



**Faculty of Science and Technology**

**The influence of edge contrast on the diversity and composition of ground beetle (Coleoptera: Carabidae) functional traits in a lowland heterogeneous landscape**

A dissertation submitted in partial fulfilment of the requirements of the degree Master by Research (MRes).

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## **Abstract**

Understanding the effects that habitat fragmentation has on biodiversity is of vital importance for both the discipline and implementation of nature conservation.

Ecological edges are transitional zones or boundaries that occur naturally between two adjacent land cover types or landscape patches. Edge effects are known to modify habitat quality within fragments, which will in turn affect the composition of species via habitat preferences. Functional diversity is now appearing as a factor of crucial importance in the determination of ecosystem processes. The functional diversity of invertebrates is directly relevant to the functioning of ecosystems. The gaining of information from functional traits can be useful in providing an insight into the mechanisms which influences the response of arthropods to changes in the environment.

Carabids (ground beetles) are well suited to studies of edge effects. Edge contrast, or the harshness of an edge, plays a vital role in explaining the distribution patterns of carabid beetles belonging to different habitat affinity groupings at forest edges. In order to research the influence of edge contrast on the functional diversity of forest carabids, 3 types of edge were defined via the stages of succession: mature forest-young forest (soft), mature forest-shrub (intermediate) and mature forest-grass (hard). Overall, 9 sites were set up (3 soft, 3 intermediate and 3 hard edges) in Ringwood Forest, Hampshire, with 9 pitfall traps per site: 3 traps set at 5 m apart at the forest edge, 3 traps set at 5 m apart at 30 m into the forest and 3 traps set at 5 m apart at 60 m into the forest. Canopy cover, soil moisture, leaf litter depth and ground vegetation type were also collected as environmental variables.

Kruskal-Wallis tests and linear mixed-effects models were used to identify the influence of both edge contrast and environmental variables on the functional diversity and Shannon diversity of carabids. It was found that carabid functional diversity and Shannon diversity follow the edge effect hypothesis, whereby diversity is greatest at the habitat edge. It was also found that the Shannon diversity of carabids was shown to be influenced by edge contrast by both the linear mixed-effects model and the Kruskal-Wallis test. Finally, it was also found that edge contrast, edge distance and the environmental variables which were tested for did not have an influence on the functional diversity of carabids.

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# **1. Introduction**

## **1.1 The Threat of Habitat Fragmentation**

The phrase ‘fragmentation’ has been used extensively within literature as an umbrella term which describes changes that occur within landscapes, including the loss of suitable habitat areas (Lindenmayer and Fischer, 2006). Landscape change via habitat fragmentation and the loss of habitats is the primary cause for declines in worldwide biodiversity (Wilcove et al., 1998), as the destruction of habitats culminates in the loss of organism populations that rely on that habitat (Fahrig, 2002). Habitat loss and habitat fragmentation are, nonetheless, two different processes (Fahrig, 2003), as the former represents the reduction of the total available habitat area, and the latter is the transformation of a given habitat from continuous matrices into discontinuous patches (Lino et al., 2019). Understanding the effects that habitat fragmentation has on biodiversity is of vital importance for both the discipline and implementation of nature conservation (Davies and Margules, 1998; Miller-Rushing et al., 2019). A given taxa’s response to the loss of habitat and fragmentation is dependent upon both landscape (regional scale) and fragment (local scale) features, with the intrinsic ecological traits of the taxa also influencing said response (Turner, 2005); this in turn can influence the distribution of populations via widely acknowledged effects on habitat edge and connectivity i.e. the extent to which movement within a landscape is altered among habitats (Ries et al., 2004; Haddad et al., 2015; Fletcher et al., 2016).

Previous studies into the effects of habitat fragmentation on biodiversity have included surveys within landscapes that have been fragmented which contain remnants of different degrees of isolation, size and age (Braschler and Baur, 2016), as well as experiments that have artificially subdivided habitats which were formally continuous (Debinski and Hold, 2000). Fragmented landscapes can have an adverse effect on many different organisms within an ecosystem, such as falling plant population sizes as a result of declining habitat quality (Roque et al., 2017), a decrease in the diversity and population size of plant pollinators due to diminishing habitat connectivity and size (Xiao et al., 2016), declines in area-sensitive grassland bird populations because of habitat fragmentation (Herkert, 1994), and a decrease in small mammal species richness stemming from a reduction in patch area (Rubio et al., 2014). However, habitat

fragmentation does not necessarily have a universally negative influence on organisms; for example, small fragments of the Atlantic Forest in Northeast Brazil have a high conservation value for forest reptiles, perhaps as a result of low densities or the absence of top-predators (Lion et al., 2016). Recently, a meta-analysis on 35 years of habitat fragmentation experiments across several spatial scales revealed that both habitat loss and fragmentation have reduced biodiversity by between 13 and 75% in five continents (Haddad et al., 2015). The paper also suggested that there is a strong negative impact of habitat fragmentation which occurs at the ‘patch-scale’ i.e. via patch isolation and increased edge effects (Haddad et al., 2015). The prevalence of habitat edges, fragmentation and habitat loss are all inextricably linked, having potentially great implications for wildlife conservation and management (Desrochers et al., 2003), and in order to understand ecological responses to the presence of habitat edges, it is crucial to understand landscape-scale phenomena, such as the impacts of habitat fragmentation within a landscape mosaic (Murcia, 1995).

## **1.2 The Edge Effect and Edge Contrast**

One common consequence of habitat fragmentation is the increase in length of edge areas (Fynn and Campbell, 2018). Ecological edges are transitional zones or boundaries that occur between two adjacent land cover types or landscape patches (Cadenasso et al., 2003; Lindenmayer and Fischer, 2006). Edge effects are known to modify habitat quality within fragments, which will in turn affect the composition of species via habitat preferences (Braschler and Baur, 2016) due to the abiotic conditions that occur at habitat edges being substantially different from those found in either adjacent habitats; this may have a direct impact on the dynamics and spatio-temporal distribution of many species, as well as modifying species interactions (competition, pollination, seed dispersal, parasitism, predation and herbivory) (Murcia, 1995). These direct and indirect biotic and abiotic changes constitute collectively towards the so-called edge effect (Murcia, 1995). The edge effect hypothesis poses that diversity is greatest in ecotones (i.e. ‘edges’) compared to in the two adjacent habitats (Odum, 1971). Since edges between habitat patches are frequently ecologically distinct from patch interiors, an understanding of ecological patterns near edges is crucial to understand landscape-level dynamics, such as the impacts of habitat fragmentation (Ries et al., 2004). It is important to focus research on edge effects in order to understand the impacts of

fragmentation, as fragmentation leads to the greater extent and availability of edges (Fynn and Campbell, 2018).

Several reviews and studies define the existence of both primary and secondary responses due to the creation of forest edges (Murcia, 1995; Harper et al., 2005). Primary responses are direct consequences as a result of the creation of an edge (e.g. damage caused to trees and biogeochemical, microclimatic or physical changes) (Magrath et al., 2013). Secondary responses consist of changes in the reproduction, growth or mortality of forest dwelling species (Harper et al., 2005). The results from single edge studies (i.e. only one type of edge, such as between two habitat types) are commonly used to predict the results of a variable density or number of edges at a coarser or broader scale (e.g., predicting the effects that forest fragmentation has on the abundance of endangered forest-specialist species) (Porensky and Young, 2013). It is suggested by Ries and Sisk (2004, 2008) that the distributional patterns of organisms in habitat patches and in edges reflects abiotic conditions (e.g. light) and the distribution of resources (e.g. nesting sites, food); however, the availability of resources and abiotic conditions are also affected by the matrix contrast (Prass et al., 2017).

According to the landscape ecology theory, as the structural similarity between two adjacent habitats increases, the edge effect is less evident due to a less abrupt edge being created; therefore, ecological flows across adjacent edges may perhaps be enhanced by reduced abruptness or sharpness and uniformity of edges (López-Barrera et al., 2007). This leads to a concept known as edge contrast, which is described as the degree to which bordering patches are structurally different from one another (Ries and Sisk, 2004) in features of ecological significance (e.g. microclimate, vegetation density and height) (Prass et al., 2017). A 'hard edge', as defined by Duelli et al. (1990), is a type of boundary where, as an edge between two adjacent habitats is crossed, there is an abrupt change in a response variable, where an organism's response at an edge can strictly be explained by the behavior of the organism in the two juxtaposed habitat types (i.e. away from the edge) (López-Barrera et al., 2007). There are two main factors which underlie differences in edge contrast: different vegetation densities within the same type of edge and differences in the mean height of vegetation between adjacent patches which form the edge; differences in edge responses for both factors are likely due to differences in edge permeability, thus resulting in different rates of ecological flows (Ries et al., 2004). Of the many studies on the effects of habitat edges on various organisms, only a

few have investigated edge contrasts i.e. the influence of different types of habitat matrices on communities in adjacent habitat patches (Noreika and Kotze, 2012).

Most studies on edge contrast have not controlled for habitat quality on either side of an edge while varying edge contrast, which in turn makes it difficult to isolate the influence of edge contrast from that of habitat quality (Ries and Sisk, 2004). An example of this is in a study by Noreika and Kotze (2012). The aim of their study was to investigate whether edge contrasts (i.e. low-, intermediate-, and high-contrast) and the presence of carabid beetle prey and competitors had an influence on the carabid assemblage and individual carabid species within an urban setting; in order to achieve this, the study investigated carabid beetle responses to different edge contrasts of urban forest: high-contrast matrix (asphalt), intermediate-contrast matrix (meadows) and low-contrast (young forest) (Noreika and Kotze, 2012). For example, dryness and open habitat associated species would be expected to respond both more strongly and positively (in terms of the quantity of individuals that are caught), to high-contrast edges than low-contrast edges, while moisture associated and forest specialist species are expected to respond inversely (Noreika and Kotze, 2012). As the literature has demonstrated, the characteristics of edge effects and edge contrast have a profound effect on the overall impact of fragmentation on both habitats and organisms, and is of vital importance for future research in order to further understand the mechanisms of fragmentation.

### **1.3 The Importance of Functional Diversity in Ecosystem Functioning**

Ecosystem functioning is an essential aspect of biodiversity, and includes ecological and evolutionary processes such as the exchange of energy, information and matter (Noss, 1990); essentially, ecosystem functioning involves processes that are carried out within an ecosystem which can be compared and quantified across multiple systems, such as herbivory or net primary production (Barnes et al., 2018). Understanding how biodiversity influences ecosystem functioning and the distribution of services could lead to the sustainable supervision of biodiversity, for the development of regionally attuned systems, and for the reinforcement of ecosystem resilience and performance (Weisser et al., 2017). While declines in ecosystem function are often closely associated with the loss of biodiversity, ecosystem functioning can also be gained or lost in a manner that does not involve any changes to the amount of species richness (Spaak et al., 2017).

Spatio-temporal variation in species diversity and composition has the ability to influence ecosystem functioning via the dispersion of functional traits that are present in local communities (Mouillot et al., 2013). Ecological experiments, meta-analyses and reviews have demonstrated that functional diversity is one of the most efficient predictors of ecosystem functioning (Petchey and Gaston, 2006; Griffin et al., 2009).

Functional diversity is a factor of crucial importance in the determination of ecosystem processes (Diaz and Cabido, 2001), and is comprised of three major components: functional divergence, functional richness and functional evenness (Mason et al., 2005). Functional evenness is the measure of the distribution of species traits within an ecosystem, functional divergence is the measure of the maximum extent of divergence of the abundance distribution of functional traits in an ecosystem within an assemblage, and functional richness is a measure of the species occupying the extent of niche space within an assemblage (Mason et al., 2005; Villéger et al., 2008; Schleuter et al., 2010). Functional traits are classified as any measurable biological characteristic of an organism that may reflect the ecological niche in which they occupy and the interactions between both other organisms and the environment, which includes aspects of their behaviour, environmental tolerances, phenology, morphology, and ecology (Levin, 2000; Diaz and Cabido, 2001). In order to achieve a mechanistic understanding of the effects of biodiversity, the functional traits of species must be considered (Buchmann et al., 2002), especially considering that ecological communities which are functionally diverse are thought to be more resilient to disturbances (Peterson et al., 1998; Standish et al., 2014).

The functional diversity of invertebrates is directly relevant to the functioning of ecosystems, such as through pest control and pollination (Spake et al., 2016). There is a common assumption that the effects of habitat fragmentation may filter species with particular sets of traits, thus leading to trait convergence (Grime, 2006) and a decrease in functional diversity in highly fragmented forests (Sonnier et al., 2014); therefore the gaining of information from functional traits can be useful in providing an insight into the mechanisms which influence the response of arthropods to changes in the environment (Barton et al., 2011; Magura et al., 2017; Ng et al., 2018). Due to the fact that functional diversity decreases in highly fragmented forests (Sonnier et al., 2014), and edges increase as a result of fragmentation (Fynn and Campbell, 2018), edge

effects, and thus edge contrast, will have an impact on the role that invertebrates have on the functioning of ecosystems (Spake et al., 2016).

## **1.4 Forest Carabid Beetles as a Study Group**

Forest edges are becoming much more abundant across the globe in many regions due to the loss of forest as a result of human activity, including resource extraction, timber harvesting, agriculture, and settlement (Harper et al., 2005). Identifying the potential impact that forest edge creation has on the functioning and diversity of forest ecosystems is important for conservation and resource management (Razafindratsima et al., 2017) The behavior of animals near the edges of forests still remains poorly understood, despite the key role that forest edges have in our understanding and management of the edge effect (Desrochers et al., 2003). Forest edges differ from the interiors of forests with respects to microclimate, as well as nutrients and energy flows which may have a direct influence on the structure, function and composition of forest ecosystems which are adjacent to such edges (Murcia, 1995; Collinge, 1996; Anderson et al., 2003). These abiotic edge effects can have an indirect impact on wildlife through changes in habitat quality near edges (Brearily et al., 2010). The creation of edges results in a gradient of microclimatic gradients; forest edges experience higher wind speeds, greater temperature extremes, lower relative humidity and more solar radiation than the forest interior (Chen et al., 1995). Despite being frequent structural components of a landscape, forest edges also have important functions in regulating biological processes, such as invasibility and dispersal ability (Ries et al., 2004). Forest coverage has been fragmented and reduced as a result of clearing, which has vastly increased the area that is covered by novel anthropogenic forms of open habitat, such as suburbs, agriculture and pasture (Stone et al., 2018). Remnant forest patches then become encircled by high-contrast edges which are adjacent to the neighbouring open (matrix) areas, thus altering the physical conditions experienced by forest microhabitats near such edges, including a correlated risk of desiccation and increased disturbance by wind (Gascon et al., 2000).

Carabids (ground beetles) are well suited to studies of edge effects (and thus edge contrast), as their taxonomy and ecology are well known, they are abundant, diverse, and they are highly sensitive to changes in the characteristics of habitats (Lövei and Sunderland, 1996), as well as being able to be grouped into moisture affinity groups (e.g. indifferent, moisture-associated, dryness-associated) and habitat association groups

(such as generalists, forest specialists, and open-habitat specialists) (Noreika and Kotze, 2012). Carabids are often strongly habitat-specific and are highly mobile at the local scale (Jopp and Reuter, 2005), and are generally acknowledged as polyphagous predators (Kotze et al., 2011), as well as being excellent indicators for environmental monitoring due to their sensitivity to changes in environmental factors (Rainio and Niemelä, 2003). The way in which carabid beetles perceive space may influence the distributions and dynamics of populations, the dispersal of individuals, home ranges and habitat selection; furthermore, the extent, spatial arrangement and volume of suitable habitats (i.e. landscape configuration and composition) may influence the long-term persistence of populations (Kotze et al., 2011).

Edge contrast, or the harshness of an edge, plays a vital role in explaining the distribution patterns of carabid beetles belonging to different habitat affinity groupings (i.e. open habitat, generalist, forest-specialist) at forest edges (Noreika and Kotze, 2012), and therefore may explain the distribution of other invertebrates belonging to different functional groups. An “invisible barrier” is created for most carabid habitat specialists as a result of changes in environmental conditions at high-contrast matrices (hard edges) within such habitats, which diminishes their value as a habitat or as a potential corridor (Prass et al., 2017). Moisture changes that affect hygrophilous carabids are also likely to affect the surrounding vegetation, which could have an impact on the microclimate (Brooks et al., 2012). The results of the study by Noreika and Kotze (2012) found that forest carabid species *Amara brunnea*, *Pterostichus oblongopunctatus* and *Cychrus caraboides* were highly sensitive to high contrast edges at the edge, but increased rapidly in population size further into the forest patches, whereas *Patrobus atrorufus*, *Calathus micropterus* and moist forest species plainly avoided high contrast edges even further into forest patches, yet seem to be negatively less affected by low contrast edges (Noreika and Kotze, 2012). It is unclear as to why there is such a varied response (i.e. positive, neutral or transitional/negative edge response (Ries and Sisk, 2004)) by forest carabid species to distance from different types of edge, but it may be due to the dispersal capability of such species (Noreika and Kotze, 2012).

To understand patterns of biodiversity along environmental gradients, trait-specific responses are of greater importance than species abundance and competition, which are usually varied in accordance with environmental variables (Jung et al., 2018). Although

the primary determinants of the spatial distribution of carabid beetles may include biotic interactions and microhabitat conditions at the local scale, identifying general patterns of carabid beetle responses to landscape features may aid in understanding how functional groups, assemblages and species effectively distribute, and to predict how they cope with current and future climatic and land-use changes (Kotze et al., 2011).

Over the course of this literature review a clear knowledge gap has developed. Each topic that has been discussed is inextricably linked to one another: fragmentation leads to the presence of habitat edges (Fynn and Campbell, 2018), which in turn leads to the occurrence of edge effects, which are known to modify habitat quality within fragments, thus impacting species composition (and ultimately functional diversity) through habitat preferences (Braschler and Baur, 2016). Functional diversity decreases in highly fragmented forests (Sonnier et al., 2014), and due to the fact that highly fragmented forests have a greater extent and availability of habitat edges (Fynn and Campbell, 2018), functional diversity will also be affected by the edge effect. Functional diversity is a major driver of ecosystem processes (Diaz and Cabido, 2001; Mason et al., 2005), which in turn will influence ecosystem function (Mason et al., 2005). Invertebrates are especially important in the functioning of ecosystems, through processes such as pollination and pest control (Spake et al., 2016). This means that the impact of fragmentation is far reaching, as fragmentation can have an impact on an ecosystem all the way down to how it functions as a whole. As the literature has shown, it is of vital importance to understand how contrasting edges impact the functional diversity of invertebrates, as this in turn will create a better understanding of how functional diversity can be gained or lost as a result of habitat fragmentation, thus improving on previous research on the edge effect, as edge contrast is an aspect of edge effects, and ultimately achieving a greater understanding on the mechanisms of fragmentation.



## **2. Aims and Objectives**

The aim of this study is to identify how carabid functional groups react to differentially contrasting edges in order to understand the patterns and variability found in previous studies, thus explaining how functional diversity can be gained or lost as a result of fragmentation, and ultimately gaining a greater understanding of the mechanisms of habitat fragmentation and how organisms respond accordingly. The method to achieve this will first be to collect samples of carabid beetles and relevant biotic and abiotic variables in the field at various locations across a variety of edge contrasts. Then, a set of statistical analyses will be employed to evaluate hypothesised direct and indirect effects by examining which variables have the greatest influence on how carabid beetle functional groups react to differentially contrasting edges, thus identifying the factors which have the greatest effect on how functional groups effectively distribute in a region consisting of a variety of edge contrasts. In order to accomplish this aim, the following predictions will be tested by using carabid beetles as a case study:

- Functional diversity will be lowest at high-contrast edges due to abrupt changes in microhabitat conditions
- Shannon diversity will be greatest at the habitat edge and will decrease into the forest interior, in line with the edge effect hypothesis
- Certain biotic and abiotic drivers (such as canopy cover and soil moisture) will be of vital importance in determining the functional diversity of carabids
- There will be certain functional groups which are associated with a specific edge contrast i.e. open habitat carabid species will be associated with high-contrast edges due to high contrast edges being more open, hygrophilous carabid species will be associated with low-contrast edges due to a smooth gradient from one habitat type to the other preventing exsiccation etc.
- Dispersal ability (i.e. wing morphology) will be the functional trait which determines the distribution, diversity and composition of functional groups at differentially contrasting edges i.e. there will be a greater prevalence of apterous

or brachypterous carabid species at low-contrast edges in order to avoid predation due to a low dispersal ability.

## **3. Method**

### **3.1 Study Area and Site Description**

The study was carried out in Ringwood Forest, Hampshire, in Southern England. Ringwood Forest contains a variety of tree species, but is mainly dominated by Corsican pine (*Pinus nigra var. maritima*) and Scots pine (*Pinus sylvestris*), with such trees being situated on podsolic soils. Other tree species found in Ringwood Forest includes Monterey pine (*Pinus radiata*), Western hemlock (*Tsuga heterophylla*), Downy birch (*Betula pubescens*), Silver birch (*Betula pendula*) and Common alder (*Alnus glutinosa*). Overstorey canopy density is relatively uniform across all forest patches, with canopy density being lowest at the forest edge and greatest in the forest interior. A variety of other habitat types can be found in Ringwood Forest, such as heathland, mostly consisting of Ling heather (*Calluna vulgaris*), grassland, which is made up of several grass species, and shrubland, which is made up of common gorse (*Ulex europaeus*) and hawthorn (*Crataegus monogyna*). The understory of the forests contain several species, including a variety of grass species, Ling heather, bracken (*Pteridium aquilinum*) and ground ivy (*Glechoma hederacea*). Understorey canopy density differs across all sites, and is dependent on the density of bracken at each site. Sites which have a greater density of bracken have a greater understory canopy density than sites that have a lower density of bracken. The topography of Ringwood Forest undulates gently between 30 m and 50 m, with the average slope seldom exceeding 1:40. There are several localised sites within Ringwood Forest which are of interest for nature conservation, and are managed by conservation organisations such as the Herpetological Conservation Trust and the Dorset Wildlife Trust. This includes three sites which are designated as Sites of Nature Conservation Interest (SNCI) by the Dorset Wildlife Trust.

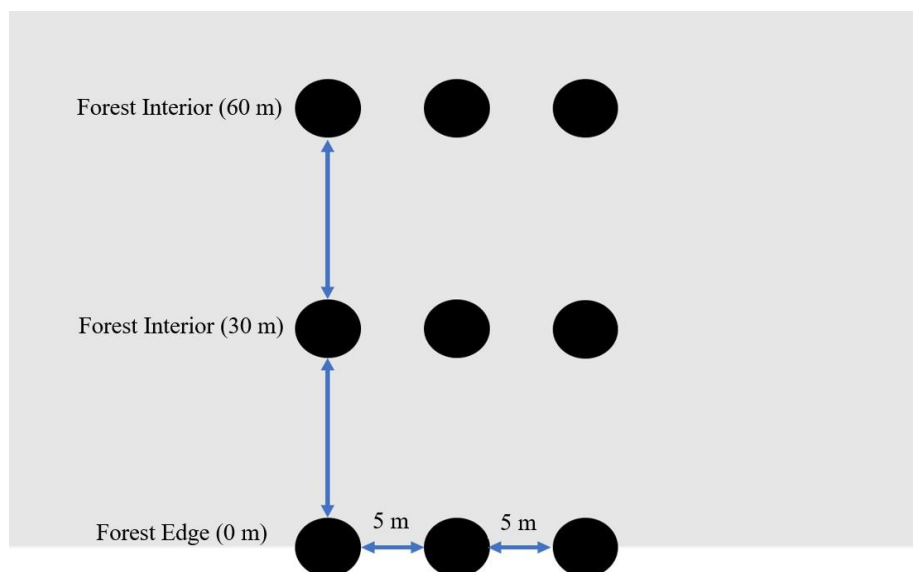
### **3.2 Study Design**

The following study design is informed by a preliminary sample collection phase (see Appendix). Three separate forest patches were selected within Ringwood Forest which were known to contain ground beetles, while also having little chance of disturbance from dogs, birds and members of the public. Another selection criteria, in order to

reduce the variability of results between forest patches, was to ensure that the same tree species were found in each forest patch: Corsican and Scots pine were the only tree species to be found in each forest patch, which were planted between 1970 and 1980. Each forest patch exhibited three different types of edge contrast: mature forest-young forest (low-contrast), mature forest-shrubland (intermediate-contrast) and mature forest-grassland (high-contrast). The three types of edge were selected based on the natural stages of succession towards mature forest i.e. grassland succeeds into shrubland, shrubland succeeds into young forest, then young forest succeeds into mature forest. Edges within this study were defined as an abrupt boundary between the mature forest and the surrounding matrix (i.e. young forest, shrubland and grassland). This therefore gave three spatial replicates of each edge contrast: three low-contrast edges (mature forest-young forest), three intermediate-contrast edges (mature forest-shrubland) and three high-contrast edges (mature forest-grassland).

Pitfall traps were placed along transects which were orientated perpendicular to the forest edge, with pitfall traps being set at the forest edge (0 m), then at 30 m and 60 m into the forest interior, thus representing one plot (Fig. 1). At each distance, three pitfall traps were set up 5 m apart. Three pitfall traps were installed to ensure that carabids can be collected at each distance, as carabids may avoid certain pitfall traps due to microhabitat conditions. This therefore gave 9 pitfall traps per transect (with 1 individual trap representing 1 site), 27 pitfall traps per forest patch, with 81 pitfall traps in total. In terms of each type of edge contrast, there were 27 pitfall traps in total over

Figure 1. Sampling design for the collection of carabids in Ringwood Forest; each black circle indicates a pitfall trap (thus representing one site) and the shaded area indicates regions of forest.



three spatial replicates: 27 mature forest-young forest pitfall traps, 27 mature forest-shrubland pitfall traps and 27 mature forest-grassland pitfall traps (Figure 2). Traps were set 30m apart in order to determine which biotic and abiotic factors determine the diversity and composition of carabid functional groups, as it is presumed that environmental variables will change over this distance. It should also be noted that due to the nature of the forest patches, it was not possible to have pitfall traps any further into the forest interior (i.e. 100 m), as this distance would be too close to another edge on the opposite side of a forest patch, thus not representing a true forest interior. Dense vegetation prevented pitfall traps being placed into the adjacent matrices (i.e. grassland, shrubs and young forest).

### **3.3 Carabid Beetle Sample Collection**

In order to collect carabid samples, pitfall traps were employed. The pitfall traps were unbaited and contained a solution of washing up liquid and water to preserve the samples and reduce the surface tension of the water to prevent the carabids from escaping, with samples being collected once a week to prevent desiccation. Stronger killing-preserving solutions, such as 70% ethylene glycol, were not permissible, as dog walkers are ubiquitous in Ringwood Forest, and ethylene glycol can be very harmful to dogs if ingested, hence why samples were collected weekly rather than monthly, as the beetles will become unidentifiable by this point. A 20 x 20 cm corrugated plastic sheet was placed 3 cm above each pitfall trap to protect the samples from rain and leaf litter. Sampling took place over a 9-week period, beginning in mid-June until the end of August. All carabids were identified to species level with the species identification key of Luff (2007). Carabid samples were pooled to the site for analysis (i.e. 81 data points, each with 9 weeks of carabid data).

### **3.4 Environmental Variables**

Environmental variables were selected based on how the environment will change between each edge type and between each distance into the forest interior i.e. to determine whether carabids react more strongly to the edge itself or to the gradient of environmental variables. All environmental variables which were collected can be found in Table 1.

Figure 2. The location of pitfall traps within Ringwood Forest at each type of edge contrast: mature forest-grassland (hard), mature forest-shrub (intermediate), mature forest-young forest (soft). Each white dot represents three pitfall traps (Refer to Figure 1 for the orientation of pitfall traps).



Table 1. Environmental variables which were collected in order to explain any variation in the functional diversity of carabids.

<b>Environmental Variable</b>	<b>Classification</b>	<b>Measurement</b>
Canopy cover	Continuous	%
Edge type	Categorical	3 categories
Ground vegetation percentage cover	Continuous	%
Ground vegetation type	Categorical	11 categories
Leaf litter depth	Continuous	Centimetres
Soil moisture	Continuous	%

Canopy cover, ground vegetation type and percentage cover, leaf litter depth and soil moisture were all collected for each individual pitfall trap. Canopy cover, leaf litter depth, ground vegetation type and percentage cover were recorded on the 17<sup>th</sup> July. Canopy cover was collected using a densiometer, with recordings being taken for each compass point (i.e. North, South, East, West) above each pitfall trap. Leaf litter depth was collected by placing a 1m by 1m quadrat over each pitfall trap, with the trap at the centre of the quadrat. Then, three random locations within the quadrat were used to record leaf litter depth by placing a ruler into the leaf litter, and recording the depth to the nearest 10 mm; these three values were then averaged to give a single total for leaf litter depth for each pitfall trap. Ground vegetation type (i.e. bare ground, bracken, dead wood, gorse, grass, hawthorn, heather, ivy, leaf litter, moss and young tree) and percentage cover was recorded by eye within a 1m by 1m quadrat, with the pitfall trap being at the centre of the quadrat.

Soil samples were taken on three separate occasions: 23<sup>rd</sup> July, 6<sup>th</sup> August and 20<sup>th</sup> August in order to account for the variation in rainfall across the length of the study period. In order to calculate the soil moisture at each pitfall trap, soil samples were taken into the lab. For each soil sample collected from each pitfall trap site, the soil was placed in a 50ml beaker, with the beaker being weighed before and after having soil placed inside the beaker. Then, all 81 beakers were placed in an oven for 48 hours at 105°C in order to remove all moisture from the soil. After the 48-hour period, the beakers were then weighed again to measure the amount of moisture that had been lost from the soil. The weight of the moisture lost was then divided by the weight of the soil without the beaker and then multiplied by 100 in order to give a percentage for the total

moisture content of the soil. This process was completed for all three of the soil sample collection dates and then average per pitfall trap.

### 3.5 Principle Selection of Carabid Functional Traits and Trait Data Collection

Functional traits were selected on an *a priori* basis using published literature (Table 2), within the constraints of the data which was available (Spake et al., 2016). Carabid functional traits were selected on the basis that such traits will be filtered by both the type of edge (i.e. edge contrast) and the distance from the edge i.e. certain traits may be associated to particular edge types and others may not appear until 30m or 60 m into the interior forest e.g. large, wingless carabid species may not be found at hard edges in order to avoid predation due to their visibility and low dispersal ability; xerophilous carabid species may be more prevalent at hard edges than other species due to their tolerance to low soil moisture levels etc.

Table 2. Carabid functional traits which were used to calculate carabid functional diversity.

Carabid Trait	Classification/Unit	Trait Category or Range	Data Source
Activity Pattern	Categorical	Diurnal/Nocturnal	(2),(4),(5),(6),(8)
Adult Feeding Guild	Categorical	Collembola Specialist/Generalist Predator/Phytophagous	(3),(4),(6),(8),(12),(15)
Adult Habitat Affinity	Categorical	Forest Generalist/Generalist/Open	(6),(7),(14)
Body Length	Continuous/mm	6.5-30	(9),(10)
Breeding Season	Categorical	Autumn/Spring/Spring and Summer/Summer and Autumn	(6),(8)
Hind-Wing Morphology	Categorical	Apterous or Brachypterous/Macropterous	(6),(9),(15)
Moisture Affinity	Categorical	Indifferent/Xerophilous	(6),(14)
Overwinter Type	Categorical	Adult Only/Adult or Larvae	(1),(8),(11),(13)

(1) Luff (1980); (2) Rijnsdorp (1980); (3) Forsythe (1982); (4) Loughridge and Luff (1983); (5) Mader et al. (1990); (6) Luff (1998); (7) Jukes et al. (2001); (8) Ribera et al. (2001); (9) Turin et al. (2003); (10) Luff (2007); (11) White et al. (2007); (12) Ward et al. (2011); (13) Jelaska et al. (2011); (14) Toïga et al. (2013); (15) Du Chatenet (2015).



## 3.6 Carabid Diversity Indices

### 3.6.1 Functional Diversity Calculation

Rao's quadratic entropy (Rao, 1982; Botta-Dukát, 2005) was used to calculate the functional diversity of carabids. It is a multiple trait functional diversity metric which describes the variation in the composition of species traits within a given community (Spake et al., 2016). Rao's functional diversity sums pairwise distances between species found within a community weighted by the relative abundance of each species (Spake et al., 2016). Rao's functional diversity is defined as:

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j$$

where  $p$  is the relative abundance vector of an  $S$ -species community,  $d_{ij}$  is the difference between the  $i$ -th and  $j$ -th species and  $FD_Q$  is an expression of the average difference between two individuals which were randomly selected with replacements (Rao, 1982; Botta-Dukát, 2005). Rao's functional diversity was computed in R 3.6.1 software (R Core Team, 2019) using the `rao.diversity` function (Rao, 1982; de Bello et al., 2007; Pillar et al., 2013) within the `SYNCSA` package (Debastiani and Pillar, 2012). The functional distances between the different species was calculated using Gower's distance metric within the `rao.diversity` function (Rao, 1982; de Bello et al., 2007; Pillar et al., 2013), which accommodates missing trait data, as well as allowing the use of a mixture of categorical, continuous and ordinal variables (Laliberte and Legendre, 2010; Sonnier et al., 2014). Rao's functional diversity has also been found to successfully identify the filtering patterns exhibited by different habitats (de Bello et al., 2009; Aubin et al., 2013). The functional diversity of all 81 pitfall trap sites was calculated individually to identify the patterns exhibited by the type of edge contrast and distance from the forest edge.

### 3.6.2 Shannon Diversity Calculation

In order to have a comparison between diversity indices, the Shannon diversity index, which is one of the most commonly used phylogenetic diversity indices in ecology (Colwell, 2009), was incorporated into the statistical analyses. The Shannon diversity index can calculate total species richness and abundance for a community in a single measure (Colwell, 2009) and is based on the percentage composition exhibited by different species (Peet, 1975). The Shannon diversity index is defined as:

$$H = - \sum_{i=1}^S p_i \ln p_i$$

where  $p_i$  is the proportional abundance of species  $i$  in a community of  $S$  species (Fisher et al., 1943; Hurlbert, 1971). Shannon diversity was calculated in R 3.6.1 software (R Core Team, 2019) using the diversity function (Fisher et al., 1943; Hurlbert, 1971) within the vegan package (Oksanen et al., 2019). The Shannon diversity of all 81 pitfall trap sites was calculated individually to identify the patterns exhibited by the type of edge contrast and distance from the forest edge, while also providing a means of comparison against functional diversity.

## 3.7 Statistical Analyses

### 3.7.1 Carabid Functional Trait Associations with Edge Contrast and Edge Distance

To identify which carabid functional traits are associated with each type of edge contrast and distance from the edge, a series of Kruskal-Wallis tests were performed. Such tests were carried out for each functional trait at each edge contrast type and edge distance. This was performed using the `kruskal.test` function within the stats package (R Core Team, 2019). A series of graphs were created also created to accompany these calculations. One graph depicts the occurrence of carabid species at each different edge type (i.e. hard, intermediate, soft), with species on the x-axis, and species abundance on the y-axis. A separate graph depicts the occurrence of carabid species at each distance from the edge (i.e. 0m, 30m, 60m), with species on the x-axis, and species abundance

on the y-axis. A table displaying the functional traits of each carabid species was also produced to accompany these graphs to identify which functional traits are associated with each type of edge contrast and distance from the edge. Any dominant carabid species were removed from these graphs, as such species skew the scale of the y-axes, thus making it difficult to identify which functional traits are associated with each type of edge contrast and distance from the edge for other, less frequently caught species.

### **3.7.2 Drivers of Carabid Functional Diversity and Shannon Diversity**

All statistical analyses were calculated in R 3.6.1 software (R Core Team, 2019). In order to evaluate the effects of environmental variables (see Table 1) on the functional diversity and Shannon diversity of carabids, linear mixed-effects models were employed. The main reason for implementing the use of linear mixed-effects models is to integrate a dependency structure into the model, thusly obtaining improved standard errors for the regression parameters compared with those produced by linear regression models (Zuur et al., 2013). Linear mixed-effects models were computed using the lmer function within the lme4 package (Bates et al., 2015). In the fixed effects portion of the global linear mixed-effects models, canopy cover, edge distance, edge type, leaf litter depth and soil moisture were included as factors and modelled as functions of the functional diversity and Shannon diversity of carabids in two separate models. In the random effects portion of the global linear mixed-effects models, plot (i.e. forest patch) was included as a factor, since pitfall traps found within a particular forest patch were expected to produce similar results and therefore cannot be considered truly independent (Spake et al., 2016). The residuals of both models were then inspected to ensure there were not any signs of non-linearity or heteroskedasticity (see Appendix). All potential models were constructed using the model.avg function (Burnham and Anderson, 2002; Lukacs et al., 2010), which allows for the comparison of models based on Akaike's Information Criterion with small-sample correction (AICc) (Burnham and Anderson, 2004) within the MuMIn package (Barton, 2019). Only models with substantial support (i.e. with a  $\Delta AICc$  value which is less than 2) (Burnham and Anderson, 2004) were included within the results. The r.squaredGLMM function (Nakagawa and Schielzeth, 2013; Johnson, 2014) within the MuMIn package (Barton, 2019) was used to determine the goodness of fit of each potential model (marginal  $R^2$ ).

In order to identify the relationship between ground vegetation and carabid functional diversity, the `cor.test` function (Hollander and Wolfe, 1973; Best and Roberts, 1975) within the `stats` package (R Core Team, 2019) was used to calculate a Spearman's rho value for each ground vegetation type, as each variable violated parametric assumptions.

### **3.7.3 Power Analysis**

A power analysis was run in order to determine the minimum sample size required to collect significant results. This was performed using the `samplesize_mixed` function (Cohen, 1988; Hsieh et al., 2003; Snijders, 2005) within the `sjstats` package (Lüdecke, 2019). Within the function, the number of cluster groups were set to 3 (i.e. number of plots) and the number of observations per cluster group were set to 27 (i.e. 9 pitfall traps for each of the three types of edge contrast). The effect size was set after the initial statistical analyses, as this value was determined based on the strength of the model(s).

## 4. Results

In total over the course of this study, 1410 individuals of carabids from 9 different species and 5 different genera were encountered: *Abax parallelepipedus*, *Amara aenea*, *Carabus arvensis*, *Carabus problematicus*, *Carabus violaceus*, *Harpalus rufipes*, *Pterostichus madidus*, *Pterostichus melanarius* and *Pterostichus niger*. The number of individuals which were caught varied from week to week, with values ranging from 228 individuals in week one to 111 individuals in week five (Fig. 3). The number of individuals caught per pitfall trap ranged from 1 to 67, with 17 individuals being encountered on average per trap. Temporal variation did seem to have an influence over some of the results (Fig. 4), as no *P. niger* individuals were caught before week three, no *A. aenea* individuals were caught after week four, no *H. rufipes* individuals were caught after week six, and no *C. arvensis* individuals were caught after week seven (Fig. 4).

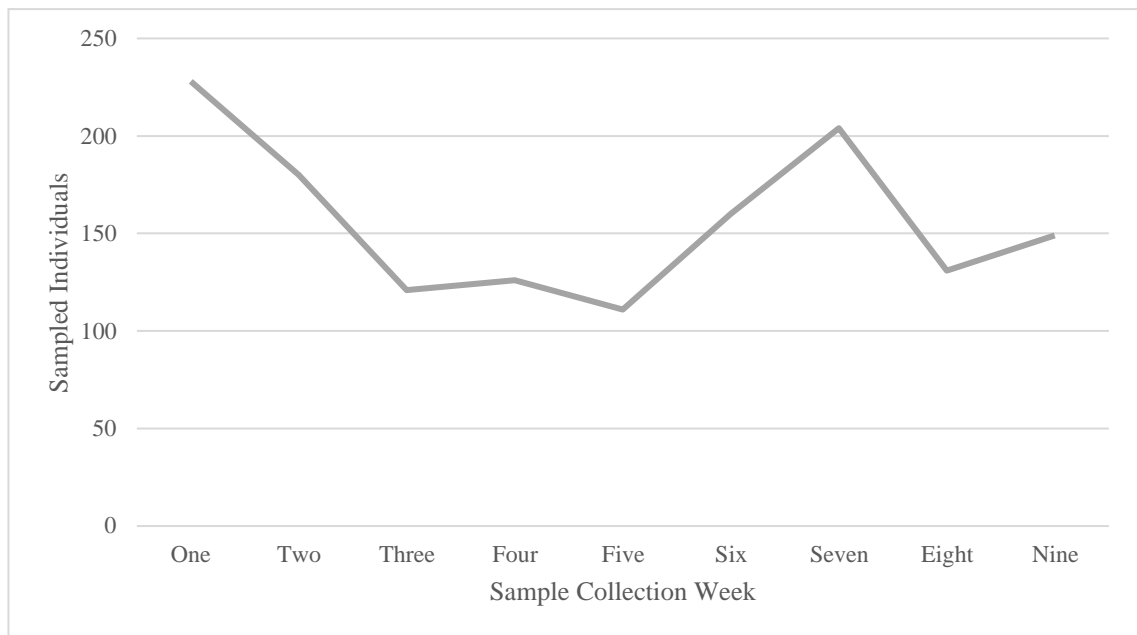


Figure 3. Weekly variation in the number of carabid individuals collected from pitfall traps over a nine-week period.

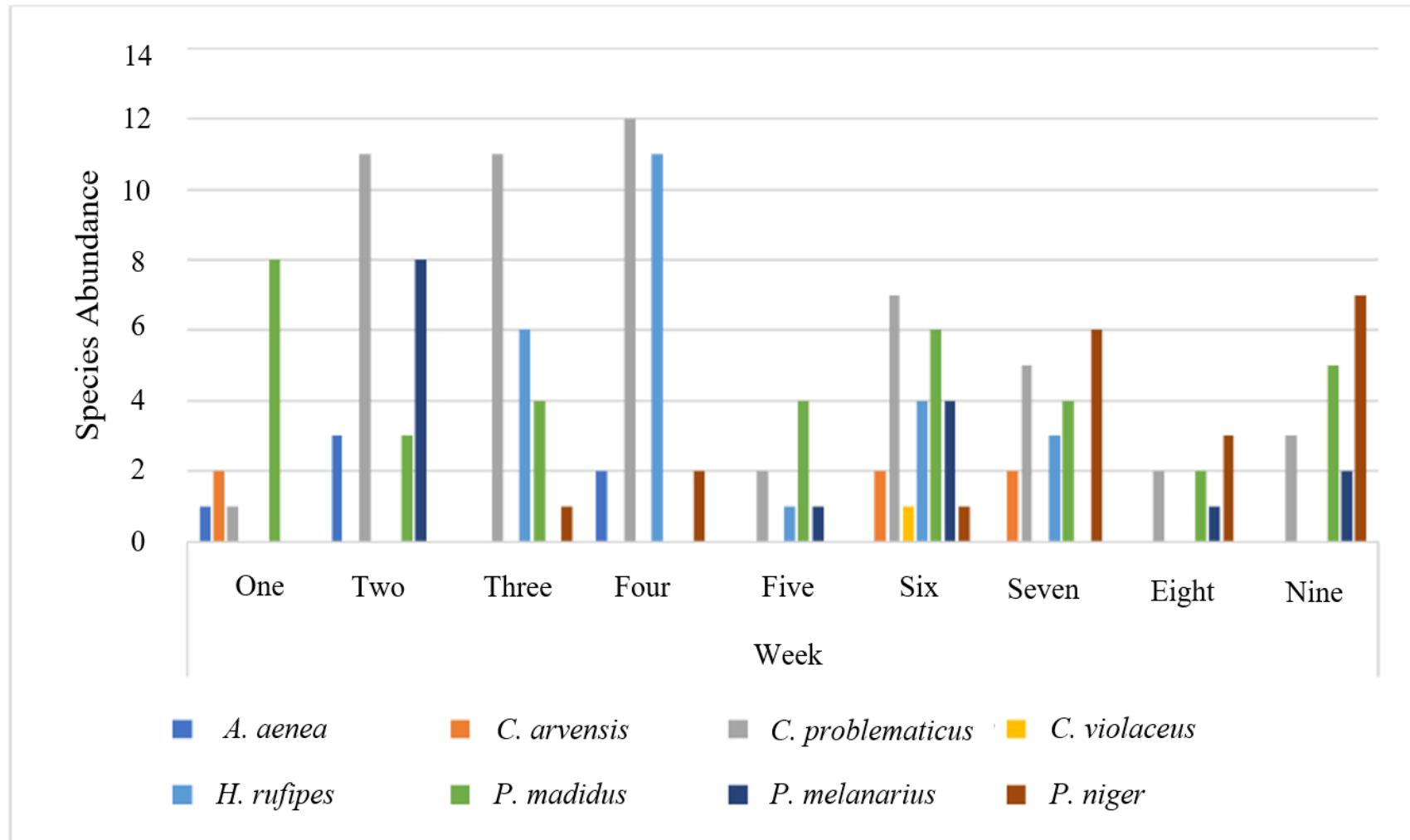


Figure 4. Species abundance of eight carabid beetle species across a nine-week study period. *A. parallelepipedus* were removed from this graph, as their abundance ranged from 101 to 228 individuals across all nine weeks, which would expand the y-axis of the graph making the other species abundances ineligible.

## 4.1 The Influence of Edge Contrast and Edge Distance on the Functional Diversity of Carabids

The results of the Kruskal-Wallis tests to identify the influence of edge contrast and edge distance on the functional diversity of carabids were not significant, with  $p$ -values of 0.065 and 0.281 respectively (Table 3).

Table 3. Kruskal-Wallis tests to identify the influence of edge contrast and edge distance on the functional diversity of carabids.

Variable	Chi-Squared	Degrees of Freedom	$P$
Edge Contrast	5.452	2	0.065
Edge Distance	2.539	2	0.281

When the functional diversity (Rao's quadratic entropy) of carabids was plotted against both edge contrast type and edge distance, a relationship seems to be apparent (Fig. 5). The graph shows that carabid functional diversity is greatest at the forest edge (0 m) and lowest at 60 m into the forest interior for both hard and intermediate edges. It was predicted that functional diversity would in fact be lowest at high-contrast edges (i.e. hard edges), therefore this result contradicts this hypothesis. For soft edges, carabid functional diversity is greatest at 60 m into the forest interior and lowest at 30 m into the forest interior. There were different degrees of variance for each edge contrast type and edge distance based on 95% confidence intervals. Variance was greatest for both hard and intermediate edges at the forest edge (0 m). Variance was relatively uniform across all edge distances for soft edges. The highest individual level of carabid functional diversity is at the forest edge (0 m) for hard edges, with a ( $FD_Q$ ) of 0.22. The lowest individual level of carabid functional diversity was at 30m into the forest interior at soft edges, with a ( $FD_Q$ ) of 0.06.

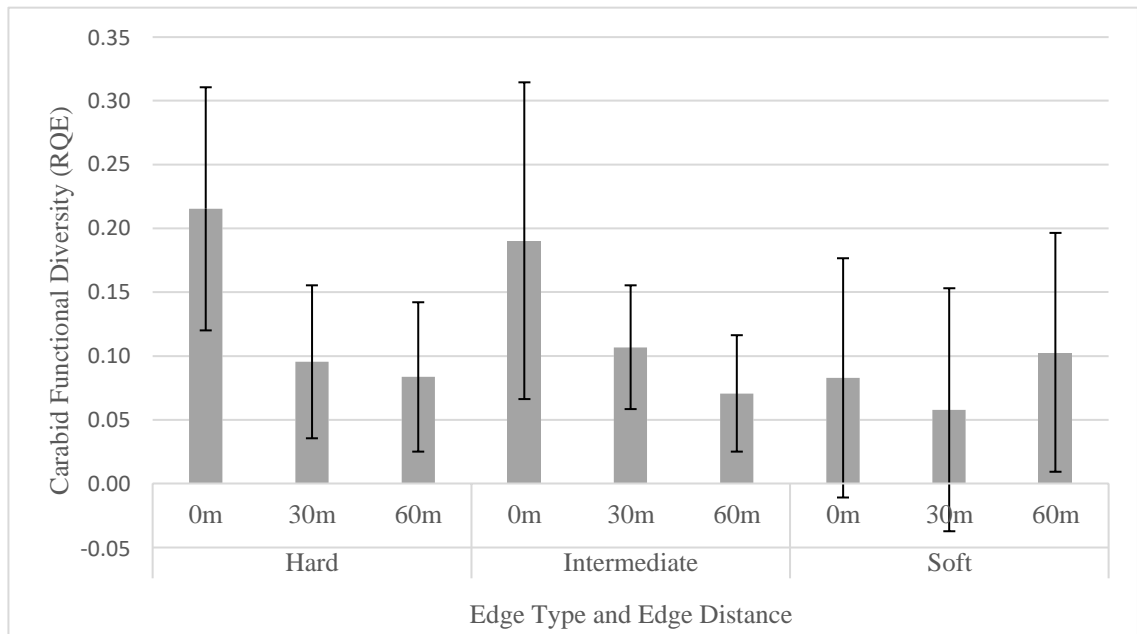


Figure 5. Mean values of carabid functional diversity calculated using Rao's Quadratic Entropy (Rao, 1982; Botta-Dukát, 2005) (RQE) with 95% confidence intervals plotted at each edge type (hard, intermediate, soft) and at each edge distance into the forest interior (0m, 30m, 60m).

## 4.2 The Influence of Edge Contrast and Edge Distance on the Shannon Diversity of Carabids

The results of the Kruskal-Wallis test to identify the influence of edge contrast on the Shannon diversity of carabids were significant, with a  $p$ -value of  $< 0.001$  (Table 4). The results of the Kruskal-Wallis test to identify the influence of edge distance on the Shannon diversity of carabids were not significant, with a  $p$ -value of 0.822 (Table 4).

Table 4. Kruskal-Wallis tests to identify the influence of edge contrast and edge distance on the Shannon diversity of carabids.

Variable	Chi-Squared	Degrees of Freedom	$P$
Edge Contrast	32.8	2	$< 0.001$
Edge Distance	0.392	2	0.822

The greatest individual carabid Shannon diversity index value (1.04) was at hard edges at the forest edge (0 m); however, this point also had the greatest level of variance with 95% confidence intervals (Fig. 6). The Shannon diversity of carabids showed a similar distribution of values to that of the functional diversity of carabids, i.e. diversity is greatest at the forest edge (0 m) and decreases further into the forest interior (30 m, 60 m). When the mean Shannon diversity index value was taken across all edge distances (0 m, 30 m, 60 m) for each edge type (hard, intermediate, soft), there was only a



difference of 0.02 between all edge types: 0.60 at hard edges, 0.61 at intermediate edges and 0.59 at soft edges.

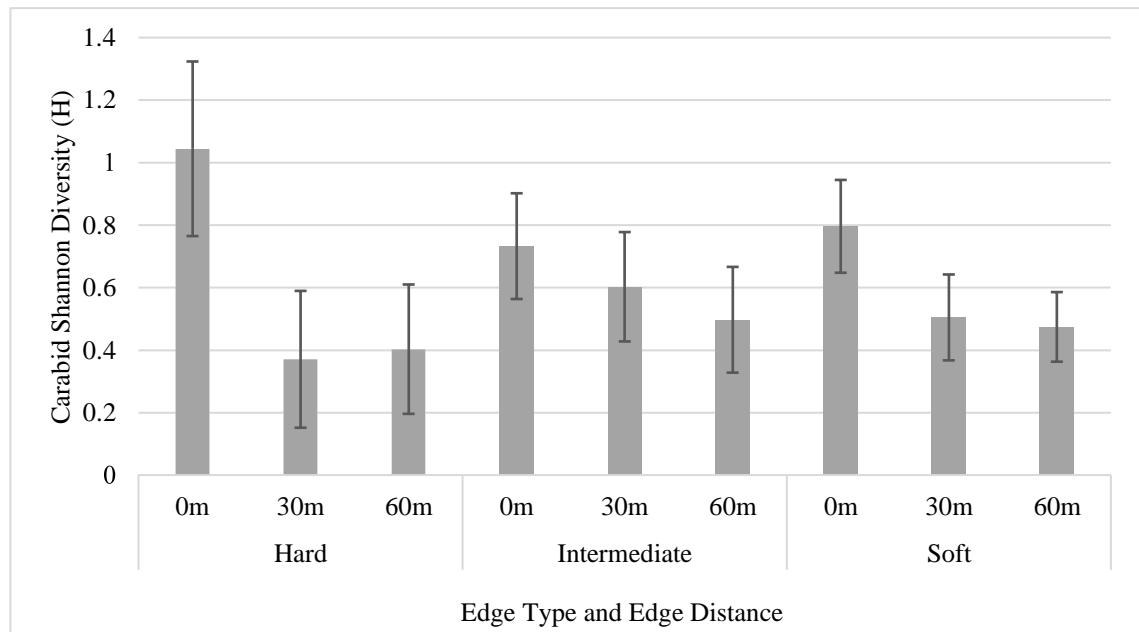


Figure 6. Mean values of carabid Shannon diversity with 95% confidence intervals plotted at each edge type (hard, intermediate, soft) and at each edge distance into the forest interior (0 m, 30 m, 60 m).

### 4.3 Edge Contrast Functional Trait Associations

Trait data for all carabid species can be found in Table 5. The occurrence of all carabid species differed between each type of edge contrast (Fig. 7). *A. parallelepipedus*, the dominant species collected in this study, were removed from the edge type species occurrence graph, with 469, 555 and 218 individuals being sampled at hard, intermediate and soft edges respectively, which would expand the y-axis values, thus making it difficult to identify the species abundances of other, lesser caught species. The results of the Kruskal-Wallis tests on the abundance of carabid functional traits at each edge contrast type (hard, intermediate, soft) were not significant (Table 6). It was predicted that certain functional groups would be present at specific edge contrasts, therefore this result contradicts this hypothesis.

Minimum and maximum size did not influence the occurrence of most carabid species at different edge types, as species of varying minimum and maximum sizes were sampled at each edge type. Both diurnal species, *A. aenea* and *C. arvensis*, were mainly sampled at hard edges, whereas nocturnal species could be sampled at each type of edge. Most species sampled within this study were generalist predators, and were

Table 5. Carabid species functional trait data. Refer to Table 2 in Method for references.

Species	Min Size (mm)	Max Size (mm)	Activity Pattern	Adult Feeding Guild	Adult Habitat Affinity	Breeding Season	Hind-Wing Morphology	Moisture Affinity	Overwinter Type
<i>A. parallelepipedus</i>	17.0	22.0	Nocturnal	Generalist Predator	Forest Generalist	Spring and Summer	Apterous or Brachypterous	Indifferent	Adult Only
<i>A. aenea</i>	6.5	8.8	Diurnal	Phytophagous	Open	Spring	Macropterous	Indifferent	Adult Only
<i>C. arvensis</i>	18.0	28.0	Diurnal	Collembola Specialist	Open	Spring	Apterous or Brachypterous	NA	Adult Only
<i>C. problematicus</i>	20.0	28.0	Nocturnal	Generalist Predator	Generalist	Spring and Summer	Apterous or Brachypterous	NA	Adult Only
<i>C. violaceus</i>	20.0	30.0	Nocturnal	Generalist Predator	Forest Generalist	Autumn	Apterous or Brachypterous	Indifferent	Adult or Larvae
<i>H. rufipes</i>	11.0	16.0	Nocturnal	Generalist Predator	Open	Summer and Autumn	Macropterous	Indifferent	Adult or Larvae
<i>P. madidus</i>	14.0	18.0	Nocturnal	Generalist Predator	Open	Spring	Apterous or Brachypterous	Indifferent	Adult or Larvae
<i>P. melanarius</i>	13.0	17.0	Nocturnal	Generalist Predator	Open	Spring	Apterous or Brachypterous	Xerophilous	Adult or Larvae
<i>P. niger</i>	16.0	21.0	Nocturnal	Generalist Predator	Forest Generalist	Autumn	Macropterous	Indifferent	Adult or Larvae

sampled at each type of edge. Both of the species that were not generalist predators, *A. aenea* and *C. arvensis*, which are phytophagous and collembola specialists respectively, were mainly sampled at hard edges.

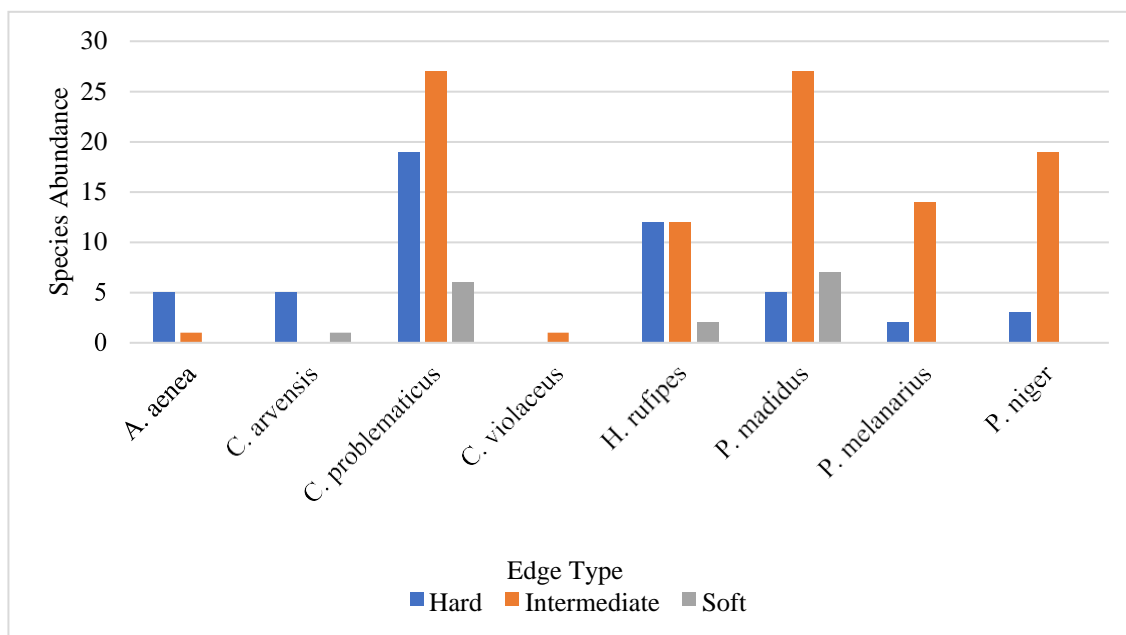


Figure 7. Species abundances of all carabid species (excluding *A. parallelepipedus*) at hard, intermediate and soft edges.

Table 6. Kruskal-Wallis tests on the association of carabid functional traits with each edge contrast type (hard, intermediate, soft).

Functional Trait	Hard			Intermediate			Soft		
	Chi-Squared	d.f.	<i>P</i>	Chi-Squared	d.f.	<i>P</i>	Chi-Squared	d.f.	<i>P</i>
Min. Size	5.58	6	0.472	2.86	6	0.827	3.87	5	0.568
Max. Size	5.15	6	0.524	2.87	6	0.825	3.29	5	0.655
Activity Pattern	4.57	6	0.600	5.43	6	0.490	4.14	5	0.529
Adult Feeding Guild	0.00	6	1.000	6.00	6	0.423	5.00	5	0.416
Adult Habitat Affinity	8.00	6	0.238	5.17	6	0.523	3.83	5	0.573
Breeding Season	8.00	6	0.238	6.15	6	0.407	6.67	5	0.247
Hind-Wing Morphology	5.69	6	0.459	5.01	6	0.543	4.88	5	0.431
Moisture Affinity	5.97	6	0.427	6.48	6	0.372	3.68	5	0.597
Overwinter Type	5.60	6	0.470	4.40	6	0.623	5.3	5	0.380

Three species sampled within this study were forest generalists: *A. parallelepipedus*, *C. violaceus* and *P. niger*. *A. parallelepipedus* were sampled at all edge types, but were mainly sampled at hard and intermediate edges. Only one *C. violaceus* individual was collected in this study, which was sampled at an intermediate edge. *P. niger* were sampled at both hard and intermediate edges, but were mainly sampled at intermediate edges. *C. problematicus* were the only habitat generalist species sampled within this study, and were sampled at all edge types, but mainly occurred at intermediate and hard edges. All of the final five species, *A. aenea*, *C. arvensis*, *H. rufipes*, *P. madidus* and *P. melanarius* were open habitat species. Both *A. aenea* and *C. arvensis* were mainly sampled at hard edges, *H. rufipes* were sampled at all edge types, but mainly hard and intermediate edges, *P. madidus* were sampled at all edge types, but mainly at intermediate edges, and *P. melanarius* were mainly sampled at intermediate edges.

Breeding season did not influence the distribution of carabid species at different edge types, as species with each breeding season (Spring, Summer and Autumn) were sampled at each edge type. Three species sampled within this study were macropterous (i.e. having fully formed wings): *A. aenea*, *H. rufipes* and *P. niger*. *A. aenea* were mainly sampled at hard edges, *H. rufipes* were sampled at all edge types, but mainly at hard and intermediate edges, and *P. niger* were sampled mainly at intermediate edges; therefore, macropterous species were sampled mainly at hard and intermediate edges. The other six species sampled within this study were apterous or brachypterous (i.e. reduced hind-wings). These species were sampled at all edge types; therefore, a lack of wings did not seem to influence the distribution of carabid species at different edge types. It was predicted that there would be a greater prevalence of apterous or brachypterous species at soft edges in order to avoid predation; however, this result contradicts that hypothesis. All species, except *P. melanarius*, were indifferent to soil moisture content, and were sampled at all edge types. *P. melanarius* is xerophilous (i.e. adapted to dry climates), and were sampled mainly at intermediate edges. Overwinter type did not influence the distribution of carabids at different edge types, as species from both overwinter types (adult only and adult and larvae) were sampled at all edge types.

#### 4.4 Edge Distance Functional Trait Associations

The occurrence of all carabid species differed between each distance from the edge (Fig. 8). *A. parallelepipedus*, the dominant species collected in this study, were removed from the edge distance species occurrence graph, with 235, 470 and 537 individuals being sampled at 0 m, 30 m and 60 m from the edge respectively, which would expand the y-axis values, thus making it difficult to identify the species abundances of other, lesser caught species. The results of the Kruskal-Wallis tests on the abundance of carabid functional traits at each distance (0 m, 30 m, 60 m) were not significant (Table 7).

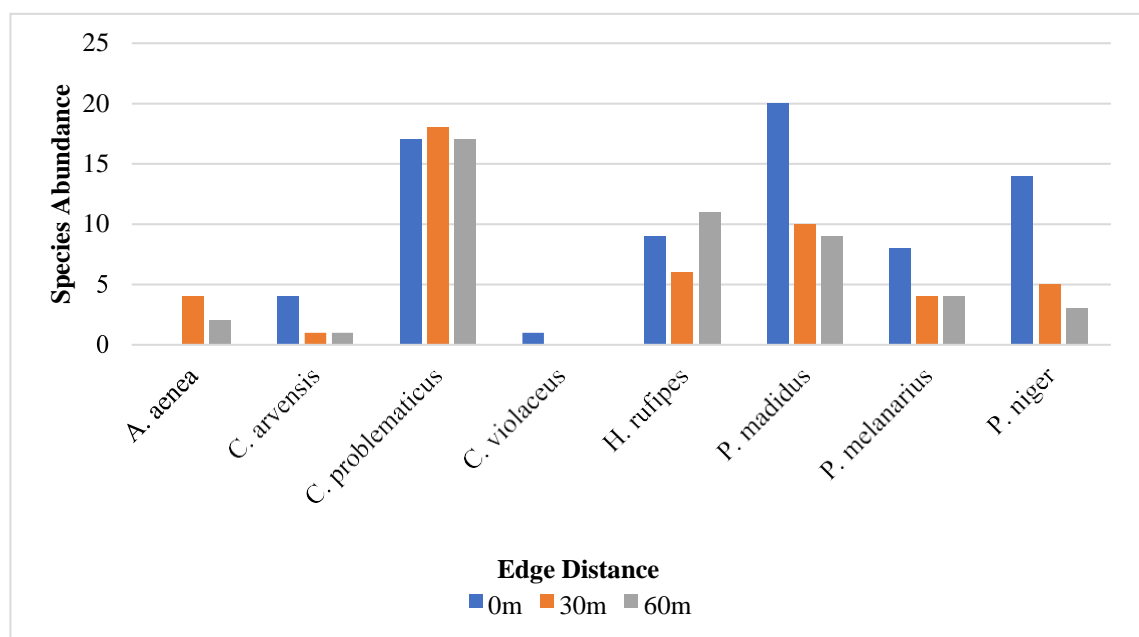


Figure 8. Species abundances of all carabid species (excluding *A. parallelepipedus*) at each distance into the forest interior: 0m, 30m and 60m.

Minimum and maximum size did not influence the occurrence of carabid species at different distances from the edge, as species of varying minimum and maximum sizes were sampled at each distance from the edge. Activity pattern did not seem to influence the occurrence of carabid species at different distances from the edge, as species of both diurnal and nocturnal activity patterns were sampled at each distance from the edge. Most species sampled within this study were generalist predators, and were sampled at each distance from the edge. *A. aenea*, which are phytophagous, were not sampled at the forest edge (0 m) at all, and were mainly sampled at 30m into the forest interior. *C. arvensis*, which are collembola specialists, were sampled at all edge distances, but were mainly sampled at the forest edge.

Table 7. Kruskal-Wallis tests on the association of carabid functional traits with each distance from the forest edge (0 m, 30 m, 60 m).

Functional Trait	0 m			30 m			60 m		
	Chi-Squared	d.f.	P	Chi-Squared	d.f.	P	Chi-Squared	d.f.	P
Min. Size	8.00	8	0.434	7.73	7	0.357	8.00	8	0.434
Max. Size	8.00	8	0.434	7.73	7	0.357	8.00	8	0.434
Activity Pattern	8.00	8	0.434	6.00	7	0.540	8.00	8	0.434
Adult Feeding Guild	8.00	8	0.434	7.52	7	0.376	8.00	8	0.434
Adult Habitat Affinity	8.00	8	0.434	5.43	7	0.608	8.00	8	0.434
Breeding Season	8.00	8	0.434	8.00	7	0.333	8.00	8	0.434
Hind-Wing Morphology	8.00	8	0.434	5.12	7	0.645	8.00	8	0.434
Moisture Affinity	8.00	8	0.434	8.00	7	0.333	8.00	8	0.434
Overwinter Type	8.00	8	0.434	6.20	7	0.517	8.00	8	0.434

Three species sampled within this study were forest generalists: *A. parallelepipedus*, *C. violaceus* and *P. niger*. *A. parallelepipedus* were found at all edge distances, but were mainly sampled at 30 m and 60 m into the forest interior. Only one *C. violaceus* individual was collected in this study, and was sampled at the forest edge. *P. niger* were sampled at all edge distances, but were mainly sampled at the forest edge. *C. problematicus* were the only habitat generalist species sampled within this study, and were sampled at all edge distances. All of the final five species, *A. aenea*, *C. arvensis*, *H. rufipes*, *P. madidus* and *P. melanarius* were open habitat species. *A. aenea* were sampled mainly at 30 m into the forest interior, *C. arvensis* were sampled at all edge distances, but were mainly sampled at the forest edge, *H. rufipes* were sampled at all edge distances, *P. madidus* were sampled at all edge distances, but were mainly sampled at the forest edge, and *P. melanarius* were sampled at all edge distances, but were mainly sampled at the forest edge.

Breeding season did not influence the occurrence of carabids at different edge distances, as species with each breeding season (Spring, Summer and Autumn) were sampled at each edge distance. Three species sampled within this study were macropterous (i.e. having fully formed wings): *A. aenea*, *H. rufipes* and *P. niger*. *A. aenea* were sampled mainly at 30m into the forest interior, *H. rufipes* were sampled at all edge distances, and

*P. niger* were sampled mainly at the forest edge; therefore, macropterous species were sampled mainly at the forest edge. The other six species sampled within this study were apterous or brachypterous (i.e. reduced hind-wings). These species were sampled at all edge distances; therefore, a lack of wings did not seem to influence the distribution of carabid species at different edge distances. All species, except *P. melanarius*, were indifferent to soil moisture content, and were sampled at all edge distances. *P. melanarius* is xerophilous (i.e. adapted to dry climates), and were sampled mainly at the forest edge. Overwinter type did not influence the distribution of carabids at different edge distances, as species from both overwinter types (adult only and adult and larvae) were sampled at all edge distances.

#### 4.5 The Influence of Environmental Variables on the Functional Diversity of Carabids

Based on model selection, none of the variables included within the linear mixed-effects models of the functional diversity of carabids have any explanatory importance (Tables 8 and 9).

Table 8. Linear mixed-effects models of the functional diversity of carabids, calculated using Rao's quadratic entropy ( $FD_Q$ ). Only the null model showed substantial support i.e. a  $\Delta AICc$  less than 2 (Burnham and Anderson, 2004). Global model is included for reference.

Model	Fixed variables included in model	df	$\Delta AICc$	AICc Weight	Marginal R <sup>2</sup>
Null		3	0.00	0.83	0.00
Global	Edge Type + Edge Distance + Canopy + Soil + Leaf Litter	9	53.97	0.00	0.09

The only linear mixed-effects model of carabid functional diversity which showed substantial support with a  $\Delta AICc$  less than 2 (Burnham and Anderson, 2004) was the null model, which contained no explanatory variables (Table 8). The null model has a marginal R<sup>2</sup> of 0.00 and the global model has a marginal R<sup>2</sup> of 0.09. None of the variables contained a  $p$ -value less than 0.05, implying that none of the variables have a significant effect on the functional diversity of carabids (Table 9).

Table 9. Full model-averaged parameter estimates, standard errors and *p*-values for the variables included in the linear mixed-effects models of the functional diversity of carabids.

<b>Variable</b>	<b>Parameter Estimate</b>	<b>Standard Error</b>	<b><i>P</i></b>
Intercept	0.618	0.521	0.236
Canopy Cover	-0.121	0.080	0.684
Leaf Litter Depth	-0.024	0.050	0.971
Edge Distance	-0.018	0.019	0.946
Soil Moisture	0.009	0.023	0.976
Hard Edge	-0.061	0.124	0.971
Intermediate Edge	-0.012	0.081	0.991
Soft Edge	-0.020	0.139	0.969

The results of the Spearman's rank correlation coefficient calculations on the relationship between ground vegetation and carabid functional diversity found no significance (at  $p < 0.05$ ) (Table 10). There was therefore no evidence for rejecting the null hypothesis (i.e. that ground vegetation has an influence on the functional diversity of carabids).

Table 10. Spearman's rank correlation coefficient calculations on the relationship between the functional diversity of carabids and ground vegetation based on each type of ground vegetation and their relative percentage covers.

<b>Vegetation Type</b>	<b>Spearman's Rho</b>	<b><i>P</i></b>
Bare Ground	0.28	0.47
Bracken	0.24	0.53
Dead Wood	0.05	0.89
Gorse	0.35	0.36
Grass	0.05	0.90
Hawthorn	0.36	0.34
Heather	-0.39	0.29
Ivy	0.38	0.32
Leaf Litter	-0.08	0.83
Moss	-0.37	0.33
Young Tree	0.20	0.61

#### **4.6 The Influence of Environmental Variables on the Shannon Diversity of Carabids**

Based on model selection, edge type (hard, intermediate, soft) was the most important variable within the linear mixed-effects models of the Shannon diversity of carabids (Tables 11 and 12).



Table 11. Linear mixed-effects models of the Shannon diversity of carabids, calculated using the Shannon diversity index. Only one model showed substantial support i.e. a  $\Delta\text{AICc}$  less than 2 (Burnham and Anderson, 2004). Global and null models are included for reference.

Model	Fixed variables included in model	df	$\Delta\text{AICc}$	AICc Weight	Marginal $R^2$
1	Edge Type	5	0.00	0.95	0.32
Global	Edge Type + Edge Distance + Canopy + Soil + Leaf Litter	9	41.84	0.00	0.35
Null		3	43.07	0.00	0.00

The only linear mixed-effects model of the Shannon diversity of carabids which showed substantial support with a  $\Delta\text{AICc}$  less than 2 (Burnham and Anderson, 2004) contained edge type as the only explanatory variable. The model containing edge type as the only fixed effect has a marginal  $R^2$  of 0.32. No other fixed effect was included in a model which had a  $\Delta\text{AICc}$  value less than 2.

Table 12. Full model-averaged parameter estimates, standard errors and  $p$ -values for the variables included in the linear mixed-effects models of the Shannon diversity of carabids.

Variable	Parameter estimate	Standard error	$P$
Intercept	2.988	0.494	<0.002
Soft Edge	-1.790	0.763	<0.002
Hard Edge	-1.226	0.765	<0.002
Intermediate Edge	-0.565	0.759	0.007
Soil Moisture	0.031	0.061	0.891
Leaf Litter Depth	0.059	0.023	0.921
Canopy Cover	0.006	0.066	0.995
Edge Distance	-0.002	0.018	0.994

## 4.7 Power Analysis

Based on the results of the power analysis, the sample size of this study was too small. When the effect size of the model was set to 0.5, the power analysis returned the findings that in order to find a significant result, there should be 98 subjects per cluster (i.e. per forest patch), with a total sample size of 293 pitfall traps. These values are 3.63 times greater than the sample size included within this study.

## **5. Discussion**

The results of this study have shown that carabid functional diversity and Shannon diversity follow the edge effect hypothesis, whereby diversity is greatest at the habitat edge. It was also found that the Shannon diversity of carabids was shown to be influenced by edge contrast (i.e. the level of habitat structural heterogeneity) by both the linear mixed-effects model and the Kruskal-Wallis test. Finally, it was also found that edge contrast, edge distance and the environmental variables which were tested for did not have an influence on the functional diversity of carabids. However, this result may be due to the distribution of certain functional groups within the test sites at each edge contrast type and edge distance, thus leading to a non-significant result.

### **5.1 The Influence of Edge Contrast and Edge Distance on the Functional Diversity of Carabids**

Although the Kruskal-Wallis tests found that both edge contrast type and edge distance did not influence the functional diversity of carabids, Fig. 4 shows that carabid functional diversity was greatest at the forest edge (0 m) for both hard and intermediate edges, which follows the edge effect hypothesis, whereby diversity is greatest at ecotones between two adjacent habitats (Odum, 1971). Hard edges (mature forest-grassland) at the forest edge had the single greatest level of carabid functional diversity. This may be due to the shrubs from the forest and herbs from the adjacent grassland contributing to the heterogeneity of the habitat, thus aiding in the differentiation and development of microhabitats (Magura et al., 2001a). As the coverage of vascular plants increases (thus contributing to greater habitat heterogeneity), the microhabitats develop into more favourable conditions for most carabid species and their larval and egg development (Magura et al., 2001). Due to the fact that the majority of the species which were caught were generalist predators, the percentage cover of plants may provide a more uniform distribution of resources in time and may increase the number of invertebrate herbivorous prey which are available for such carabid species (Niemelä and Spence, 1994; Niemelä et al., 1996). Hence, carabid functional diversity is greatest at the forest edge of mature forest-grassland edges. Soft edges (mature forest-young forest) had the lowest level of functional diversity of all edge types examined within this study. This could perhaps be due to how carabids perceive edges, i.e. mature forest-

young forest edges are not considered ‘true’ edges, possibly down to minute differences in microhabitat conditions between mature forest and young forest.

A comparable study by Magura (2016), which had pitfall traps placed at 50 m and 60 m from grassland-forest edges in both the forest interior and grassland, found that functional diversity of carabids was affected by an asymmetrical species distribution, with functional diversity being greater in the grassland; therefore, in the study by Magura (2016), the forest edge impeded the dispersal of open habitat species into the forest interior by operating as an impervious filter for such species (Strayer et al., 2003). It should also be considered that none of the species sampled within this study were forest specialists. Only three types of adult habitat affinity were observed within this study: habitat generalists, forest generalists and open habitat specialists. This could have been due to local extinctions of forest specialist species as a result of invasions by open habitat and forest generalist species (Magura et al., 2017). This in turn had an effect on the functional diversity calculations of forest interior pitfall traps, with such values being lower than at the forest edge.

The results of this research, that the functional diversity of carabids was not influenced by edge contrast or edge distance, may be due to well-known issues which occur with the use of pitfall traps. Species of carabid react differently to pitfall traps, therefore the rates at which such species are caught will also differ, thus leading to incomparable results between species (Kotze et al., 2011). *A. parallelepipedus* was the dominant species sampled within this study, and was sampled at nearly all pitfall traps, with it occurring on several occasions that *A. parallelepipedus* were the only species to be collected from certain pitfall trap sites over the entirety of this 9-week study. It could therefore be concluded that *A. parallelepipedus* were the most ‘catchable’ species encountered within this study. This means that when calculating Rao’s quadratic entropy (Rao, 1982; Botta-Dukát, 2005) for such sites where only *A. parallelepipedus* individuals were sampled, a carabid functional diversity value of 0 was returned. The fact that *A. parallelepipedus* was the dominant species sampled within this study may be due to individuals of this species (i) being able to outcompete other, lesser caught species by occupying a greater range of ecological niches, or (ii) being more mobile at the local scale (as can be inferred by *A. parallelepipedus* individuals being sampled at all edge types and edge distances), and able to have a greater home range than other species.

## 5.2 The Influence of Edge Contrast and Edge Distance on the Shannon Diversity of Carabids

The results of the linear mixed-effects model found that edge contrast type was the most important variable in determining the Shannon diversity of carabids (Table 6 and Table 7). Shannon diversity was greatest at the forest edge (0 m) for each edge type (hard, intermediate and soft), with Shannon diversity being greatest at the forest edge of hard edges (Fig. 4). This result follows the edge effect hypothesis, whereby diversity is greatest at ecotones between two adjacent habitats (Odum, 1971). Previous studies on the influence of edge effects on carabids have also demonstrated that diversity was higher at the forest edge than in the forest interior of forest-grassland edges (Báldi and Kidbenedek, 1994; Magura and Tóthmérész, 1997; Magura and Tóthmérész, 1998; Magura et al., 2001a; Magura et al., 2001b; Magura, 2017). The shrubs from the forest and the herbs from the adjacent grassland contribute considerably towards the habitat heterogeneity of hard forest edges, while also supporting microhabitats to develop and differentiate (Magura et al., 2001a), which may explain why the Shannon diversity of carabids was greatest at hard forest edges.

## 5.3 The Influence of Edge Contrast and Edge Distance on the Distribution of Carabid Functional Traits

This study found that edge contrast and edge distance did not have a significant influence on carabid functional traits; however, when the data is scrutinised, the results do not seem to be congruous with previous studies. Of the five species sampled within this study which were open habitat specialists, only one species was both small and winged (*A. aenea*) and only one other species (*H. rufipes*), was winged (Refer to Table 2 for references). The remaining three species were all average size (relative to other carabid species) and apterous or brachypterous (i.e. reduced hind-wings). The greatest number of open habitat species would be expected to be found at the forest edge (0m) of hard edges (mature forest-grassland), as canopy cover is lowest at such points; however, that was not the case in this study. *C. arvensis*, *P. madidus* and *P. melanarius* were the only open habitat species where at least half of all individuals were sampled at the forest edge, but several individuals of each species were found within the forest interior at 30

m and 60 m. *A. aenea* were not found at the forest edge at all, and were mainly sampled at 30 m into the forest interior. *H. rufipes* were sampled at all edge distances, but most individuals were found at 60 m into the forest interior, with the second greatest number of individuals being sampled at the forest edge.

This result was perhaps to have been expected, as edges which are created and maintained via forestry (group felling, forest management and clear felling) such as is seen in Ringwood Forest, appear to be permeable by open habitat and generalist species (Strayer et al., 2003), as these edges allow such species from the adjacent, non-forested habitat to inhabit the forest interior, with forest specialist species also being able to move in the opposite direction (Magura et al., 2017). The invasion of generalist and open habitat species into the forest interior may cause a decline or local extinction of intrinsic forest interior specialist species and thus facilitate or increase further invasions by non-local species (Magura et al., 2017). This may go some way towards explaining why both canopy cover and edge distance did not have an influence on the functional diversity of carabids: the species which would be expected to be found at the forest edge where canopy cover is lowest, were in fact also found within the forest interior. Due to open habitat carabid species being found within the forest interior, it may be suggested that such species have a high dispersal ability; said species may be mobile at the local scale in order to hunt for prey which can only be found within the forest interior, and in fact consider open habitats (i.e. at the forest edge) as their 'home' habitat.

Hind-wing morphology is perhaps not the greatest indicator of dispersal ability, as species within this study which were expected to be found at the forest edge (0 m) and were also apterous or brachypterous (i.e. reduced hind-wings) were found at all edge distances, which implies that such species have a high dispersal ability and are able to travel over great distances from their home ranges (i.e. open habitats such as at the forest edge). One way to remedy this would be to include the mark-and-recapture of carabids in order to find how far such species can travel over a set period of time (e.g. two weeks) and over a set distance (e.g. capture species at the forest edge (0 m) and recapture species at 30m and 60m into the forest interior) in order to quantify the dispersal ability of carabids. Another approach to consider would be to have symmetrical pitfall traps into both the forest interior and the adjacent habitat, e.g. 60 m into grassland, 30 m into grassland, at the forest edge (0 m), 30 m into the forest interior and 60 m into the forest interior.

In a meta-analysis by Brouwers and Newton (2009), it was found that forest specialist carabids moved more slowly than generalist carabid species (Brouwers and Newton, 2009). This may explain why there were no forest specialists found within this study, as pitfall traps are more likely to catch more mobile species at the local scale. It was also found within the meta-analysis by Brouwers and Newton (2009) that the body size of carabids was positively correlated with rate of movement. This may also explain the lack of smaller carabids being found, as such species may be less mobile at the local scale than larger carabid species, such as those found in this study.

#### **5.4 Environmental Drivers Influencing the Functional Diversity of Carabids**

The results of the linear mixed-effect model found that none of the environmental variables which were collected had an influence on the functional diversity of carabids (Table 8 and Table 9), with ground vegetation also being found to not be an important driver in influencing the functional diversity of carabids (Table 10). In contrast, previous studies have found that canopy cover was an important variable in determining carabid functional diversity, with carabid functional diversity decreasing as canopy cover increases (Jukes et al., 2001; Gibb and Cunningham, 2010; Spake et al., 2016). This is due to the fact that as canopy cover increases, open habitat species are expected to decrease (Spake et al., 2016). Traditionally, open habitat species have different functional traits to that of forest specialists, with such species typically being smaller in size and tending to be macropterous (i.e. winged) (Jelaska and Durbešić, 2009). The open habitat species sampled within this study had relatively different functional traits from those that had previously been studied, e.g. in the study by Jelaska and Durbešić (2009).

Were this study to have been conducted for a longer period of time, and over a two-year period, such as in the study by Spake et al. (2016), it would perhaps be unlikely that so many pitfall traps would return a carabid functional diversity value of 0. This could occur for two reasons. Firstly, a greater number of carabid species may be collected, as certain carabid species may emerge from hibernation as adults or their pupal stages (Barlow, 1970) either earlier or later in the year to align with their breeding season, i.e.

spring-breeding and Autumn-breeding (Sota, 1987). Secondly, several species have a life cycle that occurs over several years, such as *C. glabratus*, which has a biennial life cycle in upland areas located in northern England (Lövei and Sunderland, 1996). Carabid species have peaks and troughs in activity, and thus abundance, either in early or late summer (Niemelä et al., 1989), which therefore requires two sampling periods (Niemelä et al., 1990). Several species of carabid have a relatively stable life cycle, whereas others show plasticity with regards to individual development (Lövei and Sunderland, 1996); therefore, the adults of such species may only occur every few years, thus carabid sample collections can differ between two consecutive years. Therefore, were this study to have been conducted for a 20-week period from the start of summer to the end of summer over two consecutive years, carabid functional diversity values of 0 could be negated for such reasons.

## **5.5 Environmental Drivers Influencing the Shannon Diversity of Carabids**

The results of the linear mixed-effects model found that edge contrast type was the most important variable in determining the Shannon diversity of carabids (Table 11 and Table 12). Edge contrast is one approach to quantify habitat structural heterogeneity (Ries et al., 2004; Ewers and Didham, 2006): high-contrast edges (i.e. mature forest-grassland) have a high level of habitat structural heterogeneity due to microhabitat conditions which occur at the ecotones between the two adjacent habitats (Magura et al., 2001a), whereas low-contrast edges (i.e. mature forest-young forest) have a lower level of habitat structural heterogeneity due to similarities in structure between the two habitats. Previous studies have also found that environmental heterogeneity has an impact on the variation in pitfall trap catches (Magura et al., 2001a; Woodcock et al., 2010).

One thing to consider is the low species diversity found within this study compared to other more regional studies on carabids. This could perhaps be explained by the fact that within this study, only one location (Ringwood Forest) was sampled. For example, in the study by Spake et al. (2016), 12 different locations were sampled, from Northern Scotland to Southern England (Spake et al., 2016). This would of course have an effect on the species diversity of carabids, as certain species may only be found in certain parts of the country or in certain habitats. Ringwood Forest was mostly dominated by Scots

and Corsican pine, which would impact on the species diversity of carabids found within this study, as certain carabid species may have a preferred type of forest. In the study by Spake et al. (2016), there were four different tree species found over the 12 sample sites (Spake et al., 2016).

## **5.6 Limitations of Study**

It could be suggested that this study was not conducted for a long enough period of time. Other studies, such as Spake et al. (2016), had a field research period that lasted 20 weeks from May to September over two consecutive years. Overall, that would give a sample collection period which is 4 times greater than that of this study, i.e. the study by Spake et al. (2016) had 40 weeks of carabid pitfall trap samples to analyse, whereas this study had a sample collection period that lasted for 9 weeks. Interestingly, the results of the power analysis suggest that in order to obtain a significant result, this study had to be roughly 3.6 times greater in scale, which perhaps could have been achieved by having a similar sample collection period as that seen within the Spake et al. (2016) study. This study had a shorter sample collection period in order to reduce the influence of seasonality, as this was outside the scope of the study; however, this may in fact have impeded the analysis of this study.

Rather than increasing temporal sampling, it could be suggested that more spatial replicates were required within this study. The power analysis found that there should be 98 pitfall traps per forest patch, with a total sample size of 293 traps. If this were to be transposed to the design used in this study (i.e. 9 traps per site, with three sites per forest patch), 12 sites with a total of 108 traps would be required per forest patch, as opposed to 3 sites with a total of 27 traps, which would give a total of 324 traps (i.e. study design should have been 4 times greater).

Another issue to consider within this study is that due to the structure of Ringwood Forest (i.e. as an actively managed plantation forest), 60 m into the forest interior from the forest edge may not be considered as a 'true' forest interior compared to other more dense forests. This issue may be reflected in the lack of any forest specialist species found within this study. It would be expected that the interior of a forest would be more dense with trees than the forest edge, however, this was not the case in Ringwood Forest. Due to it being a plantation forest, the majority of trees are evenly spaced out,



with this also being the case within the forest interior. It may be that forest specialist species require dense forests with a high percentage of canopy cover within the forest interior, which may go some way towards explaining why there were no forest specialist species found within this study.

There were also several other limitations within this study. One such limitation includes the placement of the pitfall traps i.e. no traps per placed into the habitat matrices adjacent to the mature forests. This was not possible due to the density of vegetation in the adjacent matrices; however, it would have given a greater insight into the functioning of the ecosystem as a whole were this possible (i.e. were the study design to have been similar to Magura (2016)). Another issue was involved with the characterisation of the edge contrast types. Hard edges (i.e. mature forest-grassland) were relatively uniform across all forest patches in terms of vegetation; however, intermediate and soft edges (i.e. mature forest-shrub and mature forest-young forest) had more variation between each forest patch in terms of vegetation. This may have had an influence on the distribution of carabids as a result of habitat preference at such edge contrasts. A final limitation of this study was the accuracy of species identification. Several species, such as *A. parallelepipedus*, *P. melanarius* and *P. niger* had very similar morphologies, which made the identification of such species difficult, and thus may have led to the misidentification of such species.

## **5.7 Limitations of Literature**

One issue with regards to edge effect studies is how the depth of an 'edge' is defined, which is discussed by Ewers and Didham (2006). They suggested that some authors may consider a weak edge effect to be an edge that does not penetrate a large distance into a particular habitat type, whereas a strong edge effect does (Ewers and Didham, 2006). They also suggest that in contrast, other authors would consider a strong effect (or edge) to be a large magnitude response across a short distance (Ewers and Didham, 2006). A paper by Gascon et al. (2000) suggested that forest edges have three stages after initial isolation, relating to the depth of an edge. Firstly, recently cut forest areas show abrupt forest edges which are subject to light penetration and lateral winds which allow for profound microclimatic changes within the forest edge (Gascon et al. 2000). Then, within landscapes that exhibit low matrix harshness, edges will be maintained, thus buffering the interior of the forest from severe initial edge effects; landscapes

which have a high degree of matrix harshness exhibit a breakdown in forest regeneration along the edge, thus resulting in a gradually receding edge and a deeper penetration of edge effects (Gascon et al., 2000). Harper et al. (2005) defined a forest edge as the convergence between non-forested and forested ecosystems or between two forests which exhibit contrasting structures or compositions, whereas a forest interior can be defined as forest which does not exhibit any edge influence (Harper et al., 2005). Thus, an edge is only as physically 'deep' as its influence over the forest. In all of these examples, there is no real physical definition on the depth of an edge, with it being common practice within the literature to use 'edge' and 'edge effects' interchangeably, with edges being as deep as their influence over a forest until the forest interior, which exhibit no edge influence. For future edge contrast studies, a standard definition on the depth of an 'edge' is required to allow for comparisons and reviews between such studies. In this study, edges were defined as an abrupt boundary between the mature forest and the surrounding matrix (i.e. young forest, shrubland and grassland). Therefore, such edges would not be considered to be deep due to the fact that there was not a gradient leading from one habitat type to another.

Another issue with regards to edge effect studies is that within the literature, there are differing definitions of edge contrast and what constitutes a 'hard' edge. With regards to the definition of edge contrast, Cadenasso et al. (2003) define edge contrast as a measure of difference in function, composition or structure of an ecosystem between adjacent land use and forest, Ries and Sisk (2004) define edge contrast as the degree to which bordering patches are different in structure from one another, and Prass et al. (2017) define edge contrast as the magnitude in variation of ecologically significant characteristics between a focal patch and the surrounding adjacent matrix. These studies demonstrate that as time goes on, the definition of edge contrast becomes more complicated in wording, but generally the basis of each definition stays the same. With regards to 'hard' edges, in the study by Brearley et al. (2010) it is discussed conceptually how residential edges which contained some garden vegetation could be considered both hard and soft, depending on how easy it is for species to traverse such edges. In practice, Brearley et al. (2010) considered major roads to be a 'hard' edge, due to little to no vegetation being found either side of the road. There was also a similar definition for hard edges within the study by Noreika and Kotze (2012). Within their study, hard (or high contrast) edges were defined as asphalt roads against forest, with the roads being at least 10 – 15 m wide. And in the study by Desrochers et al. (2003),

hard edges are not defined in any more detail beyond simply open areas which are adjacent to forests. It should be noted that the definition of hard edges found in this study was more alike to intermediate edges found in previous studies, as most previous studies on edge contrast define hard edges almost as a literal habitat boundary, such as roads or residential areas, as opposed to a different habitat type (i.e. grassland) found within this study.

## **5.8 Implications of Study**

There are several implications that can be concluded from the results of this study. One such implication is that in order to maintain or increase the level of carabid functional and Shannon diversity, a high level of habitat structural heterogeneity is required. Carabid functional diversity and Shannon diversity was greatest at the forest edge of hard edges (i.e. mature forest-grassland) due to such edges having the highest level of structural heterogeneity (of all edge contrasts within this study), and thus allowing species from both adjacent habitats to be found within such ecotones, possibly due to microhabitat conditions at such areas. For future land management and carabid beetle conservation efforts, the level of high-contrast edges (i.e. mature forest-grassland) should be implemented, maintained or increased in order to increase the level of carabid functional and Shannon diversity at forest edges, thus maintaining or increasing the level of ecosystem functioning at such habitats.

Another implication of this study is that both carabid functional diversity and Shannon diversity follow the edge effect hypothesis, whereby diversity is greatest in ecotones between two adjacent habitats (Odum, 1971). This will further have an impact on future land management and carabid beetle conservation, as this study found that habitat edges are vital for carabids, and therefore in order to maintain or increase such levels of diversity, future nature reserve designs should contain 'islands' of mature forest surrounded by grassland, thus maintaining or increasing the level of ecosystem function of such sites. A final implication of this study is the need to use more than one diversity index when analysing populations of species. When the Shannon diversity of carabids is considered on its own, the communities of carabids encountered within this study appear to be relatively healthy. However, when functional diversity is also considered, such carabid communities do not appear as healthy. This is due to the dominant species encountered in this study, *A. parallelepipedus*, making up 88% of individuals caught in

pitfall traps. This drove down functional diversity for several pitfall trap sites where only the dominant species was encountered. Ultimately, this will decrease the level of ecosystem functioning at such sites.

## **6. Conclusion**

This study has shown that the functional diversity of carabids is congruous with the edge effect hypothesis, whereby diversity is greatest at the forest edge and decreases into the forest interior. The raw data also shows that functional diversity is in fact greatest at the forest edge of high-contrast edges, where habitat structural heterogeneity is greatest. This study has also shown that edge contrast is the main driver in influencing the Shannon diversity of carabids. The results also showed that the Shannon diversity of carabids followed a similar distribution to that of the functional diversity of carabids, whereby diversity was greatest at the forest edge and decreased into the forest interior, with diversity also being greatest at hard edges.

It was also shown in this study that edge contrast and edge distance did not have an influence on carabid functional diversity and the distribution of carabid functional traits at different edge contrasts and edge distances. Edge contrast and edge distance also did not influence the distribution of carabid functional traits within this heterogeneous landscape; however, this may be due to certain carabid species (i.e. open-habitat species) being encountered within the forest interior as opposed to at the forest edge. It should also be noted that the specific site sampled within this study possibly had a great effect on the low species diversity and lack of forest specialists found within this study due to the nature of Ringwood Forest being an actively managed forest plantation.

One thing that this research has demonstrated is that it is both important and useful to incorporate more than one type of diversity index into a study. If Shannon diversity were to have been the only diversity index to be used in this study, it could be assumed that the carabid communities were relatively healthy. However, when functional diversity is considered, the carabid communities do not look as healthy, with one species, *A. parallelepipedus*, being the dominant species, making up 88% of all pitfall trapped individuals. This in turn drove down the functional diversity of carabids at each pitfall trap, which will ultimately have an impact on ecosystem functioning. It could perhaps also be suggested that a proper definition for depth of edge is required in future edge contrast studies to allow greater comparison and reviews of such studies.

## **7. References**

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## **8. Appendices**

### **Appendix A – Preliminary Study Design**

Six temperate forest patches which border three different types of habitat within Ringwood Forest were selected. One 35 m long transect were be set up per site in a zig-zag design (while also ensuring that there is a 5 m distance between traps), with one pair of traps (5 m apart) being placed at 5 m into the matrix (i.e. immediately adjacent to the edge), at the edge, and at 5, 10, 15, 20, 25 and 30 m into each forest patch. This resulted in 16 traps per site, and thus 96 traps in total. The six sites included three different edge types: high contrast (grassland-forest), intermediate contrast (shrubland-forest) and low contrast (young forest-forest) edges. In order to collect the carabid samples, pitfall traps with a 60 mm diameter and an 80 mm depth were used. A solution of washing up liquid and water was used to preserve the samples, with samples being collected once a fortnight to prevent the samples becoming unusable. The traps were also covered with a 20 x 20 cm corrugated plastic square, as this will protect the samples from rain and leaf litter. Pitfall traps were set between early May to early June in order to inform the official sample collection phase of this study. The main goal of the preliminary sample collection phase was to determine how pitfall traps should be allocated in the primary sample collection phase i.e. how many pitfall traps should be placed along each transect, how long each transect should be, how many pitfall traps should be placed at each distance from the forest edge (0 m) and which environmental variables should be collected.

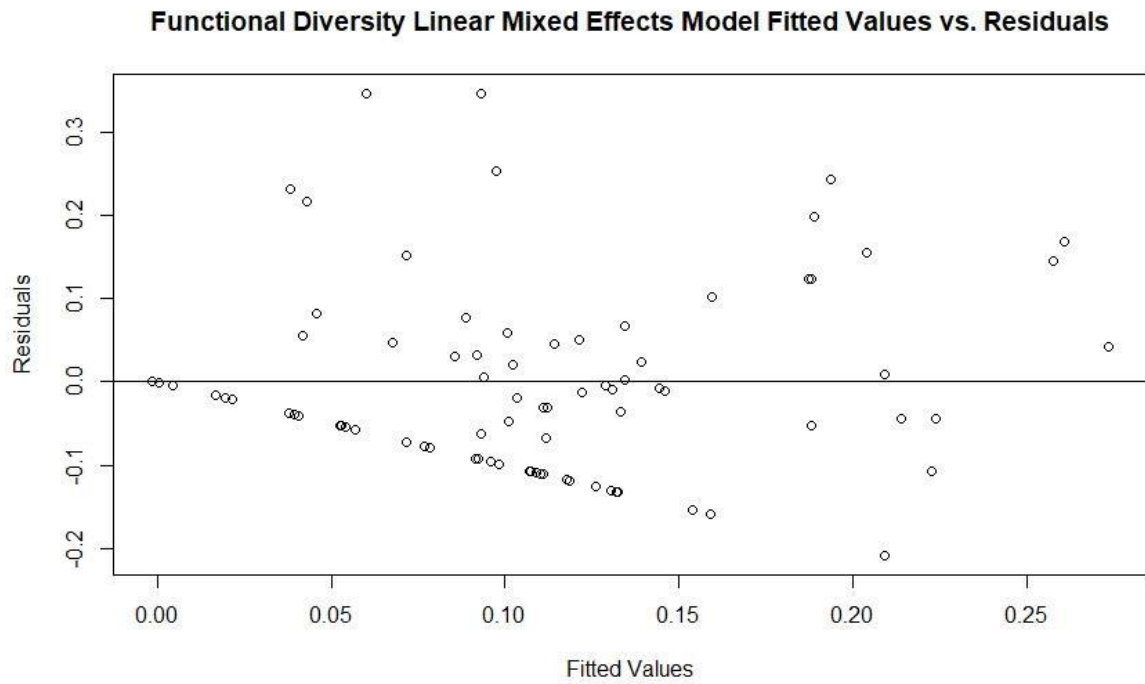
## Appendix B – GPS Position of all Pitfall Traps

Plot	Distance	Edge Type	Site	Latitude	Longitude
1	0	Intermediate	1.1.1	50.876948	1.838358
1	0	Intermediate	1.1.2	50.876994	1.838355
1	0	Intermediate	1.1.3	50.876904	1.838361
1	30	Intermediate	1.2.1	50.876939	1.837919
1	30	Intermediate	1.2.2	50.876977	1.837916
1	30	Intermediate	1.2.3	50.876903	1.837919
1	60	Intermediate	1.3.1	50.876933	1.837503
1	60	Intermediate	1.3.2	50.876976	1.837503
1	60	Intermediate	1.3.3	50.876889	1.837507
1	0	Soft	2.1.1	50.876464	1.834871
1	0	Soft	2.1.2	50.876509	1.834873
1	0	Soft	2.1.3	50.876419	1.834869
1	30	Soft	2.2.1	50.876461	1.834437
1	30	Soft	2.2.2	50.876500	1.834434
1	30	Soft	2.2.3	50.876420	1.834435
1	60	Soft	2.3.1	50.876455	1.834019
1	60	Soft	2.3.2	50.876501	1.834019
1	60	Soft	2.3.3	50.876410	1.834019
1	0	Hard	3.1.1	50.877746	1.835039
1	0	Hard	3.1.2	50.877791	1.835027
1	0	Hard	3.1.3	50.877705	1.835066
1	30	Hard	3.2.1	50.877710	1.834616
1	30	Hard	3.2.2	50.877754	1.834605
1	30	Hard	3.2.3	50.877665	1.834619
1	60	Hard	3.3.1	50.877677	1.834194
1	60	Hard	3.3.2	50.877723	1.834186
1	60	Hard	3.3.3	50.877630	1.834203
2	0	Intermediate	4.1.1	50.880633	1.838131
2	0	Intermediate	4.1.2	50.880665	1.838180
2	0	Intermediate	4.1.3	50.880605	1.838075
2	30	Intermediate	4.2.1	50.880829	1.837838
2	30	Intermediate	4.2.2	50.880600	1.837891
2	30	Intermediate	4.2.3	50.880798	1.837785
2	60	Intermediate	4.3.1	50.881031	1.837552

2	60	Intermediate	4.3.2	50.881058	1.837608
2	60	Intermediate	4.3.3	50.880999	1.837491
2	0	Hard	5.1.1	50.882388	1.838328
2	0	Hard	5.1.2	50.882393	1.838256
2	0	Hard	5.1.3	50.882383	1.838448
2	30	Hard	5.2.1	50.882118	1.838313
2	30	Hard	5.2.2	50.882118	1.838242
2	30	Hard	5.2.3	50.882118	1.838385
2	60	Hard	5.3.1	50.881848	1.838304
2	60	Hard	5.3.2	50.881848	1.838233
2	60	Hard	5.3.3	50.881848	1.838376
2	0	Soft	6.1.1	50.883384	1.835734
2	0	Soft	6.1.2	50.883389	1.835663
2	0	Soft	6.1.3	50.883373	1.835804
2	30	Soft	6.2.1	50.883115	1.835689
2	30	Soft	6.2.2	50.883117	1.835618
2	30	Soft	6.2.3	50.883110	1.835759
2	60	Soft	6.3.1	50.882846	1.835662
2	60	Soft	6.3.2	50.882846	1.835732
2	60	Soft	6.3.3	50.882846	1.835658
3	0	Soft	7.1.1	50.882512	1.849765
3	0	Soft	7.1.2	50.882557	1.849760
3	0	Soft	7.1.3	50.882467	1.849779
3	30	Soft	7.2.1	50.882479	1.849338
3	30	Soft	7.2.2	50.882552	1.849338
3	30	Soft	7.2.3	50.882437	1.849347
3	60	Soft	7.3.1	50.882449	1.848906
3	60	Soft	7.3.2	50.882486	1.848901
3	60	Soft	7.3.3	50.882410	1.848901
3	0	Hard	8.1.1	50.881438	1.850613
3	0	Hard	8.1.2	50.881482	1.850613
3	0	Hard	8.1.3	50.881394	1.850623
3	30	Hard	8.2.1	50.881415	1.850186
3	30	Hard	8.2.2	50.881457	1.850179
3	30	Hard	8.2.3	50.881371	1.850182
3	60	Hard	8.3.1	50.881396	1.849758
3	60	Hard	8.3.2	50.881438	1.849751

3	60	Hard	8.3.3	50.881354	1.849751
3	0	Intermediate	9.1.1	50.880443	1.847910
3	0	Intermediate	9.1.2	50.880476	1.847958
3	0	Intermediate	9.1.3	50.880413	1.847857
3	30	Intermediate	9.2.1	50.880287	1.848260
3	30	Intermediate	9.2.2	50.880330	1.848286
3	30	Intermediate	9.2.3	50.880257	1.848207
3	60	Intermediate	9.3.1	50.880131	1.848607
3	60	Intermediate	9.3.2	50.880168	1.848650
3	60	Intermediate	9.3.3	50.880094	1.848565

**Appendix C - Carabid Functional Diversity Linear Mixed-Effects  
Model Residual Plot**



# Appendix D - Carabid Shannon Diversity Linear Mixed-Effects Model

## Residual Plot

