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Ground-dwelling invertebrates in reforested conifer plantations

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Abstract

15 Plantation forests are an important part of the forest estate in many countries. In Ireland, they
cover around 9% of the land area and many that are commercially mature are now being felled
and reforested. The potential biodiversity value of such second rotation forests has yet to be
determined, yet this may be particularly significant in Ireland where cover of semi-natural
woodland is only 1%. Invertebrates are a vital component of forest biodiversity, functioning as
20 decomposers and pollinators, to herbivores, predators and prey. Spiders and Carabid beetles are
often used in biodiversity assessment as they are easily captured using pitfall traps, are
taxonomically well known and respond to changes in habitat structure. This study aimed to
examine spider and Carabid beetle diversity in second rotation Sitka spruce (*Picea sitchensis*)
plantations at different stages of the forest cycle (5 yrs, 8-12 yrs, 20-30yrs, 35-50yrs), and
25 compare the spiders captured in second rotation forests with those from first rotation. Spider and
beetle diversity was influenced by stand structural development in second rotation plantations
with numbers of forest-associated species increasing over the forest cycle. Overall, spider
richness declined over the forest cycle and this was related to decreasing cover of field layer
vegetation and fewer open-associated species. In contrast, total beetle richness increased and
30 became more specialised over the forest cycle which may be related to slower colonisation of
disturbed areas by beetles in comparison with spiders, and fewer open specialists at the early
stages of second rotation. Spider assemblages were distinguished between rotations. This may be
related to differing habitat conditions in second rotation forests including dryer soils with lower
pH, differing vegetation complexity and presence of brush piles. Few of the forest species
accumulated during first rotation were retained and the early stages of second rotation forest cycle

was characterised by a generalist open fauna. Nonetheless, as the forest cycle progressed the spider assemblages between rotations became more similar. Current forest policy supports retaining over-mature trees and creating a mosaic of different aged stands within a plantation. Such measures may provide refuge for forest species after clearfell. In countries where forest fragments exist in a landscape dominated by agriculture, consideration should be given to the capacity of mature forest adjacent to felled stands to support forest species, and to the configuration of over-mature areas retained after felling.

Key Words Spider; Carabid beetle; Forest Plantation; Forest Management; Biodiversity Conservation

1. Introduction

Although plantation forests constitute just 8% of the wooded area of Europe they are an important resource in countries such as Ireland, the UK and Denmark, where they constitute over 70% of national forest estates (MCPFE 2007). In the past plantations have primarily been established for timber production, but more recently there has been increasing focus on the value of alternative sources such as recreation, biodiversity and carbon sequestration (Zandersen et al., 2007; Brainard et al., 2009; Yousefpour and Hanewinkel, 2009). Furthermore, as Sustainable Forest Management is now a global objective, forest policy must address biodiversity, conservation and social objectives according to the principles of sustainable development. Recent research suggests that plantation forests can support a relatively diverse flora and fauna in comparison with semi-natural or naturally regenerating forests (Kattan et al., 2006; Marcos et al., 2007; Taboada et al., 2008), and has recognised their contribution to biodiversity in landscapes dominated by intensive agriculture (Oxbrough et al., 2007). In Ireland approximately 10% of the land area is forested, but only 1% is native or semi-natural woodlands (Forest Service, 2007). Government targets aim to increase total forest cover to 14% by 2030, primarily through plantation establishment (COFORD, 2009). Similar large-scale afforestation schemes are currently being implemented in other European countries with low semi-natural forest cover (Division of Forest Policy, 2004; Forestry Commission, 2004). The majority of plantations in Ireland were established in the last 75 years through the state owned forest agency (Forest Service, 2007). Today increasingly large forest areas are entering a second rotation, having been clear felled and replanted. In the future, when the afforestation schemes have been completed, such forests are likely to represent the majority of the national forest estate.

Invertebrates are an important component of forest biodiversity, inhabiting all areas from the soil and litter layers, to herb and understory layers, and the canopy. They have functional importance in food webs acting as herbivores, predators, as a food source for mammals and birds (Buse and Good, 1993; Gunnarsson 1996), and also as decomposers and pollinators (Kevan, 1999; Chamberlain et al., 2006). Spiders and Carabid beetles are frequently used to assess habitat 'quality' in various forested ecosystems (Pearce and Venier, 2006). These ground-dwelling predators are relatively easily captured and identified, and their ecology and behaviour is well known compared with other invertebrate taxa. In addition, both spider and Carabid beetle species are sensitive to changes in vegetation structure (Ings and Hartley, 1999; Sanders et al., 2008) which is often dependent on canopy species or forest structural development (Oxbrough et al., 2005; Mullen et al., 2008).

In the last decade, a relatively large body of work has explored invertebrate ecology in secondary forests which are either naturally regenerating or plantation (Barbaro et al., 2005; Buddle et al., 2006; Yu et al., 2008; Ziesche and Roth, 2008). These studies are typically conducted in stands surrounded by large areas of mature forest or at least a mosaic of different structural stages (Siira-Pietikainen et al., 2003; Schowalter et al., 2005; Siira-Pietikäinen and Haimi, 2009). However, in countries like Ireland, where most plantations are established on previously open land and embedded in an agricultural landscape, the potential biodiversity value of second rotation plantations has yet to be determined. In this context, this study aims to:

1. Examine spider and Carabid diversity in second rotation plantations across the forest cycle.
2. Examine whether spider diversity differs between first and second rotation plantations.
3. Identify habitat features and management practices in second rotation stands that may benefit invertebrate diversity in successive rotations of plantation forests.

This targeted research will improve our understanding of how invertebrate diversity can be maintained in second rotation forests and inform the management of successive rotations throughout Europe.

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2. Materials and methods

2.1 Study Sites

The 43 study sites were monoculture plantations of Sitka spruce (*Picea sitchensis*). This non-native conifer is the most widely planted species in Ireland, accounting for 52% of the total

stocked area (Forest Service, 2007). Four age classes were selected to represent the major structural stages of the forest plantation cycle: Tree establishment (5 years); Canopy closure (8-12 years); Time of first thinning (20-30 years); Commercial maturity (35-50 years). Rotation status (first or second) of the sites was determined using the databases of Coillte, the main forest landowner in Ireland, and verified after consultation with historical maps. Sites were selected to give a representative geographical spread and located in clusters where possible to aid the logistics of fieldwork (Figure 1). Sites within a cluster included several age classes matched for environmental attributes (i.e. soil, elevation, drainage). All sites were a minimum of 4ha in size and 100m in width. Twenty three first rotation sites were sampled during 2001-02 with between four and seven replicate sites for each age class; and 20 second rotation sites were sampled during 2007 with five replicates of each age class. Where possible these second rotation clusters were located in close proximity to those of the first rotation sampled previously (Figure 1).

The spider fauna of the first rotation stands used in this study was examined by Oxbrough et al. (2005). Oxbrough et al. (2005) found significant variation in the structural development of first rotation stands within an age class and thus used structural groupings rather than stand age to represent the different stages of the forest cycle. These groups were determined with a hierarchical clustering method using the following structural attributes: percentage canopy cover, tree height, and mean diameter at breast height. Using this method the stands in the current study were allocated to the following structural groups: Pre-thicket, Thicket, Closed-maturing, Reopening, Mature (Table 1). The Pre-thicket, Thicket and Mature structural groups contained only stands from the 5 year old, 8-12 year old and 35-50 year old age classes respectively, however the Closed-maturing and Reopening groups included stands from several age classes.

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2.2 Invertebrate sampling

Pitfall traps were used to collect spiders and Carabid beetles, a widely used method to sample ground-dwelling invertebrates in forested habitats (Oxbrough et al., 2005; Mullen et al., 2008; Yu et al., 2008; Ziesche and Roth, 2008). Although an efficient method, it should be noted that pitfall captures are dependent on a species' density and activity and thus are not a measure of absolute abundance. Five sampling plots were established in each of the first rotation stands. Species accumulation curves revealed that three of the plots in the first rotation sites sampled between 81-85% of the species from all five plots. Thus three pitfall plots were established in each of the second rotation stands to allow greater between-site replication. Plots were located in

representative areas of site in terms of stand structure and vegetation cover, were a minimum of 50m apart and were not within 50m of the forest edge. Each plot consisted of five pitfall traps spaced 2-4m apart which were pooled for the analyses. Pitfalls consisted of a plastic cup, approximately 7cm in diameter and 9cm in depth. Two drainage holes were cut horizontally, 1 cm from the top of the cup and traps were filled with ethylene glycol to a depth of 1cm to act as killing and preserving agent. Traps in the first rotation stands were set in mid June in either 2001 or 2002 and were left *in-situ* for 9-10 weeks giving a total of 64-71 trap days. Traps in second rotation stands were set in mid May in 2007 and were left *in situ* for 12 weeks giving a total of 84 trap days. Pitfall contents were collected approximately every three weeks.

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Considerable animal disturbance at two sites in 2007 meant they were re-sampled during 2008. To reduce the impact of animal disturbance, a combination of protective wire mesh boxes (mesh size approximately 3cm to allow invertebrates to pass through) and wire mesh 'roofs' held 5cm above the ground by plastic pegs and attached to electric fence units was used. To identify any potential influence of the protective devices or of sampling across years two further 'control' sites were re-sampled in 2008 which were located in close proximity to the disturbed sites, were of similar age class and had a full set of pitfall traps collected during the previous year for comparison. For both spiders and Carabid beetles analyses revealed that species richness and assemblage structure did not differ significantly between the control sites across the years so these data were pooled.

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The spiders were sorted from first and second rotation pitfall samples and adults identified to species level using Roberts (1993). Carabid beetles (hereafter referred to as beetles) were sorted from second rotation plantations (data not available for first rotation stands) and adults were identified to species level using Luff (2007). Species from both taxa were assigned to habitat preferences using the literature (primarily Roberts, 1993; Forsythe, 2000; Harvey et al., 2002; Luff, 2007).

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30 2.3 Environmental variables

Within each sampling plot metrics of stand structure were recorded including canopy cover (by hemispherical photography), diameter at breast height (DBH) and tree height.

Soil was taken at each plot and organic content and pH were determined. Cover of vegetation layers was estimated within a 1m² quadrat surrounding each of the five pitfall traps in a plot using the following classification: ground layer vegetation (<10cm); lower vegetation layer (>10cm - 50cm); upper vegetation layer (>50cm - 200cm) and understory layer (>200cm). Coverage was estimated to the nearest 5%, with values of 1-5% recorded as 3%, and those of <1% allocated 0.5%. Other ground cover types (i.e. rocks, bare soil, litter) and the amount of dead wood in each of the following categories were also recorded using this method: Coarse Woody Debris (CWD, diameter ≥10cm at widest point); Fine Woody Debris (FWD diameter <10cm); Brush pile (accumulated dead wood as a result of felling/thinning). Lastly, litter depth was measured within each quadrat. For analyses, a mean value was calculated across the five quadrats to obtain a representative value per plot.

2.4 Data analysis

Non-metric Multidimensional Scaling (NMS) was used to examine spider and beetle assemblages across the second rotation forest cycle using relative abundance data and the following parameters: Sorensen distance measure; 500 maximum number of iterations; Random Starting coordinates; 100 runs with real data; Step down in dimensionality (Initial step length = 0.2); 50 runs with randomized data. Indicator Species Analysis was used to determine species which were affiliated with particular stages of the forest cycle (McCune and Grace, 2002). One-way ANOVA with Tukey post-hoc test was used to examine trends in species metrics (richness, relative abundance and Berger-Parker dominance index). Where data did not meet parametric assumptions after transformation a non-parametric Kruskal-Wallis with Nemenyi post-hoc test was used (Zar, 1996). To examine the relationship between spider and beetle diversity and the environmental parameters within each structural group Spearman's rho non-parametric correlation was used. The two most structurally developed age classes (Reopening and Mature) were pooled to ensure there were a sufficient number of plots for these correlation analyses.

To ensure that first and second rotation datasets compared captures from the same time of year the individuals collected in first three weeks of the second rotation dataset were excluded from analyses between rotations. This gave a total of 64-71 traps days for the first rotation stands and 60-64 trap days for the second rotation. To correct for this difference in sampling effort total species richness was standardised to 60 trap days. This was done by constructing individual-based rarefaction curves for each sampling plot (Gotelli and Colwell, 2001). The number of individuals

along the X axis of the rarefaction plot were then standardised by trap-days using the formula: $(n_i/N) \times T$, where n_i is the number of individuals at the i th point along X axis, N is the total number of individuals and T is the total number of sampling days. This method is more desirable than using un-standardised rarefaction curves based on numbers of individuals which are not suitable for comparison between different habitats (Magurran, 2008).

First and second rotation stands were sampled in different years and so the potential influence of annual fluctuations on spider activity-density should be considered. Although the more abundant species are likely to be present across both years rare species may not (Norris, 1999; Relys et al., 2002). To examine this, species composition, in the form of NMS ordination was carried out both with and without rare species. Singletons were considered to be rare species, but doubletons were included as they had the chance of being sampled in either year of study (Norris, 1999). Despite singletons constituting 24% of the total species sampled across both data sets NMS ordination (presence-absence data) revealed a near identical spread of sampling plots (Pearson correlation of Axis 1 scores between ordinations $r = 0.94$, $p = <0.0001$ and Axis 2 scores 0.60 , $p = <0.0001$). Thus any influence of rare species between sampling years was minimal. NMS ordination and Multi-Response Permutation Procedures (MRPP) using presence-absence data were used to examine trends in spider assemblages between rotations within each structural group. MRPP utilises the test statistic T and associated P value, with more negative values of T representing a stronger separation between groups. However, the derived P value is not independent of sample size, so the chance-corrected within-group agreement statistic A is used to illustrate homogeneity within groups. When $A = 0$ then heterogeneity within groups is equal to that expected by chance and when $A = 1$ then all samples within groups are identical. With ecological data values of A are often <0.1 and values >0.3 are considered high (McCune and Grace, 2002). ANOVA F and Mann-Whitney U were used to examine differences in species metrics and environmental variables.

Bonferroni corrections were applied to ANOVAs and correlations and percentage cover data were Arc sin transformed. All multivariate analyses were out carried in PC ORD Version 5.10 and ANOVAs and correlations in SPSS Version 15.0. Rarefaction curves were constructed using Biodiversity Pro.

3. Results

A total of 12,661 spiders were identified belonging to 134 species and 13,442 beetles from 47 species. The most abundant spider species were from the Linyphiidae family and included *Lepthyphantes zimmermanni* (17%), *Saaristoa abnormis* (8%) and *Monocephalus fuscipes* (8%).

5 The most abundant beetle species were *Abax parallelepipedus* (54%), *Pterostichus melanarius* (15%) and *P. madidus* (9%).

3.1 Invertebrate diversity across the forest cycle of second rotation plantations

10 Two axes were recommended by the NMS ordination of spider assemblages (Figure 2) which together represented 79% of the variation in the second rotation data set (Axis 1 = 62%, Axis 2 = 17%). Across Axis 1 the plots were distinguished by structural development with the Pre-thicket and Thicket plots separated relatively well into their respective structural groups. In contrast, the more developed stands overlapped with each other and were more tightly clustered across both
15 axes. Cover of upper and lower field layer vegetation and organic content of the soil were positively correlated with this axis whilst canopy cover, litter depth, cover of needle litter and fine woody debris displayed a negative relationship. Across Axis 2 half of the Pre-thicket plots along with three Mature plots from the same site were separated from the others and cover of vascular ground vegetation was positively correlated with this axis.

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The NMS ordination of beetle assemblages represented 94% of the variation in the second rotation data set with a three dimensional solution recommended (Figure 3). Axis 1 accounted for 40% of this variation whilst axes 2 and 3 represented 30% and 24% respectively. Across Axis 1 the Pre-thicket and Thicket plots were broadly separated from those with a more developed canopy with the exception of three plots from the same Pre-thicket site. Axis 1 was positively
25 correlated with organic content of the soil and negatively correlated with soil pH and also longitude. Across Axis 2, the majority of the Pre-thicket plots were separated from the Thicket stands and some of the more mature plots, which is likely to be related to their greater cover of lower field layer vegetation. *Abax parallelepipedus*, which represented 54% of the total captures,
30 was highly positively correlated with Axes 1 ($r = 0.87$) and 2 ($r = 0.74$), thus these axes are likely to be highly influenced by the presence of this species, particularly in the tightly clustered group of Thicket stands, where few other species were present. Axis 3 did not represent any changes in assemblage structure across the forest cycle, however it may reflect differences in the presence of two species which do not appear to occur in high numbers together i.e. *P. melanarius* which

constituted 15% of the total captures was negatively associated with Axis 3 ($r = -0.43$) and *P. niger* which constituted 4% of the captures, was positively associated with this axis ($r = 0.69$).

- 5 Spider species richness was significantly greater in the younger stands than in those with a more developed canopy whilst beetle species richness increased in the later stages of the forest cycle (Table 2). For both taxa richness and relative abundance of open habitat species was greatest in the Pre-thicket stands whereas the richness and relative abundance of forest-associated species increased with forest structural development. A similar trend was shown by the Berger-Parker dominance index for spiders, which was significantly higher towards the end of the forest cycle.
- 10 The relative abundance of beetle species with a preference for shaded habitats was greatest in the Thicket stands, as was dominance, however this is likely to reflect captures of *A. parallelepipedus* which is associated with shaded habitats, and was the most abundant beetle at this structural stage and the whole dataset.
- 15 Nearly four times as many spider species were identified by Indicator Species Analysis in the Pre-thicket plots than in any of the other structural groups, seven of which were associated with open habitats (Table 3). By contrast, only four species were affiliated with the Thicket plots, all of which were habitat generalists. In the more structurally developed groups, between two and four species were identified and these were predominately associated with forested habitats. Indicator
- 20 Species Analysis identified one beetle species in the Pre-thicket stands which has a preference for open habitats (Table 4) whereas for the Thicket structural group, no species were identified. One species was identified as an indicator of the Closed-maturing structural group and this was associated with forested habitats. For the Reopening group eight species were identified, two of which were associated with shaded or forested habitats, but also one with open habitats whereas
- 25 of the four species identified in the Mature structural group only one had a preference for forested habitats.

3.2 Relationship between environmental variables and invertebrates in second rotation forests

- 30 In the Pre-thicket stands, species richness of both spiders and beetles was positively related to cover of lower field layer vegetation (Table 5). A similar trend was observed for the richness of open-associated spiders and they were also positively related to soil pH and negatively related to needle litter and upper field layer cover. In contrast, dominance and beetles associated with shaded habitats were negatively related to lower field layer and positively related to canopy and

upper field layer cover. In the Thicket stands spider richness, abundance and open-associated species were negatively related to canopy cover, canopy height, mean DBH and brush cover whereas forest species were positively related to cover of canopy, brush and litter depth. In the Thicket stands, beetle richness and abundance was positively related to needle litter cover and soil pH and open species relative abundance was negatively related to brush. In the more developed structural groups abundance and dominance of both spiders and beetles were positively related to canopy height, cover and mean DBH. Furthermore, beetles associated with forested or shaded habitats were positively related to litter depth and cover and negatively related to ground and lower field layer vegetation. Across the structural groups there were no significant correlations between the species metrics and FWD, CWD and soil organic content.

3.3 Spider diversity between first and second rotation plantation forests

The NMS ordination of spider assemblages represented 81% of the variation in the dataset and recommended two axes (Figure 4), with Axis 1 accounting for 50% and Axis 2 for 31%. Overall, the spider assemblages were distinguished by both rotation and structural development; first and second rotation plots were separated from each other but arranged in a similar pattern with increasing structural development. The most distinct group was the first rotation Pre-thicket plots which were clearly distinguished from all of the other plots across Axis 1, and was negatively related to soil pH. In addition, the difference between Pre-thicket and Thicket second rotation plots was not as great as that of first rotation. In contrast, the more developed stands displayed similar levels of variation across the axes for both first and second rotation. Variables related to tree development such as canopy cover and height, were positively associated with both axes whereas lower field layer cover was negatively associated with both axes. In each of the structural groups, the spider assemblages differed significantly between rotations though in the Reopening group the difference was not as large (MRPP, Pre-thicket: $T = -14.8$, $P = <0.0001$, $A = 0.27$; Thicket: $T = -14.7$, $P = <0.0001$, $A = 0.22$; Closed-maturing: $T = -9.4$, $P = <0.00001$, $A = 0.10$; Reopening: $T = -2.1$; $P = 0.03$, $A = 0.09$; Mature: $T = -4.2$, $P = <0.0007$, $A = 0.09$). It should be noted, however, that for the more developed structural groups $A = \leq 0.1$, indicating a high level of heterogeneity within each rotation as well as between rotations.

Overall, 44 of spider species sampled were unique to first rotation stands and 19 to second rotation. For both rotations the majority of the unique species were encountered in the early stages of the forest cycle (Table 6), however in the first rotation stands the number of unique

species was also relatively high in the Mature structural group. Both expected (corrected for trap days) and observed species richness were significantly higher in first rotation than second rotation stands across all stages of the forest cycle with the exception of the Pre-thicket stands. The number of species with a preference for open habitats was generally lower in second rotation stands, though this difference was only significant in the Mature structural group. A significantly greater number of species with a preference for forested habitats were sampled in the Pre-thicket second rotation stands. This is in contrast with the Mature structural group where a greater number of these species were sampled in the first rotations stands.

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3.4 Environmental variables in first and second rotation plantation forests

Structural variables (canopy cover, mean DBH, tree height) were similar between rotations during the early stages of the forest cycle although canopy cover was significantly greater in second rotation Pre-thicket stands than in those of first rotation (Table 7). However, towards the end of the forest cycle canopy height and mean DBH, and canopy cover and DBH were greater in second rotation for the Reopening and Mature groups respectively. In contrast cover of FWD was greater in first rotation stands in the later stages of the forest cycle, though this was only significant in the Mature structural group. Overall, cover of ground vegetation was significantly greater in second rotation stands, though not in the Closed-maturing group, whilst cover of field layer vegetation was greater in first rotation stands, though only significantly so for the Thicket and Mature groups. Soil pH was higher in the forest rotation stands at the beginning of the forest cycle but did not differ significantly in the more developed stands. Needle litter cover showed contrasting trends being greater in first rotation Thicket stands and higher in second rotation Closed-maturing stands.

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4. Discussion

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4.1 Spider and beetle diversity across the forest cycle of second rotation plantations

In second rotation plantations, the spider and beetle fauna were influenced by stand structural development, with increasing canopy cover and subsequent changes in vegetation and litter layers affecting species composition and richness. Both taxa are influenced by changes in habitat structure, which can provide hiding places for active hunters, protection from predators, greater

prey availability and a more stable microclimate (Thiele, 1977; Uetz, 1991). Such change across the forest cycle is well-documented for these taxa in temperate forests of planted and natural origin (Oxbrough et al., 2005; Buddle et al., 2006; Mullen et al., 2008; Ziesche and Roth, 2008). In this study, the relationship between beetles and forest development was less clear than that for spiders, and may be confounded by geographical location. Jukes et al. (2001) found that latitude was an important determinant of assemblage structure in conifer plantations across Britain. In Ireland a longitudinal gradient of wetter and warmer weather in the west to dryer conditions in the east (Holden et al., 2003) influences plant species distribution (Poole et al., 2003) and may also be important for Carabid beetles (Figure 3).

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For both taxa the Pre-thicket stands supported the most species open habitat species and the lowest number of forest species. This is to be expected at the early stages of the forest cycle where small trees (<3m) have little impact on the surrounding vegetation. The majority of spider indicator species identified in these stands were associated with open habitats, suggesting a predominately open fauna is supported at the Pre-thicket stage. Total richness of both taxa and open species of spiders were positively related to lower field layer vegetation, suggesting this as a potential indicator of species richness for ground-dwelling invertebrates in young second rotation forests as well as those of first rotation (Oxbrough et al., 2005). In contrast to spiders, beetles exhibited relatively low species richness in the Pre-thicket stands. Previous studies of Carabid beetles in plantation forests have had contrasting results with some reporting highest species richness in the early stages (Mullen et al., 2008; Taboada et al., 2008), some during later stages (Jukes et al., 2001) and some reporting relatively little change across the forest cycle (Day and Carthy, 1988). In the present study only one beetle species was identified as an indicator in the Pre-thicket stands suggesting that they support a generalist fauna which is common across the whole forest cycle. Consequently, this lack of open specialists may be contributing to the lower species richness observed at this stage of the forest cycle. Underlying differences in soil conditions influence beetle fauna (Cole et al., 2005), and may reflect major habitat differences such as plant species composition, soil pH and moisture. In this study, since four of the five Pre-thicket stands were on moderate-poorly drained peaty soils with low pH, it is possible that such soils support fewer beetle species than other open habitats.

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At the Thicket stage, around the time of canopy closure, richness and relative abundance of spiders associated with forest habitats increased and the assemblages formed an intermediate group between those in the Pre-thicket and the more structurally developed. The spiders were

directly influenced by tree development: total richness and open species were negatively associated with canopy cover, canopy height and mean DBH whereas forest species were positively related to cover of canopy cover and litter depth. Additionally, forest associated spiders were positively related to cover of brush piles, which may add structural complexity to a thicket habitat that generally has little vegetation cover. This suggests that the Thicket stage represents a transition from open to closed canopy habitat which can support both open and forest specialists (Oxbrough et al., 2005). The beetle assemblages were characterised by low species richness and little variation between the stands dominated by the shade-associated species *A. parallelepipedus* (80% of the captures), and there were no indicator species identified for this stage suggesting a generalist beetle fauna. Additionally, cover of canopy or vegetation layers was not an important determinant of beetle richness in the Thicket stands suggesting that whilst this stage supported both open and forest spider species, the shady conditions were no longer suitable for open beetle species, but forest species had yet to colonise in significant numbers.

15 In the later stages of the forest cycle, spider species richness declined suggesting fewer species can exploit the conditions after canopy closure. This is likely related to a corresponding reduction in vegetation complexity, which is important for spider diversity, over the forest cycle (Ferris et al., 2000). Furthermore, the species composition of stands separated by 100km was relatively similar suggesting that closed canopy conditions are more important in determining spider assemblages than local factors. By contrast, beetle species richness was greater in stands with a more developed canopy and the assemblages exhibited relatively similar levels of variation in the more developed stands as the Pre-thicket stage. Such trends have previously been observed in plantations (Jukes et al., 2001; Mullen et al., 2008; Yu et al., 2008). The presence of relatively high numbers of indicator species in more mature stands suggests a more specialised fauna.

25 Spiders colonise new areas by ground movement and aerially through ballooning, whereas Carabid beetles rely flight or movement along the ground. Consequently, after clearfelling, it may take longer for beetle species associated with undisturbed or forested habitats to colonise, leading to a gradual increase in beetle richness over the forest cycle.

30 As the canopy developed, both taxa supported increasing numbers of forest- or shade-associated species, which were positively related to factors indicating structural development (e.g. canopy cover, mean DBH). Following canopy closure, forest specialists from both taxa are likely to benefit from the structural diversity provided by increased cover of ground vegetation and litter layers (Oxbrough et al., 2005; Buddle et al., 2006; Mullen et al., 2008; Taboada et al., 2008).

Indeed, in this study beetle species associated with forested or shaded habitats were related to cover and depth of litter layers and negatively related to ground and lower field layer vegetation. Oxbrough et al., (2005) have shown that forest associated spiders are positively related to ground-vegetation, however no such relationship was found in this study. Furthermore, litter depth was negatively associated with overall spider abundance in the Reopening and Mature group, despite previous reports to the contrary (Uetz, 1979; Wagner et al., 2003). These litter layers were comprised of needles rather than leaves, but as the dominant forest cover in Ireland was historically deciduous broadleaved trees (Mitchell, 1995), these forest spiders may not be adapted to exploiting such litter layers. Overall, there were relatively few significant relationships between spiders associated with forested habitats and the environmental parameters suggesting that other factors may influence the assemblages, from small scale parameters such as humidity and temperature (Ziesche and Roth, 2008) to those acting at the larger scales including the shape and distribution of forest cover in the landscape (Barbaro et al., 2005).

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4.2 Does spider diversity differ between rotations of plantation forests?

Spider assemblages were distinguished by rotation as well as structural development, the most distinct being those of first rotation Pre-thicket. By contrast, second rotation Pre-thicket plots were not as clearly distinguished from the more developed stands. First and second rotation Pre-thicket stands supported similar numbers of open associated species, however first rotation stands had twice as many unique species as second rotation. In first rotations, rare or specialist species typical of pre-planting habitats can persist in the early stages of the forest cycle (Oxbrough et al., 2006), though these species will not remain once the canopy closes (Oxbrough et al., 2005). Therefore, open species sampled in the early stages of second rotation are likely to have colonised from surrounding areas rather than be retained from the pre-afforestation habitat. Open habitat spiders can colonise stands relatively quickly after clearfelling (Buddle et al., 2000; Matveinen-Huju et al., 2009). In this study indicator species associated with second rotation Pre-thicket stands included several species ubiquitous in open habitats, including the active hunting spiders *P. pullata* and *P. amentata* which are known to disperse by ballooning (Richter, 1970). This suggests that whilst second rotation Pre-thicket stands can support open species, they are more likely to comprise a generalist open fauna, which can exploit newly disturbed open land.

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Between rotations the younger stands differed in vegetation and edaphic characteristics. Soil pH was lower in second rotation Pre-thicket and Thicket stands even though both rotations were on

similar peaty soils. Over the forest cycle soils typically grow more acidic (Salmon et al., 2008), and so the early stages of second rotation plantations are likely to reflect those of mature forest from the previous rotation. Second rotation stands may also have had dryer soils due to a reduction in soil moisture during the first rotation caused by the canopy and root system (Babel, 1977) but also drainage measures (Forest Service, 2003). Additionally, remnant plant species associated with mature stands, present at the end of the first rotation, may be retained for several years after clear felling (Cooper et al., 2008). In this study, the early stages of second rotation had a higher ground vegetation cover predominately comprised of mosses, and the Thicket stands had a lower cover of lower field layer vegetation. This combination of factors is likely to be important for spiders, particularly for their influence on vegetation complexity.

A greater number of forest-associated species were sampled in second rotation Pre-thicket stands than those of first rotation. Such species may be remnants from the previous rotation. For instance, *Tapinocyba pallens* is typically recorded in mature forests (McFerran, 1997) and was sampled in second rotation Pre-thicket stands, but not those of first rotation. Whereas species shared between rotations included *Lepthyphantes zimmermanni* and *Monocephalus fuscipes*, both of which are commonly found in hedgerows as well as forested habitats, and may have been present prior to afforestation (Oxbrough et al., 2006). Despite this, the difference of forest-associated species between rotations was low (Table 6). The persistence of forest-associated species or their ability to re-colonise after felling, may be influenced by availability of suitable refugia including the amount of forest in the surrounding area and retained forest patches within felled stands (Schowalter, 1995; Siira-Pietikäinen and Haimi, 2009). Current forest biodiversity guidelines recommend the retention of over-mature trees during felling, but make no explicit mention of how they should be selected, in terms of patch size or shape (Forest Service, 2000). Moreover, although the guidelines recommend a mosaic of various aged stands in larger plantations, further forest planning measures may be required to ensure that clearfelled blocks are located close to mature stands for the purposes of retaining forest species.

In the Thicket stage, forest associated spiders were positively related to the cover of brush, which was a notable feature in the early stages of second rotation forests. Castro and Wise (2009) have shown that fine woody debris can influence spider species composition, and suggest that its influence on the spider fauna may be more notable in younger forests, whereas Jonsell et al. (2007) found that felling residues of just 1-4cm diameter can support red listed saproxylic beetles species. Current forest biodiversity guidelines recommend leaving dead wood in the form of

standing or downed logs to benefit saproxylic species (Forest Service, 2000), but make no mention of the management of brush piles from a biodiversity perspective. Since brush is likely to become a feature of future plantations further research is required to examine their potential to support biodiversity.

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Spider assemblages between rotations were most similar in the later stages of the forest cycle, emphasizing the importance of canopy cover in shaping the fauna. However, overall species richness was significantly greater in first rotation stands at all stages, with the exception of Pre-thicket. Greater vegetation structure may explain the difference in species richness, as first rotation stands had a greater cover of lower field layer vegetation whereas in second rotation stands ground vegetation cover was greater. In the mature stands, these differences may be explained by the much lower canopy cover in first rotation stands, which is probably due to higher thinning levels or a longer time since thinning that has allowed lower field layer vegetation to develop. It is also possible that conditions in second rotation plantations are better for tree growth i.e. more suitable soil conditions, leading to larger tree canopies and less potential for the development of structurally diverse vegetation layers.

Ideally, successive rotations would support a greater number of forest species than first rotation, however as discussed previously few forest species are retained during the open stages of second rotation forests, a similar trend has also been observed for plants (Cooper et al., 2008). In fact, there were more forest species in first rotation mature forests than in second, although the actual difference was very low (Table 6). It is clear that once a stand is felled the accumulated forest-associated spider fauna is lost. Although forest policy supports leaving over-mature trees to provide a refuge for such species, it is currently unclear the extent to which consideration is being given to over-mature trees when felling operations are planned. Despite the fact that such considerations may be difficult in regions where plantations are relatively small and productivity may be adversely affected, allowing potential refuges for forest species is important to ensure they are retained into the next rotation.

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5. Conclusions

In order to maintain or enhance invertebrate diversity in successive rotations of plantation forests the objectives of management plans should be clarified. If the goal is to enhance overall plantation diversity then the presence of stands across a range of ages, but particularly Pre-

5 thicket, will be beneficial. However, if the goal is to create a more 'natural' forest state in
plantations then management should concentrate on promoting habitat and micro-habitat features
that enhance the diversity of invertebrates associated with forests including structural attributes
and litter layers. Future research in landscapes such as Ireland, where plantations are
predominately surrounded by intensive agriculture and cover of semi-natural woodland is low,
should give particular consideration to the capacity of mature forest adjacent to felled stands to
support forest species, to the size and shape of over-mature patches and to the potential of
continuous cover forestry. Additionally, the fauna supported in native woodlands should be
examined to identify the 'ideal' forest biota. Such information is vital to inform management
10 plans of forest rotations into the future.

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Table 1. The number of sites and sampling plots within each structural group.

	No. of sites	No. of plots	Original age class (no. of plots)
<i>Pre-thicket</i>			
1 st Rotation	4	20	5 yrs (20)
2 nd Rotation	5	15	5 yrs (15)
<i>Thicket</i>			
1 st Rotation	5	25	8-15 yrs (25)
2 nd Rotation	5	15	8-15 yrs (25)
<i>Closed-maturing</i>			
1 st Rotation	8	40	8-15 yrs (15) 20-30 yrs (15) 35-50 yrs (10)
2 nd Rotation	5	15	20-30 yrs (15)
<i>Reopening</i>			
1 st Rotation	2	10	20-30 yrs (5) 35-50 yrs (5)
2 nd Rotation	2	6	35-50 yrs (6)
<i>Mature</i>			
1 st Rotation	4	20	35-50 yrs (20)
2 nd Rotation	3	9	35-50 yrs (9)

Table 2. Mean (\pm SE) values of species metrics across the forest cycle of second rotation forests. Significance tested with parametric ANOVA (F) and non-parametric Kruskal-Wallis (H) with Tukey and Nemenyi posthoc tests respectively. Test statistics in bold are significant after Bonferroni correction.

	Pre-thicket (P)	Thicket (T)	Closed-maturing (C)	Reopening (R)	Mature (M)	ANOVA df _{4,54}	Post Hoc comparisons
Spiders							
Species richness ^b	22.3 \pm 1.5	16.9 \pm 1.0	12.9 \pm 0.8	12.8 \pm 1.3	13.1 \pm 0.7	$F = 13.43^{***}$	P>T,C,R,M; T>C
Dominance	0.22 \pm 0.02	0.25 \pm 0.03	0.30 \pm 0.02	0.35 \pm 0.03	0.33 \pm 0.03	$F = 3.97^{**}$	P<R,M
Open species richness	5.53 \pm 0.65	2.07 \pm 0.53	0.27 \pm 0.12	0	0.11 \pm 0.11	$H = 42.66^{***}$	P>T,C,R,M; T>C,R,M
Forest species richness	3.53 \pm 0.40	4.29 \pm 0.30	5.67 \pm 0.35	6.83 \pm 0.75	6.00 \pm 0.33	$F = 10.07^{***}$	P<C,R,M; T<R,M
Open relative abundance	0.26 \pm 0.04	0.06 \pm 0.03	0.01 \pm 0	0	0.01 \pm 0	$H = 43.81^{***}$	P>T,C,R,M
Forest relative abundance	0.15 \pm 0.03	0.29 \pm 0.03	0.66 \pm 0.04	0.72 \pm 0.05	0.77 \pm 0.03	$F = 50.27^{***}$	P<C+R+M; T<C,R,M
Beetles							
Species richness ^b	9 \pm 1.2	7.1 \pm 1.1	8.3 \pm 0.8	13.2 \pm 5.4	12 \pm 0.9	$F = 4.29^{**}$	T<R,M
Dominance	0.49 \pm 0.04	0.83 \pm 0.05	0.61 \pm 0.05	0.33 \pm 0.13	0.45 \pm 0.04	$F = 16.53^{***}$	T>P,C,R,M; C>R
Open species richness	2.20 \pm 0.48	0.93 \pm 0.29	0.53 \pm 0.17	1.00 \pm 0.41	0.89 \pm 0.26	$H = 16.79^{**}$	P>T,C
Shaded species richness	1.73 \pm 0.18	1.93 \pm 0.22	2.93 \pm 0.26	3.50 \pm 1.43	3.67 \pm 0.24	$H = 29.06^{***}$	P<C,R,M; T<R,M
Forest species richness	0.40 \pm 0.13	0.57 \pm 0.17	1.20 \pm 0.18	2.17 \pm 0.88	1.33 \pm 0.33	$H = 20.82^{***}$	C>P, R>P+T
Open relative abundance	0.17 \pm 0.03	0.01 \pm 0.01	0.01 \pm 0	0.01 \pm 0	0.02 \pm 0.01	$H = 34.74^{***}$	P>T,C,R,M
Shaded relative abundance	0.45 \pm 0.05	0.84 \pm 0.05	0.61 \pm 0.06	0.46 \pm 0.19	0.57 \pm 0.07	$H = 22.28^{***}$	T>P,R
Forest relative abundance	0.01 \pm 0	0.01 \pm 0	0.07 \pm 0.03	0.03 \pm 0.01	0.01 \pm 0	$H = 28.89^{***}$	P,T<C,R

^b Square root transformed; ANOVA significance: *P = \leq 0.05; **P = \leq 0.01; ***P = \leq 0.001

Table 3. Spider species identified in each structural group by Indicator Species Analysis and their habitat preference. Species with a significant indicator value (P = <0.05) are shown.

	Indicator Value (%)					Habitat preference
	Pre-thicket (n = 15)	Thicket (n = 14)	Closed-maturing (n = 15)	Reopening (n = 6)	Mature (n= 9)	
<i>Pardosa pullata</i>	70***	1	0	0	0	Open
<i>Pocadicnemis pumila</i>	68***	9	0	0	0	Open
<i>Dismodicus bifrons</i>	53**	14	0	0	0	Generalist
<i>Walckenaeria vigilax</i>	47**	0	0	0	0	Generalist
<i>Pardosa nigriceps</i>	46**	2	0	0	0	Open
<i>Trochosa terricola</i>	45**	2	0	0	0	Generalist
<i>Peponocranium ludicrum</i>	40**	1	0	0	0	Generalist
<i>Bathyphantes parvulus</i>	40**	0	0	0	0	Open
<i>Metpobactus prominulus</i>	36*	0	0	0	0	Generalist
<i>Ero cambridgei</i>	33**	0	0	0	0	Generalist
<i>Pardosa amentata</i>	33**	0	0	0	0	Open
<i>Lepthyphantes ericaeus</i>	33**	6	12	0	3	Generalist
<i>Nerienne clathrata</i>	31*	2	0	0	0	Generalist
<i>Pocadicnemis juncea</i>	30*	2	0	0	0	Open
<i>Oedothorax gibbosus</i>	26*	3	0	0	0	Open
<i>Walckenaeria acuminata</i>	3	47**	6	1	5	Generalist
<i>Agyneta ramosa</i>	32	42**	12	2	5	Generalist
<i>Agyneta conigera</i>	1	37**	2	0	0	Generalist
<i>Ozyptila trux</i>	1	33*	0	0	0	Generalist
<i>Monocephalus fuscipes</i>	3	21	38***	15	13	Forest
<i>Pelocopsis nemoralis</i>	0	0	38**	2	1	Forest
<i>Centromerus dilutus</i>	0	10	35*	13	10	Generalist
<i>Lepthyphantes zimmermanni</i>	6	7	32*	31	23	Forest
<i>Diplocephalus latifrons</i>	0	0	4	54***	33	Forest
<i>Asthenargus paganus</i>	2	6	17	40**	13	Forest
<i>Robertus lividus</i>	7	11	13	36*	5	Generalist
<i>Lepthyphantes tenebricola</i>	0	0	2	21	55**	Forest
<i>Lepthyphantes flavipes</i>	0	0	6	4	48**	Forest

Significance of Monte Carlo tests: * P= <0.01; ** P= ≤0.005; ***P = ≤0.001

Table 4. Beetle species identified in each structural group by Indicator Species Analysis and their habitat preference. Species with a significant indicator value (P = <0.05) are shown.

	Indicator Value (%)					Habitat preference
	Pre-thicket (n = 12)	Thicket (n = 14)	Closed-maturing (n = 15)	Reopening (n = 6)	Mature (n= 9)	
<i>Carabus granulatus</i>	63***	4	1	2	13	Open
<i>Cychrus caraboides</i>	1	1	53***	21	7	Forest
<i>Pterostichus madidus</i>	1	0	0	77***	16	Generalist
<i>Notiophilus biguttatus</i>	0	0	11	63***	24	Shaded
<i>Calathus rotundicollis</i>	0	0	0	61***	4	Forest
<i>Pterostichus nigrita</i>	16	12	8	42**	5	Generalist
<i>Loricera pilicornis</i>	0	0	1	38**	15	Generalist
<i>Pterostichus melanarius</i>	7	5	14	38*	29	Generalist
<i>Amara Plebeja</i>	0	0	0	33*	0	Generalist
<i>Bembidion lampros</i>	6	1	0	30*	0	Open
<i>Nebria brevicollis</i>	0	0	0	36	55**	Shaded
<i>Pterostichus niger</i>	0	0	1	1	44**	Generalist
<i>Leistus terminatus</i>	1	2	3	10	33*	Generalist
<i>Paranchus albipes</i>	0	0	0	0	22*	Generalist

Significance of Monte Carlo tests: * P= <0.05; ** P= ≤0.01; ***P = ≤0.001

Table 5. Relationship between species metrics and environmental variables within each structural group (n = number of plots). Only significant (P < 0.05) Spearman's Rho correlations are shown and the direction of the relationship indicated with + or – respectively. Correlations significant after Bonferroni correction are shown in bold.

	Prethicket (n = 15)	Thicket (n = 14)	Closed maturing (n = 15)	Reopening + Mature (n = 15)
<i>Spiders</i>				
Total species richness		-Canopy cover**		
Abundance		-Canopy cover**	-Soil pH*	-Litter depth*
Dominance			+Canopy height* +Mean DBH*	+Canopy cover*
Open species richness	+Lower field layer*	-Mean DBH* -Canopy cover** -Brush*		
Forest species richness		-Ground vegetation* +Litter depth**		
Open relative abundance	+Lower field layer** -Upper field layer* -Needle litter cover* +Soil pH*	-Canopy height* -Canopy cover* +Lower field layer* -Brush**		
Forest relative abundance		+Canopy cover* +Brush**		+Mean DBH*
<i>Beetles</i>				
Species richness	+Lower field layer*	+Soil pH**		
Abundance		+Needle litter*	+Canopy height*** +Mean DBH**	+Soil pH*
Dominance	-Lower field layer* +Canopy cover*	-Soil pH* -Brush*	+Mean DBH*** +Litter depth**	
Open species richness	+Soil pH*			
Shaded species richness		+Soil pH***		
Forest species richness				
Open relative abundance	+Brush**	-Brush**		
Shaded relative abundance	-Lower field layer** +Upper field layer* +Canopy cover* -Soil pH*		+Mean DBH** +Litter depth* -Brush**	
Forest relative abundance				-Ground vegetation* -Lower field layer* +Needle litter**

Spearman's Rho correlation significance: * P= <0.05; ** P= ≤0.01; ***P = ≤0.001

RA = Relative Abundance; S = Species Richness

Table 6. Total number of unique species and mean \pm SE spider species richness (S) between first and second rotation plantation forests within each structural group. Significance tested with parametric ANOVA (F) and non-parametric Kruskal-Wallis ANOVA (H). Test statistics in bold are significant after Bonferroni correction (P <0.05).

	Unique species	Observed S	Expected S [†]	Open S	Forest S
<i>Pre-thicket (n = 35, df 1,34)</i>					
1st Rotation	24	17.0 \pm 1.4	16.5 \pm 1.3	4.9 \pm 0.5	1.1 \pm 0.2
2nd Rotation	12	17.5 \pm 1.6	17.3 \pm 1.6	4.2 \pm 0.7	2.7 \pm 0.3
ANOVA	-	n.s	n.s	n.s	F = 17.3***
<i>Thicket (n = 42, df 1,41)</i>					
1st Rotation	22	18.8 \pm 0.8	17.7 \pm 1.1	1.8 \pm 0.3	4.6 \pm 0.3
2nd Rotation	6	13.2 \pm 1.1	13.1 \pm 0.7	1.3 \pm 0.4	3.7 \pm 0.3
ANOVA	-	F = 16.8***	F = 12.6***	n.s	n.s
<i>Closed-maturing (n = 49, df 1,48)</i>					
1st Rotation	9	14.0 \pm 0.4	13.2 \pm 0.3	0.34 \pm 0.1	5.4 \pm 0.2
2nd Rotation	3	11.3 \pm 0.8	11.2 \pm 0.7	0.2 \pm 0.1	5.2 \pm 0.3
ANOVA	-	F = 8.3**	F = 12.9***	n.s	n.s
<i>Reopening (n = 15, df 1,14)</i>					
1st Rotation	4	14.6 \pm 0.8	13.9 \pm 0.7	0	6.6 \pm 0.5
2nd Rotation	1	11.2 \pm 1.4	11.1 \pm 1.4	0	6 \pm 0.6
ANOVA	-	F = 5.4*	n.s	n.s	n.s
<i>Mature (n = 28, df 1,27)</i>					
1st Rotation	13	17.8 \pm 1.1 a	17.0 \pm 1.0 a	1.0 \pm 0.2	6.7 \pm 0.2
2nd Rotation	2	11.4 \pm 0.7 a	11.4 \pm 0.7 a	0	5.8 \pm 0.3
ANOVA	-	F = 16.7***	F = 14.6***	U = 36**	F = 7.2*

*P = \leq 0.05; **P = \leq 0.01; ***P = \leq 0.001

[†] Standardised by trap day; ^a Data square root transformed

Table 7. Mean \pm SE environmental variables between first and second rotation forests within each structural group. Significance tested with parametric ANOVA (F) and non-parametric Kruskal-Wallis ANOVA (H). Test statistics in bold are significant after Bonferroni correction. Only environmental variables with a mean coverage of >5% within a structural group are included.

	Canopy cover (%)	Canopy height(m)	Mean DBH (cm)	Fine Woody Debris (%)	Ground vegetation (%)	Lower field layer vegetation (%)	Needle Litter (%)	Soil pH
<i>Pre-thicket (n = 35, df 1,34)</i>								
1st Rotation	27.5 \pm 3.1	2.4 \pm 0.2	3.4 \pm 0.4	0	6.3 \pm 0	52.3 \pm 0.1	0.1 \pm 0.1	5.3 \pm 0.2
2nd Rotation	47.7 \pm 3	2.9 \pm 0.1	3.4 \pm 0.1	0.12 \pm 0.1	47.7 \pm 4.9	57.3 \pm 8.9	0.2 \pm 0.1	4.2 \pm 0.1
ANOVA	F = 20.2***	n.s	n.s	n/a	U = 6***	n.s	n/a	U = 27***
<i>Thicket (n = 42, df 1,41)</i>								
1st Rotation	78.3 \pm 2.9	6.1 \pm 0.4	12 \pm 0.5	0.8 \pm 0.2	33.1 \pm 4.8	25.1 \pm 4	53 \pm 4.9	5.1 \pm 0.1
2nd Rotation	80 \pm 4.1	6.3 \pm 0.3	9.3 \pm 0.9	2.3 \pm 0.5	77.4 \pm 6	2.3 \pm 0.6	24.6 \pm 6	4 \pm 0.1
ANOVA	n.s	n.s	F = 8.25**	n/a	F = 33.7***	U = 91.5**	U = 73.5***	U = 16.5***
<i>Closed-maturing (n = 49, df 1,48)</i>								
1st Rotation	86 \pm 1.6	12.4 \pm 0.4	19.3 \pm 0.7	11 \pm 2.1	18.1 \pm 2.9	0.5 \pm 0.5	75.9 \pm 2.5	4.6 \pm 0.1
2nd Rotation	90 \pm 3	13.9 \pm 1	18.7 \pm 1	6.1 \pm 1.5	13.1 \pm 4.2	0.1 \pm 0	84.7 \pm 7.3	4.3 \pm 0.1
ANOVA	n.s	n.s	n.s	n.s	n.s	n/a	F = 23.2***	n.s
<i>Reopening (n = 15, df 1,14)</i>								
1st Rotation	69.1 \pm 4.7	19.2 \pm 0.4	21.1 \pm 1	17 \pm 4.3	16.5 \pm 3.1	7.6 \pm 6.2	67.6 \pm 6.6	4.6 \pm 0.2
2nd Rotation	80.8 \pm 2.7	21.5 \pm 0.5	31.7 \pm 2.2	8.6 \pm 2	44.2 \pm 12.5	0.1 \pm 0.1	60.1 \pm 11.9	4.2 \pm 0.2
ANOVA	n.s	F = 11.38**	F = 26.8***	n.s	U = 9*	n.s	n.s	n.s
<i>Mature (n = 28, df 1,27)</i>								
1st Rotation	53.3 \pm 1.8	21.9 \pm 0.4	37.0 \pm 1.3	15.5 \pm 2.0	60.7 \pm 4.4	29.6 \pm 5.7	21.8 \pm 4.5	4.57 \pm 0.08
2nd Rotation	71.7 \pm 4.1	26.4 \pm 0.9	37.3 \pm 1.8	8.3 \pm 1.4	91.6 \pm 10.4	6.3 \pm 2.3	21.9 \pm 6.9	4.40 \pm 0.16
ANOVA	U = 27.5**	F = 33.4***	n.s	U = 45*	U = 38.5*	U = 41*	n.s	n.s

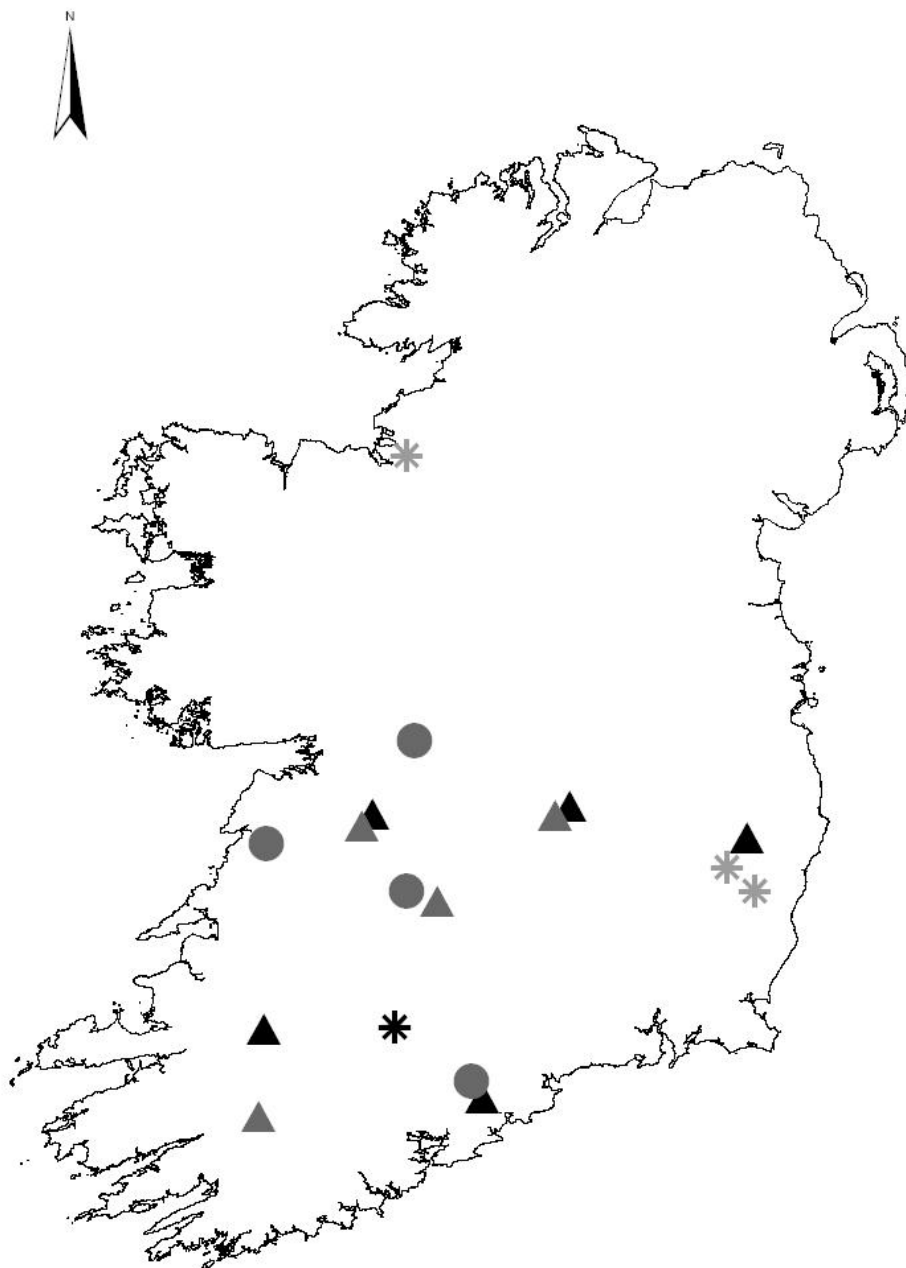


Figure 1 Distribution of study site clusters and individuals sites, grey symbols represent first rotation stands and black symbols second rotation stands: ▲ cluster of sites (all age classes); ▲ cluster of sites (age classes 2-4); ● age class 1; *age class 4.

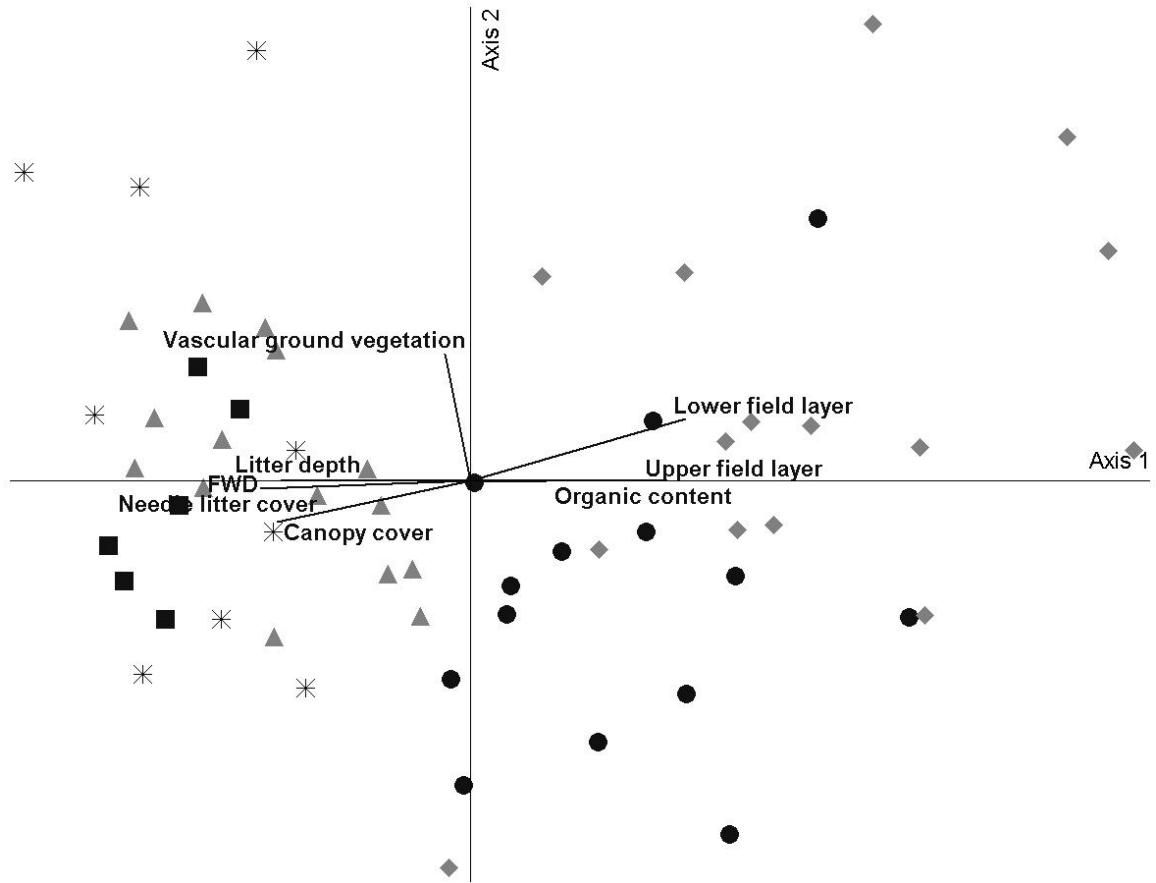


Figure 2 NMS ordination of spider assemblages across second rotation forest cycle: ◆ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Reopening; * Mature. Variables with a Pearson correlation coefficient significant of $P < 0.05$ are shown. Cumulative variation in the original dataset explained by the ordination is 79%: Axis1 = 62%, Axis 2 = 17%, Final Stress = 18.1; Final Instability = 0.0001.

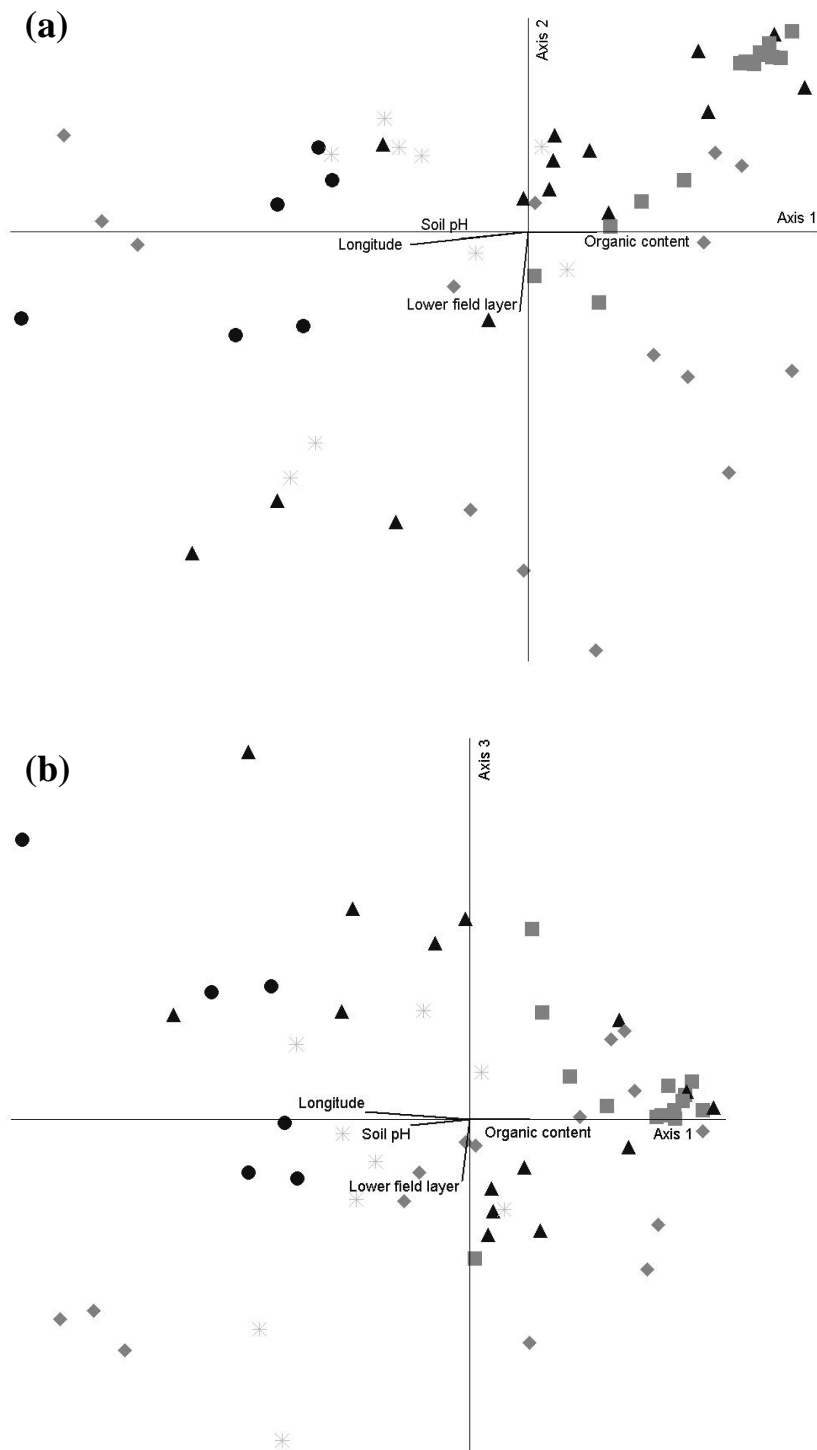


Figure 3 NMS ordination of beetle assemblages across the forest cycle of second rotation plantations: a) Axes 1 and 2; and b) Axes 1 and 3. Structural groups are shown by ◆ Pre-thicket, ■ Thicket, ▲ Closed-maturing, ● Reopening, * Mature. Cumulative variation in the original dataset explained by the ordination is 94%: Axis1 = 40%, Axis 2 = 30%; Axis 3 = 24%, Final Stress = 9.30; Final Instability = 0.0001.

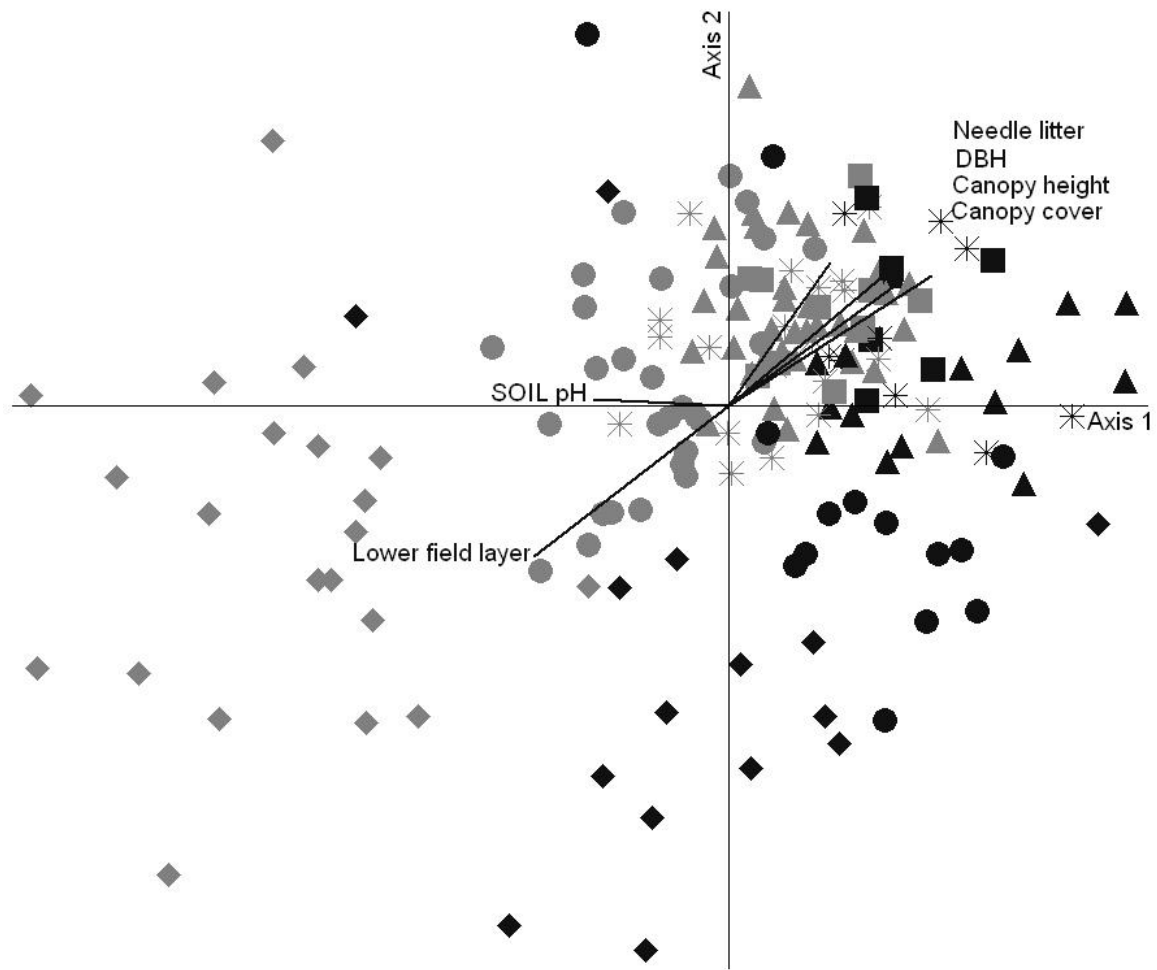


Figure 4: NMS ordination of spiders in first (grey symbols) and second (black symbols) rotation plantations at different stages of the forest cycle: ◆ Pre-thicket; ● Thicket; ▲ Closed-maturing; ■ Reopening; * Mature. Cumulative variation in the original dataset explained by the ordination is 81%: Axis1 = 50%, Axis 2 = 31%, Final Stress = 21.42; Final Instability = 0.0006.