

Microhabitat preference of native and invasive small mammal species in logged-forests of Sabah, Borneo



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A thesis submitted in partial fulfilment of the requirements for
the degree of Master of Research of Imperial College London
and Diploma of Imperial College London

September 2012

Abstract

Invasive species pose one of the greatest threats to biodiversity. This study explores the extent that human disturbance to natural ecosystems facilitates the spread of non-native species, using the example of a small mammal community in logged-forest, Sabah, Borneo. The microhabitat preference and niche overlap between three native species of small mammals and the invasive *Rattus rattus* was examined. Species showed significant differences between the used microhabitats compared with spatially matched, alternative microhabitats. This microhabitat preference was not found to differ significantly between the species considered, although *R. rattus* showed the greatest preference for heavily disturbed habitats. At a finer spatial scale species shared a common preference for fallen wood and avoidance of leaf litter. No overall difference was found in substrate preference between species, although variation existed in the use of rare terrestrial forest substrates. These results are discussed in the context of developing appropriate management regimes to limit the penetration of invasive *R. rattus* into tropical forests.

1. Introduction

Tropical forest ecosystems are home to two thirds of the world's terrestrial biodiversity (Gardner *et al.* 2009). Yet the combined influence of anthropogenic forest degradation and invasive species is set to make these ecosystems the focus of future extinction (Bradshaw *et al.* 2009). Southeast Asia is a region of particular concern as it hosts the greatest per country endemism of mammals and birds and is experiencing the fastest rate of habitat conversion (Sodhi *et al.* 2010). Borneo in particular contains exceptional species diversity (Myers 2000, Meijaard and Sheil 2007). In the Malaysian state of Sabah, approximately 48% of the remaining forests are found within protected areas (Marsh *et al.* 1996). However outside of these protected areas the majority of remaining forests have been modified or disturbed (Aiken and Leigh 1992). With this large area of land existing in an altered state, it is of central importance to conservation to understand how biological communities persist in altered habitats (Hansen *et al.* 2001).

Small mammals play a key role in biological communities, acting as both seed predators and dispersers (Asquith et al 1997, Wells and Bagchi 2005, Wells et al. 2009). High small mammal densities in human-induced predator free habitats, has been hypothesized to cause elevated seed predation and slow forest regeneration (Terborgh *et al.* 2001). Small mammals are also important prey items for large avian and mammalian predators (Puan *et al.* 2011, Wilting *et al.* 2006). It has often been reported that in tropical forests, populations of small mammals tend to increase after logging activity (Adler and Levins 1994, Pardini 2004, Lambert 2006). Changes in the abundance of this functionally important group in altered forests may cause knock on effects at other trophic levels (Grassman *et al.* 2005).

In heavily altered landscapes, the introduction of invasive species poses a severe threat to native biota already under stress from habitat modification (Kot *et al.* 1996, Kupfer *et al.* 2006). The highly successful pioneer species *Rattus rattus* has recently been observed in a logged forest of Sabah, Borneo (Wearn *et al.*, unpublished data). This species is normally restricted to urban areas (Payne and Francis 2007).

Changes in the presence and abundance of species in a landscape may be explained by knowledge of species' preference for particular habitat features (Manly *et al.* 2002). Habitat selection can be considered on a hierarchal scale: from the geographic range of species (Schoen, and Kirchhoff 1985), to individual home range within a landscape (Dotter and James 1998, Nakagawa *et al.* 2007), to selection for specific habitats within a home range (Spitz and Janeau 1995, Bertolino 2007), and finally, to fine scale selection for specific features within a habitat (Wells *et al.* 2006).

This study focussed on the fine-scale habitat preference of three native and one invasive species of small mammal. Preference is the likelihood that a habitat will be selected if offered on an equal basis with alternatives (Johnson 1980). Optimal foraging theory states that individuals should seek to maximise their fitness and reproductive success by maximising the ratio of energetic gains to costs (Charnov 1976). In the case of small mammals, the greatest cost of all is the instant and absolute loss of fitness by predation (Bouskila, 2001). Therefore we may predict that small mammals will show preference for habitats with abundant food resources and minimal predation risk. In this study

The spool-and-line technique (Miles *et al.* 1981, Mendel and Viera 2003) was trialled to answer the following questions:

1. What microhabitat features are preferentially used by native and invasive species of small mammal in logged forest?
2. Is there significant overlap in the microhabitat use of invasive and native species?

These findings are discussed in the context of the potential for competition and replacement of native species of small mammal by the invasive pioneer species *R. rattus*.

2. Materials and Methods

2.1 Study site and species

This study focuses on a complex of four species belonging to the Muridae family (rats and mice) which are thought to utilize similar habitat (Payne and Francis 2007): the red spiny rat (*Maxomys surifer*), a wide spread generalist species with a characteristic red coat, Whitehead's rat (*Maxomys whiteheadi*), which is classified as Vulnerable on the International Union for the Conservation of Nature red list (IUCN 2012), the partially arboreal long-tailed giant rat (*Leopoldamys sabanus*), and the invasive black rat (*Rattus rattus*), which had not been previously reported in forests of this region of Sabah.

The study was conducted within the Stability of Altered Forest Ecosystems (SAFE) project site in Sabah, Malaysian Borneo (Ewers *et al.* 2011). Small mammal trapping was carried out in an 8000 ha area of twice logged secondary forest displaying varying levels of forest disturbance. The continuous forest of the SAFE project area is connected to a large (> 1 million ha) area of similar forest to the north, and is otherwise surrounded by an oil palm plantation matrix. Three trapping grids were established within blocks D and F of the SAFE project experimental setup (Figure 1), in order to encompass a gradient of logging intensity and forest modification. Grids were located more than a kilometre from the forest edge and were all connected by continuous forest.

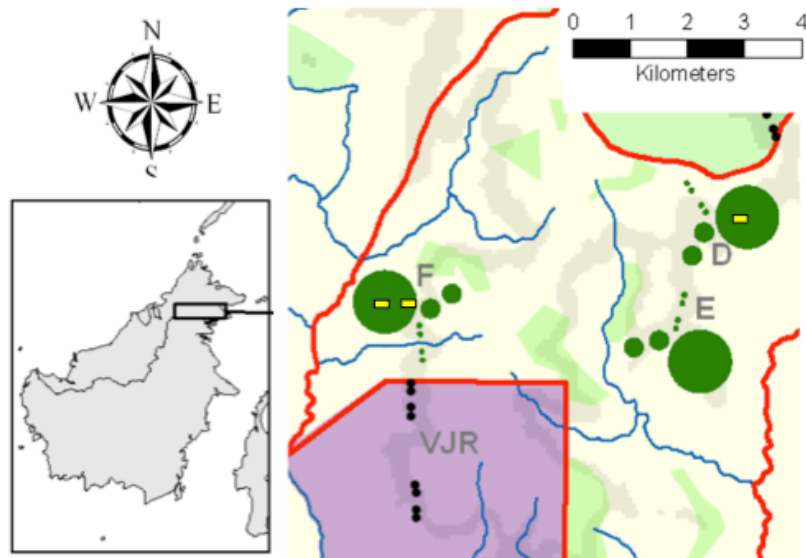


Figure 1 Three trapping grids (yellow rectangles) were established within an area of continuous secondary forest (red outline) situated in blocks D and F (green circles) of the SAFE experimental area. A small Virgin Jungle Reserve (VJR, purple) with lower disturbance was located to the south of the experimental area, with oil palm plantations to the east and west (outside red line). Grids were positioned to control for elevation and slope. Figure adapted from Ewers *et al.* (2011).

2.2 Trapping protocol

Trapping grids consisted of 48 trap stations separated from each other by a distance of 23 meters and arranged in a four by 12 rectangular pattern. At each station, two locally made wire-mesh traps (280x140x140mm) were positioned within a ten metre radius of the centre of the station and the GPS location recorded. A total of 96 traps were setup on each grid. Traps were equipped with a plastic cover to provide shelter and baited with palm oil fruit. Each grid was trapped for two weeks, trapping on alternate days. Trapping was conducted for three months between May and July of 2012. Traps were checked in the morning and all captured small mammals were injected with a unique passive induced transponder (PIT) tag under the skin, identified to species, sexed and weighed as part of an on going mark-recapture experiment. Animals were anaesthetised using diethyl ether during processing to reduce any pain or stress caused by the PIT-tagging. Once they had recovered from the anesthetic, all animals were released at the point of capture.

2.3 Microhabitat preference

To effectively quantify a species' habitat preference, habitat measurements must be made at the spatial scale at which the species makes selection choices (Manly *et al.* 2002). For example, we may ask which habitat does the species choose given a number of known and contrasting alternatives? The spool-and-line technique (Anderson *et al.* 1987) is ideally suited to studying fine-scale microhabitat preference as it allows even very subtle route choices to be quantified (Wells *et al.* 2006, Harris *et al.* 2006). This method involves attaching a bobbin of thread (the spool) to an animal and tying the end of the thread to any fixed structure (vegetation or rocks) at the point of release. The spool unravels from the inside, so that as the animal moves, the thread plays out without resistance, wrapping around vegetation and rocks in its path (Boonstra and Craine 1985). In this way the spool track precisely replicates the movement behaviour of the spooled individual. Deviations and route choices are therefore observed at the spatial scale experienced by the individual (Cox *et al.* 2000). This provides three-dimensional information on microhabitat preference both at the order of several meters and at the fine scale of what specific substrate was used for movement. Importantly, such detailed information could not be gleaned from radio-telemetry or trapping data alone (e.g. 1985; Key and Woods 1996; Dennis 2002 and 2003).

Spools (nylon quilting cocoons, weight between 1 and 2.5g, length between 100 and 200m, Danfield Ltd) were attached to the four study species during processing of trapped individuals. The spools were wrapped in a thin layer of cling film, followed by a layer of electrical tape to prevent snagging on vegetation. The cling film layer prevented the electrical tape from attaching directly to the spool. This ensured that the final reels of thread played out without resistance and the animal could discard the spool without incident. The weight of spools was adjusted to less than five percent of the individual's body weight. This weight ratio followed that used in radio-tracking studies so as to avoid disturbing the animal's activity (Kenwood 2001). A small fur clip was made dorsally between the shoulder blades and spools were attached to the under-

fur using acrylamide gel (Loctite ®). Spool tracks were followed with a GPS the day after release.

2.4 Spatial autocorrelation and preliminary trials

Repeated habitat measures along a path suffer from spatial autocorrelation since measures closer together in space will be more similar than those measured further apart (Moore and Swiharte 2005). The degree of correlation between equally spaced observations along the spool track depends on:

- 1) The linear rate of habitat change in the environment – the observed change in habitat per metre.
- 2) Path tortuosity – how directly the small mammal moves between habitat types.

The distance along the spool track at which the small mammal experiences the changes in habitat depends on the interaction between 1) and 2).

Preliminary trials were conducted to estimate the separation distance at which repeated measures on the spool track become independent from each other. Forest density was used as a proxy for the scale at which microhabitat units vary. This was measured by repeated spherical densiometer readings (Englung 2000) taken at five-meter intervals along sample spool tracks, so matching the separation used by Harris *et al.* (2006). The correlation between observations at 5, 10, 15 and 20 metres apart was assessed using the autocorrelation function (ACF) in R 2.13.2 (R development core team 2012). Slight correlation was found between consecutive five metre recordings (covariance = 0.21), but this dropped to a negligible value at ten metre intervals (covariance = 0.09) and so this separation distance was used for making repeated microhabitat observations along the spool track.

2.5.1 Microhabitat covariates

The first ten metres of each spool track were discarded as a flight response (Harris *et al.* 2006). Then after every ten metres, nine microhabitat variables were measured (Table 1). The microhabitat was defined as the area within a one-meter radius of the spool. The height above ground was recorded as arboreal behaviour in particular habitats may be beneficial to small mammal survival by reducing the risk from predominantly terrestrial predators and introducing physical barriers between aerial predators (Montgomery and Gurnell 1985, Buesching *et al.* 2008). The density of forest strata from the ground ($\leq 0.5\text{m}$ above ground), understory ($> 0.5\text{m} \leq 3\text{m}$), mid-storey ($> 3 \leq 20\text{m}$) and canopy ($> 20\text{m}$) was recorded to test whether species' spatial use patterns were driven by structural components of different vertical strata (Putker *et al.* 2008). Four further covariates indicating potential resource availability and predation risk risk were also recorded (Table 1).

In addition the rainfall and lunar phase were recorded each day (Table 1). Rainfall may influence small mammal movement by masking the noise of travel across complex substrates (Vickery and Bider 1981). Variation in moonshine was predicted to influence the visibility of the microhabitats, making some locations less desirable when well lit by a full moon (Kotler *et al.* 1991).

Table 1. Descriptions of microhabitat continuous variables (Cont.) and scoring system for categorical variables.

Covariate	Factor level	Description
Density of forest strata	1	Density between 0-25%
	2	Density between 26 and 50%
	3	Density between 51 and 75%
	4	Density between 76 and 100%
Total canopy closure	Cont.	A was spherical densiometer was placed on the ground at arms length. Four readings were taken at right angles from the spool track direction of travel, with the researcher kneeling in a central position on the spool. An average of these scores was generated for use in the analyses.
Forest quality	1	Heavily disturbed. Grass or open logging trail. No trees vegetation not above 1m
	2	Heavily disturbed by logging. Herbaceous with No large trees above sapling size
	3	Different strata not clearly defined, occasional tall trees
	4	Taller more continuous canopy
	5	Undisturbed primary rainforest
Tree basal area (m²/ha)	Cont.	A relascope (Gove 2001) was held at eye level 53cm from the researcher whilst a 360° rotation was made about the central position of the spool track. The number of trees viewed as larger than the 1cm opening in the relascope was counted and the number multiplied by two to give an estimate of tree basal area (m ² /ha).
Predator avoidance score	1	Spool visible from all sides
	2	Spool visible from one side and above or from two sides
	3	Spool visible from one side or above
	4	Spool not visible from either side or above
Height	1	Height above ground ≤0.5 m
	2	Height above ground > 0.5 m ≤ 3 m
	3	Height above ground > 3 m ≤ 10 m
	4	Height above ground > 10 m
Rainfall	1	No rain
	2	Light rainfall in night, ground slightly wet on arrival in morning
	3	Heavy rainfall throughout night, ground still very wet in morning
Lunar phase	1	¼ to no moon
	2	¼ to ¾ moon
	3	¾ to full moon

2.5.2 Comparison of used vs unused microhabitat

Previous studies using the spool-and-line technique to compare the movement of small mammal species have tended not to record control observations for the spool track (Mendel and Viera 2003, Wells *et al.* 2004). In this way, it has been possible to compare small mammal behaviour between species, but not compared to the surrounding environment. Few studies have collected observations of possible alternative “unused” habitat (Richard and Armstrong 2010). Harris *et al.* (2006) made control observations for a spool track by taking a random bearing at the same starting point as the trap release point and walking in a straight line of equal distance to the spool track along this bearing, taking recordings at intervals (Figure 2a). This allows for comparison against an alternative route at the spatial scale of the whole spool track.

To achieve a finer scale comparison of used vs unused microhabitat, this study explicitly linked used vs control microhabitat observations. For each ten metre microhabitat observation along the spool track, the microhabitat of one spatially matched location was also recorded. The location of these control observations were taken by walking ten metres in a straight line on a bearing relative to the spool track of 45° , 135° , 225° , or 315° selected sequentially (Figure 2b). In this way all paired, used and control observation had a fixed spatial separation in a randomised orientation.

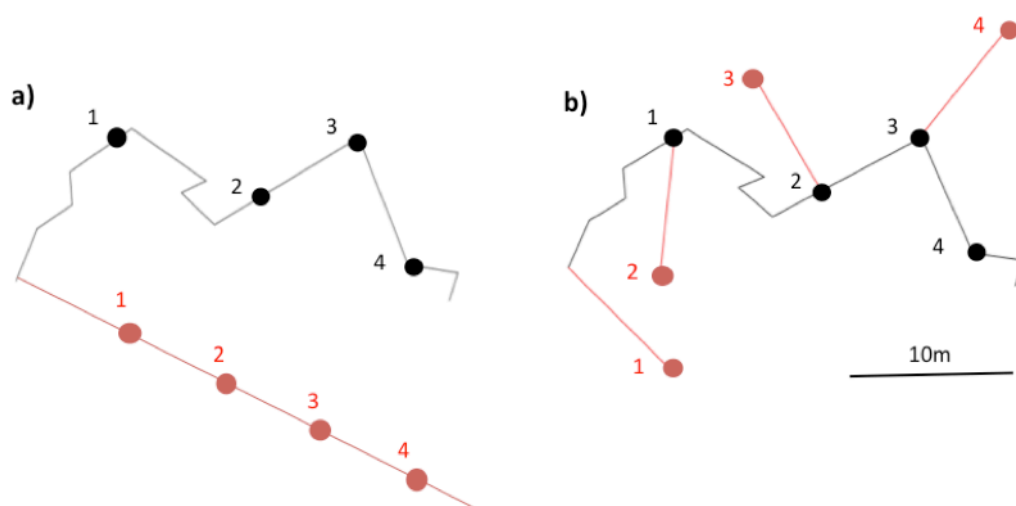


Figure 2. comparison of the control methods used by Harris et al 2006 (a) and this study (b) plotted using the recorded spool track of a male *M. Surifer* with the spool track (black) and control track (red). Numbers 1-4 illustrate how the sequential microhabitat observations of the used track (black circles) are spatially linked to the control track (red circles) .

2.6 Fine scale substrate use

The preference of species for particular structural elements of the forest was investigated by examining the frequency that spool tracks passed over particular substrates (Table 2). The distance between different substrates on the forest floor is much smaller than the distance between different microhabitats. Therefore the dominant substrate was characterised for each step of the spool track (Wells *et al.* 2006). A step was defined as the straight-line distance with no change of direction greater than 20°. In this way the substrate used for each significant change of direction was recorded. One control measurement was taken for each step by walking the same distance as the step, on a bearing taken sequentially at either 45°, 135°, 225° or 315° to the direction of spool track. In this way the substrate chosen at each major change of direction was compared with a possible alternative. The distance and bearing of each step was also recorded.

Table 2. Dominant substrate categories and definitions.

Substrate abbreviation	Definition
LL	Leaf litter - Ground covered by a thin layer of leaves.
SLL	Suspended leaf litter - Found where ground vines and low lying vegetation have been covered by a continuous layer of fallen leaves, providing excellent cover for small mammals. Identified where the spool track moves through rather than over the leaf litter substrate.
BG	Bare ground.
RK	Rock.
ST	Streambed - Dry stream beds provide excellent sunken travel routes for small mammals that is enclosed on two sides and so concealed from view.
FW	Fallen wood - Any dead woody debris lying on the ground e.g log, tree stump, branch etc.
V	Vines – All non-woody shoots and herbaceous structures.
FP	Footpath – clearly marked trails.

2.7 Statistical analysis

A key characteristic of the data collected by repeated measures taken at intervals along the spool is that a nested structure was attributed to the data. To accommodate this, mixed effects models were used to nest observations taken on the same track within individuals using the R packages nlme and lme4 (R development core team, 2012, Bates *et al.* 2011, Pinheiro *et al.* 2011). In addition the rainfall and lunar phase were incorporated into models as random effects.

2.7.1 Analysis of spatial behaviour

Extent of arboreal behaviour was compared between the two partially-arboreal species by generalised linear mixed-effects models with a poisson error structure. Step lengths were log transformed and compared by mixed effects models fitting the individual's mass as a random effect (R development core team). Trapping data from this study together with long-term trapping data (Wearn unpublished data) was used to estimate home range sizes for *M. surifer* (the most commonly trapped species). The minimum convex polygon method (Worton 1987) was used to estimate home ranges for individuals that had been trapped at five or more different locations in ArcGIS 9.2 (ESRI 2006). Individuals' body mass, sex and spool track straight-line distance (as a proxy for nightly foraging distance) was used to predict home range size.

2.7.2 Microhabitat analysis

In the assessment of species' preference for microhabitat components priority was given to modelling the correlation of microhabitat covariates. This was done through a redundancy analysis in the vegan package of R 2.13.2 (R development core team 2012, Oksanen *et al.* 2011). In this way the variation amongst co-varying variables was maximised along principle components. Variables were measured on different scales, so standardisation of values between variables was carried out by dividing the value of each variable by the sum total of values for that variable. The heavily correlated nature

of the microhabitat variables prevented the confident analysis of which individual microhabitat variables drove species microhabitat preference (Figure 1 Appendix). As the majority of variation was captured within the first principle component (PC1 52%), PC1 scores were used as the only response variable. Mixed-effects models nested paired used and control observations within spool tracks, within individuals (R development core team, 2012).

2.7.3 Step analysis

The strength of preference for each substrate was estimated at the scale of each spool track. Preference for substrate x was calculated as the number of steps where substrate x was recorded, divided by the number of times the same substrate was recorded in the matched control steps. This gives a measure of the number of times that a substrate is used, standardised between tracks by the availability of the substrate in the local environment. In this way a score greater than one indicates a preference for use of that substrate and a score less than 1 indicates preference for avoiding that substrate. Preference scores were compared between substrates and species by mixed-effects models (R development core team, 2012).

3. Results

3.1 Species' spatial behaviour

In total 53 spools were attached to 41 individuals: 15 *M. surifer*, 13 *M. whiteheadi*, nine *L. sabanus* and four *R. rattus*. The total spool track followed was 3.4km with a mean spool length of 64m (SE= 44.3m).

All species were trapped on all grids and individuals of different species displayed a large amount of spatial overlap in their terrestrial foraging behaviour (Figure 3). However, some vertical segregation of space was observed as spools of *L. sabanus* and *R. rattus* were followed into the canopy. While both *Maxomys* species remained terrestrial (Figure 4A), *L. sabanus* and *R. rattus* had mean heights of 1.05m and 0.87m above ground respectively. No significant difference was observed in the height above ground of the two arboreal species (estimated difference 0.21m, S.E= 0.41, P=0.61). Lunar phase explained a large proportion of the variance in spool track height (0.373), but rainfall did not influence variance (<0.001).

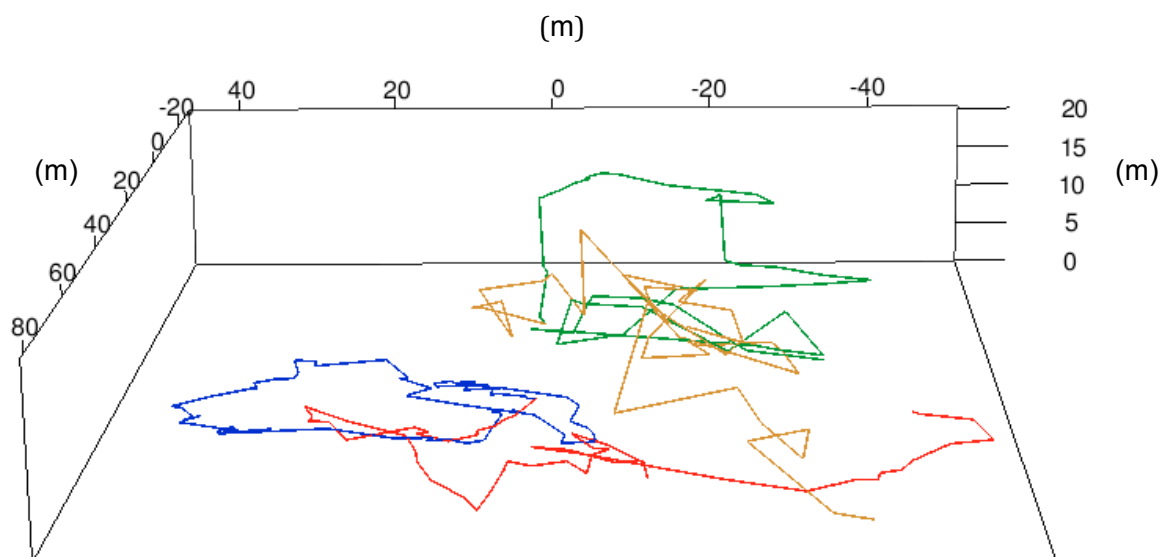


Figure 3. Plotted geographical position of one spool track for each study species that had been released on the same day. Zero scores on axes denote the midpoint of the trapping grid. *M. surifer* (red), *M. whiteheadi* (Blue), *L. sabanus* (green), *R. rattus* (orange).

M. surifer had the longest mean step length at 2m, and *M. whiteheadi* the lowest at 1.79m (Figure 4B). No significant differences existed between species, with the greatest difference between the two *Maxomys* species ($T= 0.87$, $DF=19$, $P=0.39$).

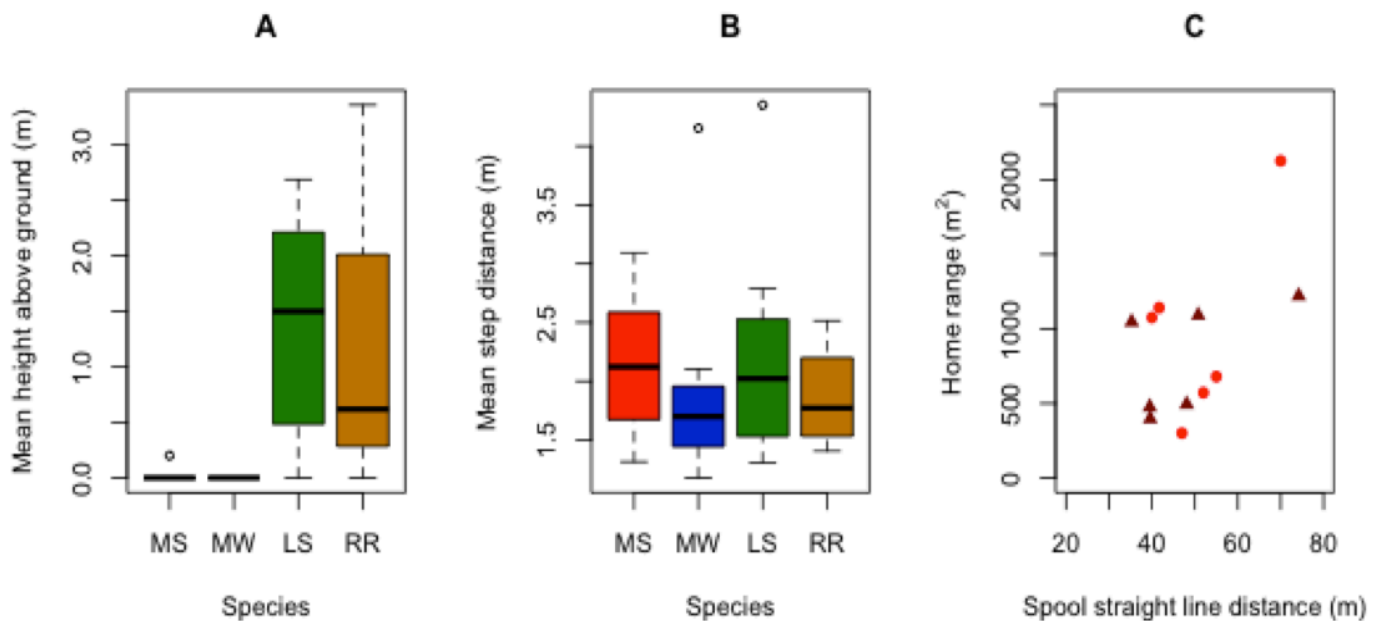


Figure 4.A Mean height above ground of *M. surifer* (MS), *M. whiteheadi* (MW), *L. sabanus* (LS), *R. rattus* (RR). Mean step length of spool tracks (B). Estimated home range of male (red circles) and female (dark red triangles) *R. surifer* (C).

Mean home range was estimated at 982m² for males (n=6) and 787m² for females (n=6). However, neither sex or body mass were significant predictors of home range size ($P= >0.50$). Spool straight-line distance was on the other hand marginally significant ($T=2.03$, $DF= 10$, $P=0.069$) (Figure 4C).

3.2 Microhabitat selection

Principle component analysis of species' microhabitat observations revealed that most of the variation between microhabitat variables could be explained by a single composite variable that summarised the transition from low to high forest disturbance. This first principle component (PC1) generated a scale moving from negative values consisting of high quality forest, canopy density and tree basal area (m²/ha), to positive scores of high understorey and ground vegetation density scores. The second principle component consisted primarily of variation in the total canopy closure variable (appendices Figure 1).

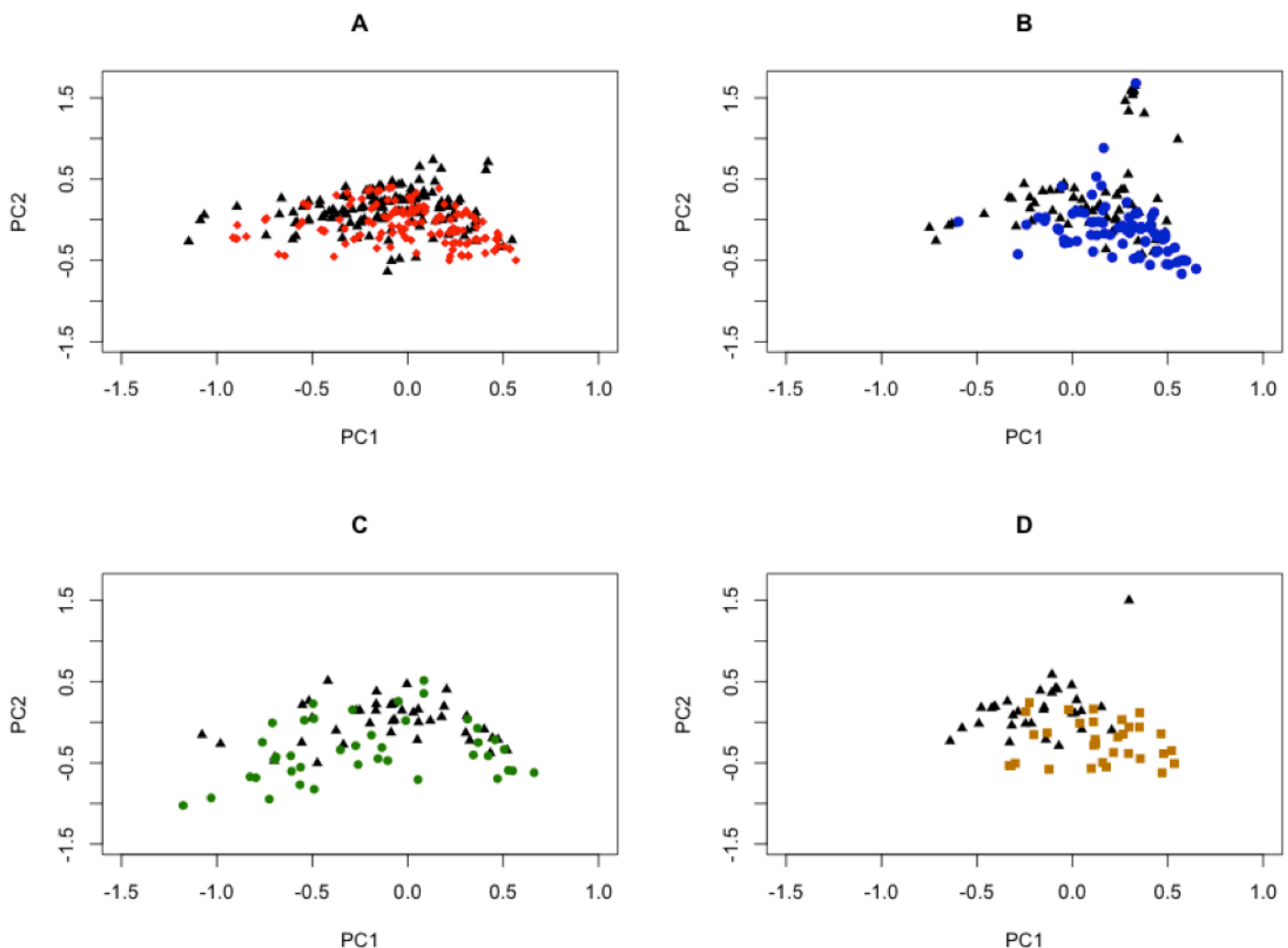


Figure 5. Species used vs control microhabitat observations plotted on the same principle component axes of a global redundancy analysis ordination of all microhabitat observations made during the study. A) *M. Surifer* used (red diamonds) and control habitat observations (black triangles). B) *M. whiteheadi* used (blue circles) and control (black triangles). C) *L. sabanus* used (green circles) and control (black triangles). D) *R. rattus* used (orange squares) and control (black triangles).

All Species showed clear patterns of preference for specific microhabitats compared with spatially matched control microhabitats (Figure 5). Species were recorded in a wide range of habitats but comparison of PC1 scores revealed that both *Maxomys* species (Figure 5A, 5B) showed significant preference for more disturbed habitats (*M. surifer* preference 0.11 SE = 0.03, df=138, $P < 0.001$, *M. whiteheadi* preference = 0.13, SE = 0.033, DF=80, $P < 0.001$). *R. rattus* showed the strongest preference for disturbed microhabitat compared with matched controls, with an estimated difference of 0.31 (SE= 0.05, df = 31, $P < 0.001$). By contrast *L. sabanus* showed the reverse pattern of preference (Figure 5C), with a marginally non-significant preference for less disturbed habitat (estimate= 0.09, SE= 0.06, DF=40, $P=0.14$).

Despite these differing trends of habitat use between paired, used and control microhabitats, no significant differences existed between species' used PC1 scores. The greatest separation existed between *M. whiteheadi* and *L. sabanus*, with *M. whiteheadi* using more degraded habitat with an estimated greater PC1 value of 0.17 (SE=0.11, DF=20, $P=0.13$).

3.3 Substrate preference

Species showed a common preference for fallen wood (estimate preference= 1.55, SE= 0.29, DF=117, $P < 0.001$), dry stream beds (estimated preference=1.21, SE=0.53, DF=117, $P = 0.025$) and avoidance of leaf litter (estimated preference= -0.55, SE= 0.24, DF=117, $P = 0.029$) (Figure 6). No significant difference was found in the overall preference between species, with the greatest difference in strength of selection between *L. sabanus* and *M. whiteheadi* (estimate = 0.283, SE=0.19, DF= 17, $P = 0.146$).

M. whiteheadi (Figure 6B) showed the strongest preference for fallen wood (estimate= 2.63, SE= 0.45, DF= 30, $P < 0.001$) and also significant selection for rocky substrates (estimate=1.68, SE= 0.68, DF= 30, $P = 0.020$). The other species with a unique

preference for a particular substrate was *R. rattus* (Figure 6B) with significant preference for suspended leaf litter (estimate= 2.08, SE= 0.765, DF= 8, P= 0.026).

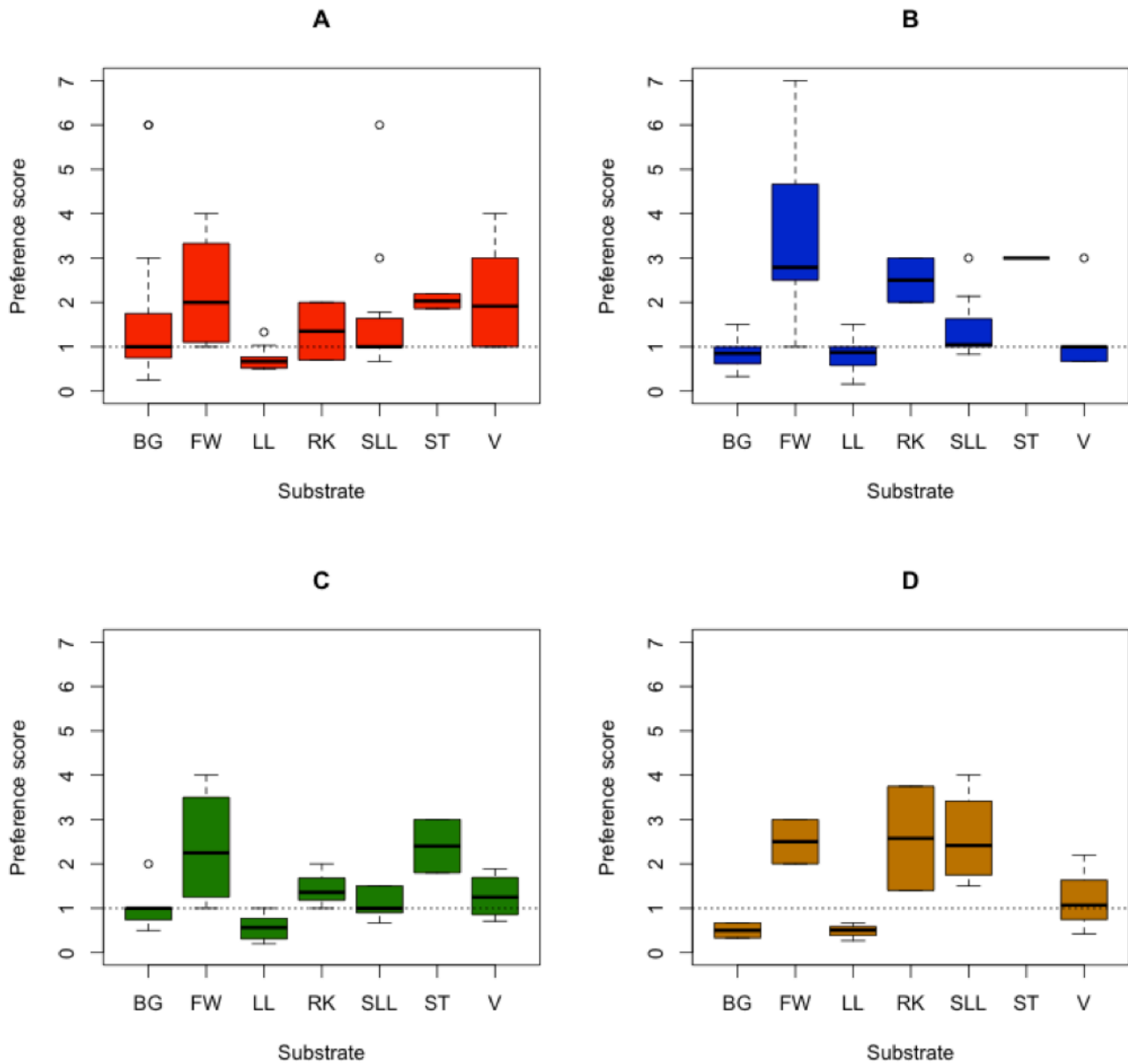


Figure 6. Preference scores of *M. surifer* (A), *M. whiteheadi* (B), *L. sabanus* (C), *R. rattus* (D) for bare ground (BG), fallen wood (FW), leaf litter (LL), rocky substrates (RK), suspended leaf litter (SLL), dry stream beds (ST) and vines (V).

4. Discussion

4.1 Spatial behaviour

4.1.1 Terrestrial space use

In this study no evidence of interspecific territoriality was observed as individuals of the different study species were recorded foraging within overlapping ranges (Figure 3). Indeed spool tracks of different species released on the same night were occasionally found to cross over each other. This home range overlap was also replicated at a finer spatial scale. Individuals from different species were recorded using the same fallen log or dry riverbed as multi-species travel routes. In the context of potential competition between native species and the invasive *R. rattus*, this suggests that scramble, rather than contest competition might define species interactions (Nicholson 1954). Records from an on going small mammal mark-recapture experiment have shown that *R. rattus* currently exists at low population density in the SAFE project area (Wearn 2012, pers. comm.). Therefore they are unlikely to have a large impact on the native small mammal community at present.

Species showed strong similarity in observed step lengths (Figure 4B). This suggests that the straight line distance of travel may be determined by proximate features of the local environment, such as logs, rocks and dense vegetation that force the individual to change direction. Such features would be experienced by all individuals foraging within similar habitat and so create a uniformity amongst species in terms of observed straight line movement. In this respect measures of step lengths may not be an indicative measure of the larger spatial scale at which an individual operates, but instead give an indication of the density of habitat features within the local environment.

4.1.2 Spatial segregation

This study represents one of the only efforts to quantify the extent of arboreal space use by *R. rattus* (Key and Woods 1996). Neither *Maxomys* species showed arboreal behaviour, however both *L. sabanus* and *R. rattus* utilised higher layers of the forest strata. No significant difference was found in the height above ground between the invasive black rat and the semi-arboreal *L. sabanus*. Indeed, the foot morphology of the two species is very similar, both having wide foot pads with small first and last toes (pers. obs.). Therefore *R. rattus* is well adapted to fully exploit the three-dimensional complexity of forest habitat. This is of particular concern as nest predation by this introduced omnivore may influence the survival success of native bird species, as has been the case on other tropical islands such as Hawaii (Amarasekare 1993). It is also interesting that the level of moonshine influenced the amount of arboreal behaviour. This may represent a behavioural response to reduce predation risk when visibility is greater.

4.2 Microhabitat preference

Small mammals are known to rely on a wide variety of food items (Endries and Adler 1997, Emmons 2000). Consequently it is not surprising that the study species foraged widely and no clear differences observed between species in the microhabitat profiles exploited (Wells *et al.* 2004).

Small mammal movement is predicted to be driven by predator avoidance and access to resources (Houston *et al.* 1993). Many interacting features of a habitat influence both these drivers (Buesching *et al.*, 2007). Both *Maxomys* species and *R. rattus* showed significant preference for the more disturbed microhabitats. Disturbed habitats were characterised by a low presence of large trees, allowing the growth of a dense ground vegetation layer. This provides excellent cover from predators. Heavily disturbed habitats may maximise both predator avoidance and resource availability, making these

habitats very desirable resources for small mammals. The greater abundance of these habitats after human disturbance may also explain why it has been observed that small mammal populations tend to increase after logging activity (Adler and Levins 1994, Pardini *et al.* 2004).

It is interesting to note that this same preference was not replicated by *L. sabanus*, which showed marked, but non-significant preference for less disturbed habitat. One explanation for this reverse trend is that the semi-arboreal *L. sabanus* benefits from exploiting resources present in the more intact canopy of less disturbed forest. This species also has a relatively much larger body size, making it more mobile. This, combined with semi-arboreal behaviour, may make this species less susceptible to predation (Montgomery and Gurnell 1985).

4.3 Fine scale substrate preference

All studied species showed clear preference for fallen wood (Figure 6). Woody debris contains high concentrations of invertebrates, a key resource for small mammals (Emmons 2000). Larger pieces of woody debris may also be used as cover, in order to reduce visual detection by predators (Browman *et al.*, 2000). This is supported by the observation that individuals in this study sometimes travelled parallel to fallen wood, close against the side. By travelling on top of such woody debris, it has also been hypothesised to provide a simple substrate to allow for faster, more efficient travel and allow small mammals to scan more effectively for predators whilst moving (Shadbolt and Ragai 2010). Therefore, in terms of foraging and predation risk, fallen wood may be an important microhabitat feature for small mammal survival.

The general pattern of avoidance of leaf litter may be explained by the complexity of this substrate inducing slow, noisy travel and greater risk of predation (Shadbolt and Ragai 2010). By contrast, the preference for suspended leaf litter by *R. rattus* and for sunken, dry river beds for by *M. whiteheadi* and *L. sabanus* may be explained by the more enclosed nature of these substrates reducing visibility to predators.

4.4 Implications of the study

The microhabitat data presented illustrates how two major threats to biodiversity in the tropics, namely habitat conversion (Brown and Brown 1992) and invasive species (Kot *et al.* 1996), may act in combination to multiply the impact on native biota. The rapid conversion of primary tropical forest to heavily logged and degraded forest forces native species into an environment that their behavioural and physical adaptations did not evolve in, so committing species to extinction (Brooks *et al.* 1999). Furthermore this study has shown that disturbance may generate habitat that is more suitable for invasive species, so promoting the spread of invasive species, which may lead to competition with native species. The findings of this study illustrate this compound effect of forest disturbance amplifying the biodiversity threat from invasive species.

This study showed that native and invasive species had no significant differences in microhabitat or substrate preference. This similar pattern of habitat use shows that invasive *R. rattus* can exploit all the same habitats as native species. Therefore once *R. rattus* has an established population in an area of forest, it will be very difficult to remove. To keep *R. rattus* populations at low densities and avoid altering the composition of the native small mammal community, management strategies might be used to generate conditions that are most unfavourable to *R. rattus*. This could be done by the wider implementation of reduced impact logging (RIL) methods (Putz *et al.*, 2008), or the rehabilitation of logged-over areas using enrichment planting (Kettle, 2010).

4.5 Directions for future research

The close relationship between spool straight-line distance and home range size indicates the role that this technique could play at illuminating behaviour at larger spatial scales. (Figure 4A). The spool track straight-line distances tended to be longer than the maximum breadth of trap estimated home ranges, suggesting that the home range estimates may be negatively biased (Ribble *et al.* 2002). This is a common

problem when trapping grids are not sufficiently large to encompass the total home range of any trapped individuals, and is exacerbated by using trapping grids with a larger perimeter to area ratio, such as the rectangular grids used in this study. The spool-and-line technique could be used in combination with trapping data to generate a more realistic estimate of small mammal home range size as it enables the movement of individuals to be tracked beyond the limits of the trapping grid.

This study emphasises how species make habitat selection choices at multiple spatial scales (Manly *et al.* 2002). Furthermore, that small-scale processes can be used to help explain large-scale phenomenon such as the invasion of *R. rattus* into altered forests. At the opposite end of the spectrum, the wider landscape context of experimental forest patches is also needed to understand taxonomic differences in response to forest modification (Gardner *et al.* 2009). Clearly studies at a range of spatial scales are needed to inform holistic management strategies that properly address the present biodiversity crisis.

Acknowledgements

With thanks to Rob Ewers and Oliver Wearn for their supervision and comments on this study. Fieldwork was funded by the Sime Darby Foundation as part of the Stability of Altered Forest Ecosystems (SAFE) Project.

Appendices

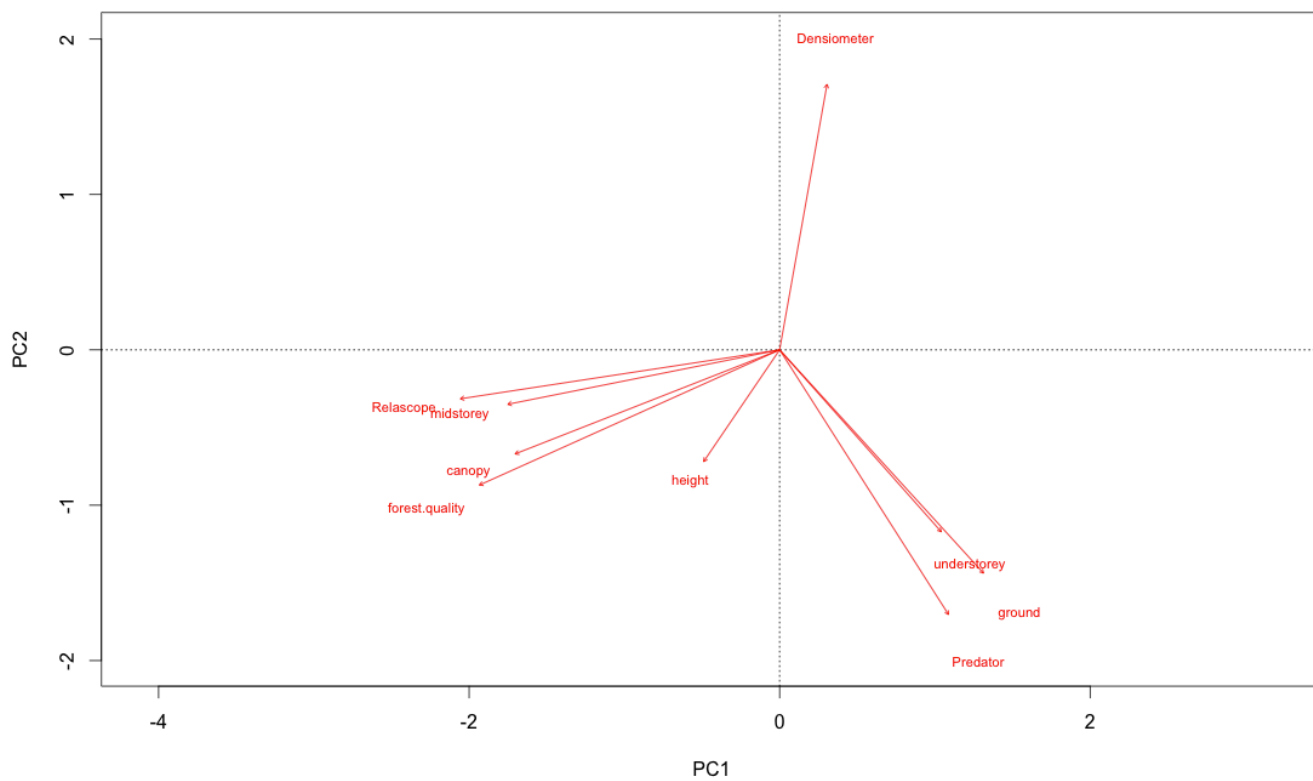


Figure 1. Directionality of variables with respect to PC1 and PC2 scores of a global ordination of all used and control microhabitat observations for study species

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