In general, narrower rides have larger nests on them, while wider rides were populated by smaller nests, consistent with predictions that nests receiving less insolation are larger. Nest abundance was greater on the north side of rides regardless of orientation, but this effect was greater for rides running east-west; the closer to north-south orientation, the less difference there was between the two sides. Finally, we found that, as predicted, the orientation of rides affected *F. lugubris* dispersal. Populations of *F. lugubris* have dispersed more quickly along rides that run in cardinal directions (N, E, S, W) than ones that run in intercardinal directions (NE, SE, SW, NW).

The importance of edge characteristics

We have shown that the orientation of edge habitats relative to north is an important factor in edge quality for *Formica lugubris* and is sufficient to have measurable effect on nest abundance and population margin expansion. Ride width is also a factor in edge quality for these wood ants; we found larger nests in narrower rides. In general, larger nests are found in shadier areas because larger nests are better able to thermoregulate (Chen and Robinson, 2014). The strong south-facing bias in nest aspect we found confirms that our other results are likely to driven by insolation, as sunlight is important for many aspects of wood ant biology. Nests lacking direct sunlight, especially small nests, may initiate foraging later (Rosengren *et al.*, 1987), have slower brood maturation (Kadochová and Frouz, 2013) and therefore potentially slower colony growth.

Dispersal along rides

In addition to ride bearing affected wood ant abundance (nest volume and number of nests, it also affects the ability of the wood ants to disperse through these plantation forests, with most rapid dispersal along rides oriented along the cardinal bearings (N-S or E-W). Although the absolute rates are low, due to the slow dispersal of *F. lugubris*, the rate of dispersal in cardinal rides is three times (15m/year) greater than intercardinal rides. We hypothesise that the slower population margin expansion observed for rides with bearings in intercardinal directions is due to a minimum threshold of insolation for newly established nests of *F. lugubris* to be viable. Above this threshold, a wood ant nest's outcomes continue to improve. We suggest that the south side of a ride with an intercardinal

bearing receives insolation below this minimum threshold, due to being shaded for most of the day by the trees on the southern side, while the north side will receive less insolation than the north side of a ride running east-west. This means nests on these bearings are in a 'worst of both worlds' environment. Due to the negative effects that shade can have on the onset of foraging (Rosengren *et al.*, 1987) and brood maturation (Kadochová and Frouz, 2013), this would result in fewer individuals and a reduced ability to form new nests in the polydomous network. Polydomy allows for food and labour sharing between nests that can help a new nest that may be non-foraging initially (Ellis and Robinson, 2015). Due to the small size of newly established nests new nests in shadier areas may require more support from neighbouring nests (Rosengren *et al.*, 1987), so being further from the centre of this network may leave new nests more vulnerable to abandonment. The combination of lower rates of nest foundation and a higher failure rate for nests that have been established further from the parental nests, could explain the reduced margins growth that we measured in shadier, intercardinal rides.

Practical implications

Given that wood ants increase biodiversity in plantation forests and may provide additional pest control benefits (Laine and Niemela, 1980; Karhu and Neuvonen 1998; Zingg *et al.*, 2018), the results that we present here may be useful in planning management of plantations. Wood ants can reduce defoliating pest burden (Karhu and Neuvonen 1998), increase aphid abundance (Frouz *et al.*, 2008), compete with other insectivores (Haemig, 1992), and change the spatial distribution of soil resources (Podesta, 2023), the effects of ride characteristics on dispersal have major implications for conservation and forest management. When planning new areas of forestry adjacent to existing populations of wood ants, or in areas where translocation of wood ants' nests is being considered (Nielsen *et al.*, 2018), we would recommend cutting fire breaks, access tracks etc. in cardinal directions, to maximise the ability of wood ants to disperse. This could also benefit other edge-specialist woodland species that rely on insolation, e.g., herbaceous plants.

On the other hand, the width of the ride should also be considered when managing forest to promote species richness or dispersal. Previous work has suggested that canopy gaps should be at least 15m wide in order to harbour species that would be shaded out in the forest interior (Oxbrough *et al.,* 2006; Smith *et al.,* 2007), and our data seem to suggest that wood ants similarly have a minimum threshold of insolation (also impacted by ride width) that allows them to thrive and disperse.

Wider ecological implications

The work presented here adds to a body of research showing that linear canopy gaps in plantation forests have important implications for forest dwelling species. The characteristics of rides, such as

width, affect the diversity or abundance of butterflies (Greatorex-Davies *et al.*, 1993), spiders (Oxbrough *et al.,* 2006; Carter *et al.,* 1991), ground beetles (Carter *et al.,* 1991), vascular plants (Sparks *et al.,* 1996; Smith *et al.,* 2007), and bryophytes (Smith *et al.,* 2007), although see also (Jokimäki *et al.*, 1998). We have shown that, in addition to the effects that ride characteristics can have on the diversity and abundance of forest species in plantation, the orientation of rides can influence the dispersal ability of an edge specialist, opening up the question of whether other species with similar habitat requirements might be similarly affected.

Managing plantations in a manner favourable to wood ant dispersal (by cutting fire breaks and other necessary linear gaps along cardinal directions) could be beneficial to other species and biodiversity in economically productive forests in two ways. Firstly, the presence of wood ants themselves can be beneficial to other species. The nests of wood ants are home to many myrmecophilous species, with over 100 myrmecophiles currently identified in wood ants' nests (Robinson *et al*., 2016; Parmentier *et al.,* 2014). Additionally, wood ants can play an important role in the dispersal of seed, including some declining and charismatic wildflowers like the endangered *Melampyrum cristatum* (crested cow-wheat) which is dispersed by wood ants and is probably range-limited by the availability of dispersers (Stachnowicz, 2013). Secondly, other species with similar habitat requirements and dispersal ability to the wood ants would benefit from the same rides as dispersal corridors as the wood ants. Due to their poor dispersal and sunlight requirement, species that might benefit from the same corridor design as wood ants are likely to be wildflowers that likewise require direct sunlight but benefit from other conditions provided by the forest edge such as protection from wind, acidic soil or edge related nutrient influx (Weathers *et al*., 2001).

On the other hand, edge specialists with the potential to benefit from improved dispersal due to edge orientation may also be pests, for example, the larvae of *Gilpinia virens,* a pine sawfly and common pest of *Pinus sylvestris*, are found in higher numbers in stands with relatively open canopies (Gawęda and Grodzki, 2020). As a result, pests such as *G. virens* may also benefit from the presence of canopy gaps cut in favourable, cardinal directions, although it should be noted that it does not necessarily follow that a preference for canopy gaps will result in the same response to different gap characteristics as we see in wood ants.

Conclusions

The potential to promote dispersal of both rare and desirable species as well as pests of canopy gaps in plantation forests makes forest edges and linear canopy gaps worthy of more detailed study. Very little work has investigated the effects of gap orientation on the dispersal ability of plants or animals that might utilise plantation forests (but see van Schalkwyk *et al*., 2022) despite the necessity of gaps

in plantations forests as fire breaks or for access for logging machinery, and the control that forestry planners have over the placement of fire breaks and other linear canopy gaps. The increase in demand for timber products and forested areas to reach carbon offset goals will likely lead to an increase in the area and intensity of plantation forests in the future (McEwan et al., 2020). If these economic and environmental goals are not to come at the detriment of biodiversity or resilience, care must be taken to ensure the development of forestry practices that allow wildlife to proliferate in plantation forests, for the ecosystem services they can provide and for the biodiversity that they represent

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Supplementary Information

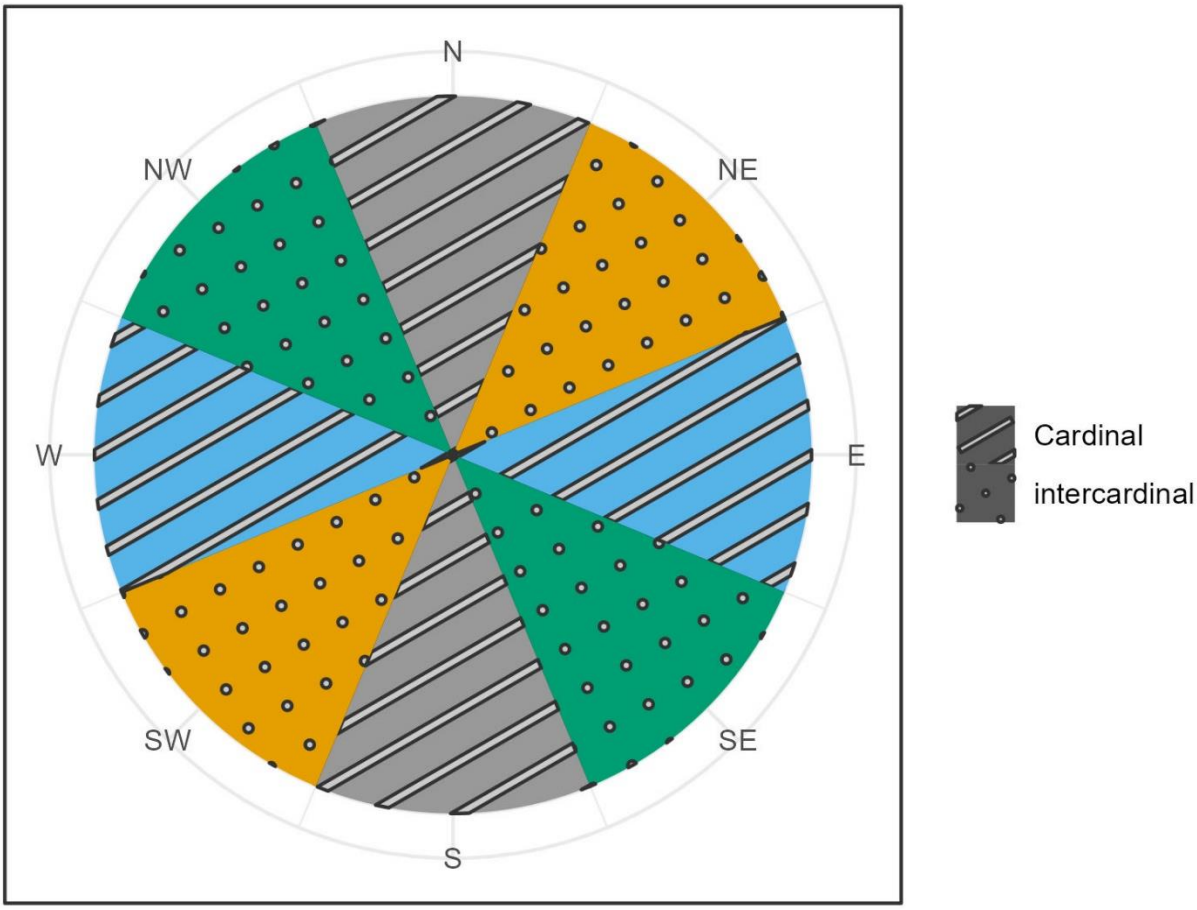

Figure S.1. We pooled the data for margins change for rides of different bearing into two categories for rides running along cardinal and intercardinal directions (+/- 22.50°) so that we could test the differences between more or less exclusive groups respectively.

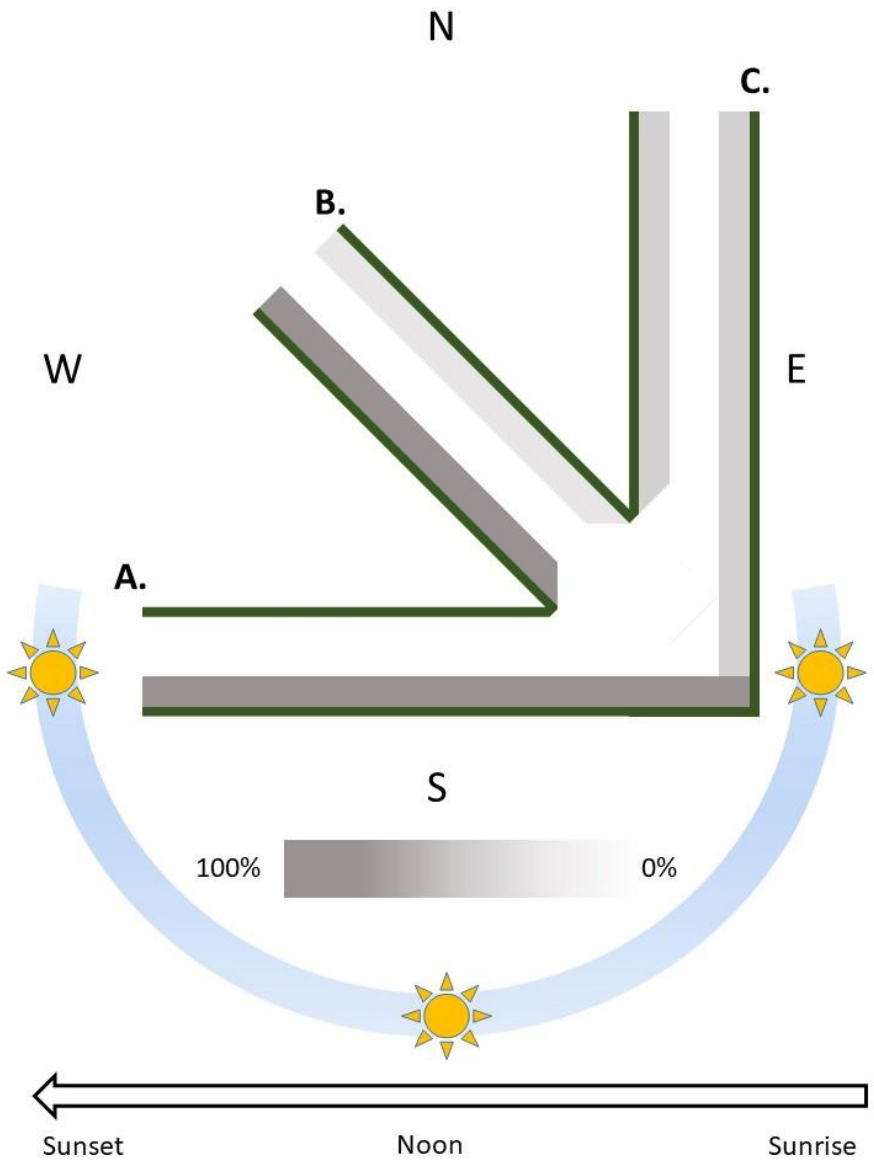

Figure S.2. An E-W ride (A) receives a full day of sun on the north side, whereas a N-S ride (C) receives half of a day of sunlight on each side (in the morning on the west side, in the afternoon on the east). Rides in intercardinal directions (e.g., B) will receive fewer hours of sunlight on the north side than and E-W ride, but still receive little or no direct sunlight on the south side. The hours of sunlight available on each side will approach 50% as the ride bearing approaches 0°, while hours of sunlight available will reach maximum asymmetry for rides bearing 90/270° (E-W). Only the north side of the ride A will be suitable for wood ants to nest, and the south will remain unsuitable for all potential bearings until the hours of sunlight reaches a threshold (between B and C) at which both sides can be utilised by the ants but are both sub-optimal compared to the north side of an E-W ride.

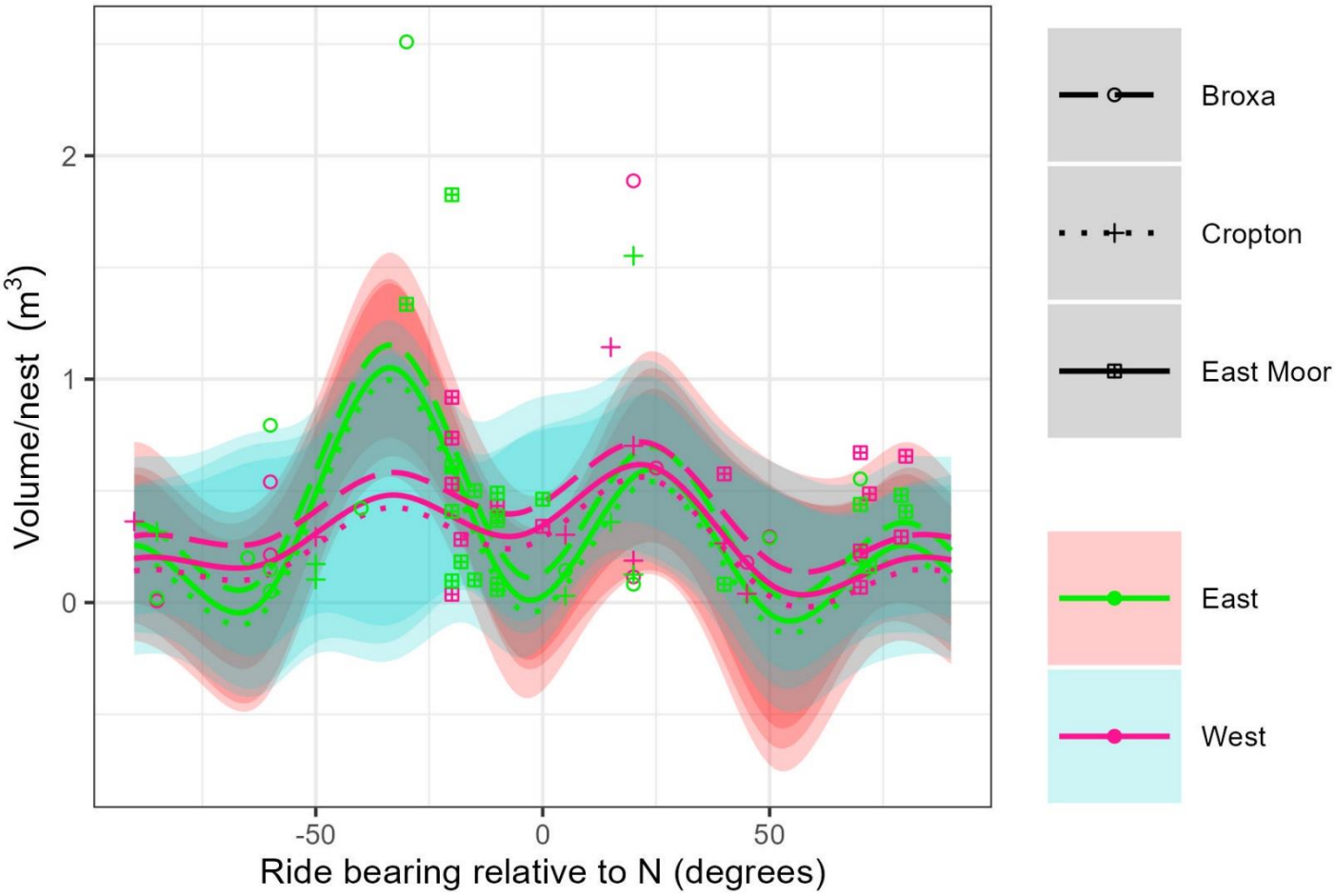

Figure S.3. Predicted values from a generalised additive model (GAM) with the formula volume per nest ≈ side + s(bearing) + s(width) + s(site) R^2 = 0.299, deviance explained = 44.2% were plotted for values of ride bearing (lines) alongside the original data (points) and 95%CIs (shaded areas). Although the east side and mean width smooths were significantly different from a line at the intercept of gradient = 0 ($p < 0.01$), there was no significant difference between the east and west smooths and no clear pattern is discernible from the plot. Based on AIC values, this was more parsimonious than the model excluding site as a smoothing term (Figure 4), however the ΔAIC = 2.278, only just outside of the widely used cut-off for supporting a more complex model. As a result, both models have been presented here.

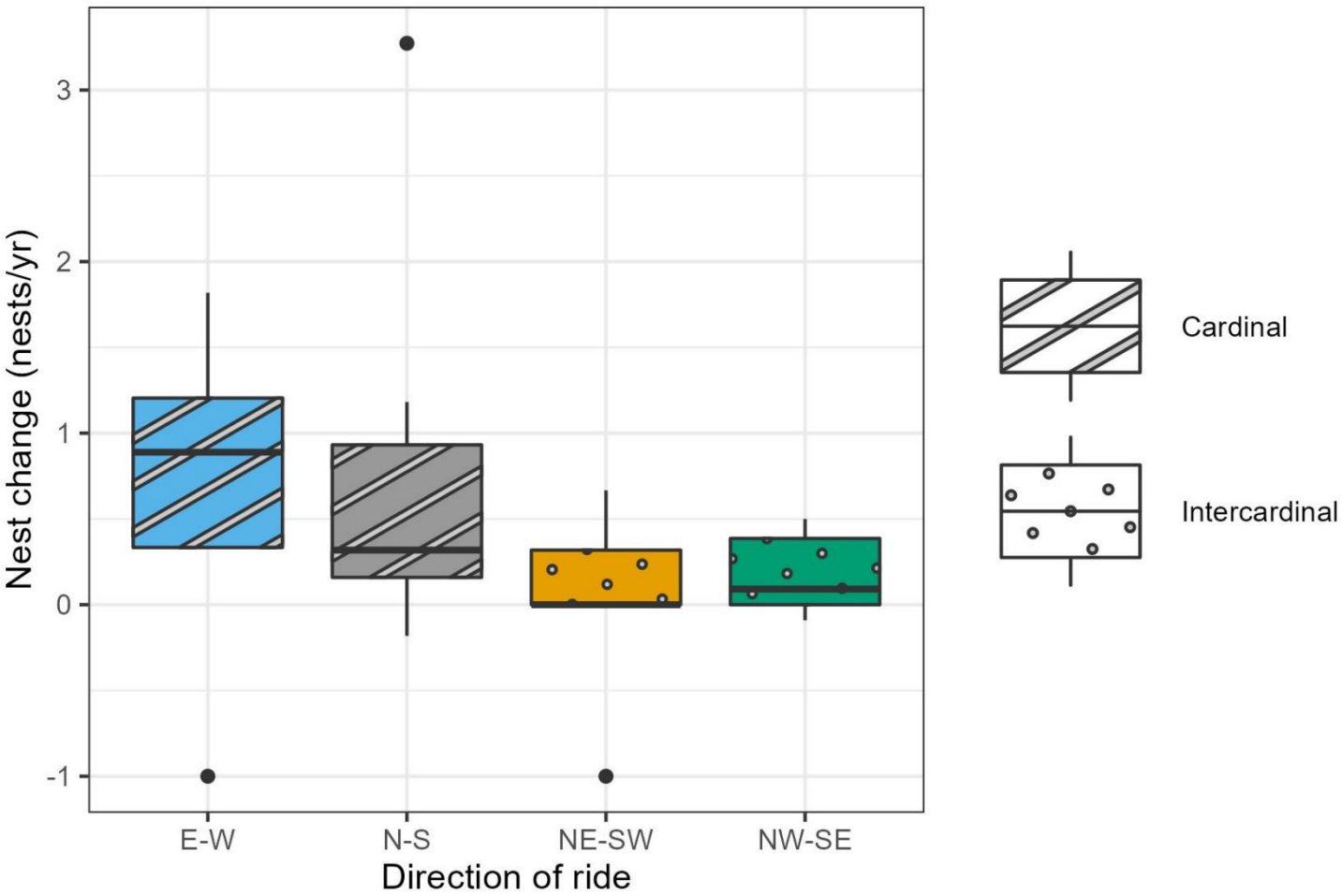

Figure S.4. The ride data were pooled by bearing so that the categories consisted of rides bearing +/- 22.5° of the cardinal and intercardinal points. E-W and N-S rides appear to have undergone slightly more (positive) change in nest number than NE-SW and NW-SE rides.

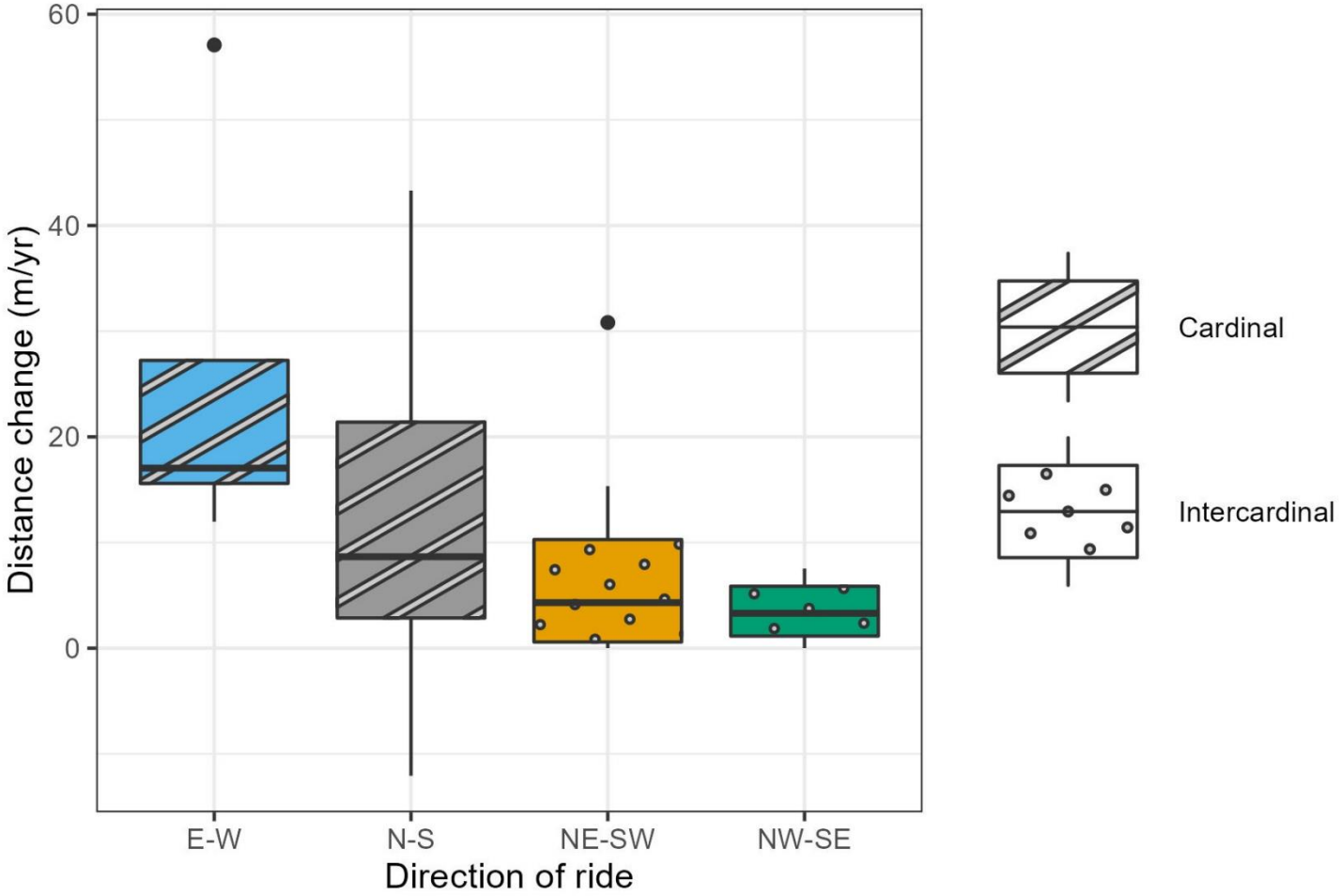

Figure S.5. We pooled the data by bearing so that the categories consisted of rides bearing +/- 22.5° of the cardinal and intercardinal points. Although the differences in distance change between category were not significant (ANOVA, $p > 0.05$), E-W and N-S rides appear to have undergone slightly more (positive) change in margins position than NE-SW and NW-SE rides.