Master of Science Thesis

The importance of novel ecosystems for biodiversity – a study of ground beetles (Carabidae) on afforested fields

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6.8.2014

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Övermark, E.:	The importance of novel ecosystems for biodiversity – a study of ground beetles (Carabidae) on afforested fields
Master of Science Thesis:	24 p.
Supervisors:	D.Sc Atte Komonen, PhD Panu Halme
Inspectors:	
August 2014	

Key Words: abundance, boreal forest, Coleoptera, compensatory habitat, disturbance, peat field, restoration, succession

ABSTRACT

Deforestation, cultivation and other land management practices are transforming ecosystems in increasingly amounts. As a consequence, exceptional anthropogenic ecosystems will arise. The importance of these novel ecosystems for biodiversity will increase in the near future as the human impact on the Earth increases. Afforested fields could in many cases be regarded as novel ecosystems: Fertilizing has long lasting effects on the physical features of the soil and the amount of nutrients is higher in afforested field than in natural forest. However, the precise outcome of vegetation development is not yet known. In Finland, the area of afforested fields is now almost 300 000 hectares and their possible positive importance for the biodiversity is still insufficiently known. Carabids are widespread group of beetles and found almost in all kinds of habitats. They are surface active predators and an important link in ecosystem processes including nutrient fluxes and food web regulation. Ground beetles reflect changes in their environment – especially disturbances caused by human actions – in short period of time. Although the effects of different land use activities to ground beetles have been studied extensively in many kinds of environments, there has been only few research focused on carabids of afforested fields. The overall aim of this study was to achieve knowledge about what kind of ground beetle species afforested fields maintain in Finland and what is their abundance and composition in these habitats. Furthermore, I studied the importance of wooded species for ground beetle species composition and community structure. I had a field experiment in former agricultural peat soils which were afforested about 25 years ago. My research included 8 study sites which were situated in Central Finland and Ostrobothnia. A total of 4018 carabid individuals representing 40 species were recorded. Overall, species composition and abundance was exceptional in comparison with managed forests. Contrary to hypothesis, the number of species and individuals did not differ between wooded species. However, the similarity of carabid community depends both on tree species and geographical location (study site) when they were considered together. Altogether, it seems that afforested fields in this study really are novel ecosystems at least in regard to carabids due to their exceptional composition and abundance in these habitats.

JYVÄSKYLÄN YLIOPISTO, Matemaattis-luonnontieteellinen tiedekunta

Bio- ja ympäristötieteiden laitos
Ekologia ja evoluutiobiologia

Övermark, E.:	Uusekosysteemien tärkeys monimuotoisuudelle – tutkimus metsitettyjen peltojen maakiitäjäisistä (Carabidae)
Pro Gradu -tutkielma:	24 s.
Työn ohjaajat:	MMT Atte Komonen, FT Panu Halme
Tarkastajat:	
Elokuu 2014	

Hakusanat: boreaalinen metsä, ennallistaminen, häiriö, korvaava elinympäristö, kovakuoriaiset, runsaus, sukkessio, turvepelto

TIIVISTELMÄ

Metsien hävittäminen, maanviljely ja muut ympäristöä muokkaavat toimet muuttavat ekosysteemejä kasvavissa määrin. Tämän seurauksena syntyy poikkeuksellisia, ihmisen toiminnasta peräisin olevia ekosysteemejä. Näiden uusekosysteemien merkitys monimuotoisuudelle kasvaa lähitulevaisuudessa kun ihmisen vaikutus Maahan lisääntyy. Metsitetyt pellot voidaan monessa tapauksessa lukea uusekosysteemeihin: lannoituksella on pitkäaikaisia vaikutuksia maaperän fysikaalisiin ominaisuuksiin ja ravinteiden määrä on metsitetyillä pelloilla suurempi kuin tavallisissa metsissä. Kasvillisuuden sukkession tarkkaa lopputulosta ei vielä tiedetä. Metsitetyt pellot käsittävät 300 000 hehtaaria Suomen pinta-alasta ja niiden mahdollinen positiivinen merkitys monimuotoisuudelle on toistaiseksi puutteellisesti tiedossa. Maakiitäjäiset ovat yleinen kovakuoriaisryhmä ja niitä löytyy lähes kaikista habitaateista. Ne ovat pohjakerroksen petoja ja tärkeä osa ekosysteemin prosesseja kuten ravinteiden kiertoa ja ravintoverkon säätelyä. Maakiitäjäiset heijastelevat muutoksia ympäristössään – etenkin ihmisen toiminnasta peräisin olevia häiriöitä – lyhyessä ajassa. Vaikka erilaisten maanmuokkaustoimenpiteiden vaikutuksia maakiitäjäisiin on tutkittu laajalti erilaisissa ympäristöissä, vain harva tutkimus on keskittynyt metsitettyjen peltojen maakiitäjäisiin. Tämän tutkimuksen tarkoituksena oli saada tietoa siitä millaisia maakiitäjäislajeja metsitetyillä pelloilla esiintyy Suomessa ja mikä on niiden runsaus ja koostumus näissä habitaateissa. Lisäksi tutkin istutetun puulajin merkitystä maakiitäjäislajiston koostumukselle ja yhteisön rakenteelle. Tein kenttäkokeen aiemmin viljelykäytössä olleilla turvepohjaisilla pelloilla, jotka oli metsitetty noin 25 vuotta sitten. Kenttäkoe piti sisällään 8 kohdetta, jotka sijaitsivat Keski-Suomessa ja Pohjanmaalla. Yhteensä 4018 maakiitäjäisyksilöä ja 40 lajia löydettiin. Kaiken kaikkiaan lajikoostumus ja -runsaus oli poikkeuksellinen verrattuna talousmetsiin. Vastoin hypoteesia, lajirikkaus ja yksilömäärä ei kuitenkaan eronnut eri puulajien välillä. Tästä huolimatta maakiitäjäisyhteisön samankaltaisuus riippui sekä puulajista että maantieteellisestä sijainnista (tutkimusalue) kun niitä tarkasteltiin yhdessä. Yhteenvetona, metsitetyt pellot tässä tutkimuksessa vaikuttaisivat todella olevan uusekosysteemejä ainakin maakiitäjäisten osalta niiden poikkeuksellisesta koostumuksesta ja runsaussuhteista johtuen.

Contents

1. INTRODUCTION

Human population has always changed its environment since prehistoric man started to log forests to give way for sedentary agriculture (Redman 1999, Ellis et al. 2010). The agricultural practices made possible for people to establish permanent settlements and allowed the rise of human civilization (Gupta 2004). However, after industrialization, the expansion of human land use has been escalating (Ojima et al. 1994, Ellis et al. 2010). Through habitat loss and fragmentation, human land use has serious consequences for biodiversity around the world (Miller & Hobbs 2002) like species loss. Deforestation and other land management practices are transforming ecosystems (Redman 1999). Land is being converted into agricultural and other purposes in increasingly amounts (Meyer & Turner 1992).

At the same time with deforestation and other land use activities, part of the previously managed lands is being abandoned or restored (Hobbs & Cramer 2007). Defining what ecological restoration exactly means is not as obvious as one might think and there are several definitions currently used. The Society for Ecological Restoration International has defined ecological restoration as: *"The process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed"* (SER 2004). Abandoned fields can in some case be returned to the preceding habitat types through restoration activities (Wall 1998, Hobbs & Cramer 2007). However, the recovery of these areas depends on the land use history, time being elapsed after cultivation, physical and chemical qualities of the soil and random factors (Jukola-Sulonen 1983).

Although the area could not be restored to the same habitat, which it was earlier, the new habitat that will arise can still be important for the biodiversity. These ecosystems which arise from human actions are called "novel ecosystems" (Hobbs et al. 2006). Other required key characteristic for novel ecosystems is the new species combination. Hobbs et al. (2006) defined novel ecosystems: "*Novel ecosystems result when species occur in combinations and relative abundances that have not occurred previously in a given biome*". Afforested fields could in many cases be regarded as novel ecosystems. Novel systems can arise for example through invasion of native ecosystems or by abandonment of intensively managed systems (Hobbs et al. 2006). The importance of novel ecosystems will increase in the near future as the human impact on the Earth increases. Novel ecosystems may, for example, be valuable environments especially when considering biodiversity. Inspite of these facts, novel ecosystems are relatively little studied (Hobbs et al. 2006) and the understanding of the ecological consequence of these systems for biodiversity is still poor (Cramer et al. 2008).

I studied the importance of novel ecosystems for biodiversity using ground beetles of afforested fields as study organisms. The importance of tree species for carabids was at special interest. Ground beetles were used as a measure of diversity and their composition and abundance was also examined. Afforested fields may contain ground beetle species in combinations and relative abundances differing from everything distinguished before. In other words, afforested fields may function as novel ecosystems or as compensatory habitats.

2. FIELD AFFORESTATION

Although the area of forest cover is globally decreasing currently, field afforestation is widely practiced in many countries (Wall 1998, O'Leary et al. 2000, Madsen 2002). In some countries the area of forest land is even increasing (Kauppi et al. 2006). EU has funded afforestation of fields from the year 1992 onward and since it has become part of EU-politics (Madsen 2002). Tax-free incentives have worked for example in Ireland, where the area of afforested fields increased considerably between years 1984 and 1995 (O'Leary et al. 2000). One aim of field afforestation is to reduce CO-emissions in the EU-region because forests absorb carbon during growth, in other words, they act as carbon sinks.

Field afforestation is taking place also in Finland. The area of afforested fields is now almost 300 000 hectares (Wall 1998, Metsätilastollinen vuosikirja 2013). Last year, the area of newly afforested field was 1693 hectares (Metsätilastollinen vuosikirja 2013). Most of this area is located in North Karelia. Nearly all are in a private ownership and almost all were funded by government. However, the intensity of field afforestation has been changing during recent decades. Afforestation was started in Finland in the late 1960s due to mechanization and agricultural overproduction (Hytönen 1999). In 1969, changes in law statute enabled to get reimbursements from afforestation of abandoned fields (Tilli & Toivonen 2000). This economical help encouraged people to afforestation and as a result, the area of afforested fields started to increase (Tilli & Toivonen 2000) and in 1993, the yearly afforested area was at its maximum (Metsätilastollinen vuosikirja 2013).

However, also the volume of afforestation varies a lot across Finland. In southern and western Finland agriculture is more intensive and the area of abandoned fields is lower than for example in eastern Finland, where most of the afforestation is done due to depopulation (Selby 1990). Topography may also affect, because in western Finland ground is more flat and, due to that, better for cultivation than more hilly landscape in eastern Finland. For the most part afforestation has focused on fields which are underproductive or already removed from agricultural use (Valtanen 1991). Despite the afforestation, the forest land cover has not changed in Finland because forests have been simultaneously transformed to agricultural and urban land (Selby 1990).

Inspite of where the field is afforested, it will become exceptional habitat during the afforestation process. Activities during agricultural use to improve crop size, like fertilizing, have long lasting effects on the physical features of the soil. Fertilizers increase the amount of organic matter and make the soil more nutrient rich (Johnson 1992, Mann 1986). The amount of nutrients is higher in afforested field than in natural forest. Wall & Hytönen (2005) measured that the soil of fields afforested 10 years ago contained significantly more nitrogen (N), phosphorous (P), kalium (K), calcium (Ca), mangan (Mg), zinc (Zn) and boron (Br) compared to continuously forested sites. Furthermore, high nutrient load seems to remain long time in the soil, because in the same study fields afforested even 60-70 years ago contained still significantly more nitrogen (N), calcium (Ca) and zinc (Zn) than continuously forested sites. Wall & Hytönen (2005) also confirmed that because of liming, soil pH is higher both 10 and 60-70 years after afforestation compared to continuously forested sites. In addition, in afforested peat fields it was common to use mineral soil as soil amendment to improve nutrient content of the soil. Mineral soil has also increased density and ash concentration and it may have changed the plough layer from peat to mold when heavily used (Wall & Hytönen 1996).

Naturally, physical and chemical features of the soil influence directly on the development of vegetation. The development is also influenced by the cultivation technique, time elapsed after cultivation and random effects (Jukola-Sulonen 1983). First after afforestation, weed plants gain ground and after that, meadow grasses will take place (Jukola-Sulonen 1983). However, the development of vegetation from field to forest species is a slow process (Wall 1998). It takes time from field vegetation to change into forest vegetation because the seed bank of weeds is large and remains very long time in the soil (Thompson et al. 1998). However, the precise outcome of vegetation development is not yet known (Wall 1998). As a result of several factors, the new forming habitat is not likely to be the same as it was before cultivation, but rather something exceptional, a novel ecosystem.

3. THEORETICAL FRAMEWORK

Disturbances belong to boreal forest ecosystem (Pickett & White 1985). According to Pickett & White (1985), disturbance is an event that modifies physical environment and affects the temporal and spatial heterogeneity of the ecosystem. For some species, new available space and resources are created, for others it is a source of mortality. In this way disturbance disturbs the community structure and further many populations. Diversity and regeneration of natural forests is maintained by different kinds of irregularly frequent disturbances like wildfires, storms, pests, parasites and some keystone species like beaver (Esseen et al. 1997, Engelmark 1999). Humans are also causing disturbances to forest ecosystems by forest management (Niemelä 1999). The extent of disturbance varies according to the area which it affects (Kuuluvainen 1994). Individual tree deaths caused by insects are small scale disturbances whereas extensive disturbances may be produced by forest fires. The intensity, extent and interval between disturbances affects what kind of structures and composition are created in forests. These structures are, for example, variation in tree species composition, size and developmental stage (Angelstam 1998). Structures in turn have immediate impact on the dynamics of populations and species whose habitat the forest is. Gray (1989) predicts that species richness would decrease as the disturbances increase. On the other hand, according to Connell`s (1978) intermediate disturbance hypothesis, the species richness would be at its maximum in a community that experiences moderate disturbances in frequent mean. Connell (1978) argued that intermediate disturbances would prevent domination of some species and therefore the community would contain both pioneer and climax stage species. Cultivation can be considered as a long lasting intensive disturbance after which afforestation will help the ecosystem begin to recover.

The regeneration of forest after disturbance is called succession. During proceeding succession, community composition and abundances of species change (Kellomäki 2005). In forest environment succession is seen as development of young forest to old one (Horn 1974). This development is highly based on competition (Horn 1974) because the early successional species are replaced by late successional species when the lighting conditions are changing in the system due to canopy closing (Bergeron & Dubuc 1989). Heterotrophic species follow this change. Finally the forest achieves climax (Odum 1971) where the older trees, which developed first after the disturbance, start to decay and make space for new tree generations (Kuuluvainen 2004).

Field afforestation is a classic example of secondary succession (Hobbs & Cramer 2007). Nevertheless, comparing ecosystems modified by human actions to natural succession development has been criticized (Walker et al. 2007). Afforestation of a field is a process caused by human activity and therefore it is not truly a natural succession process. Still, afforestation of a field could be thought as a kind of a middle point in the longitudinal axis where other end describes natural ecosystem and the other intensively utilized system (Sanderson et al. 2002).

4. GROUND BEETLES AND AFFORESTATION

Ground beetles (Coleoptera: Carabidae) are one of the best known species groups in northern hemisphere (Niemelä et al. 2000). Carabids are abundant and found in all kinds of habitats except deserts. This is why they are usually classified into forest, open land and generalist species (Niemelä et al. 1988). Ground beetles belong to predaceous beetles (Adephaga) and most carabids truly are predatory, but species feeding on both plant material and carcasses also occur (Lövei & Sunderland 1996). One of the most important mortality sources for carabids is predators, although pathogens and parasites may also be important for younger developmental stages. In other words, ground beetles occur almost globally, they are seen as the most important surface active predators of ground layer, which consume a wide range of food types and are themselves food to other species. Overall, ground beetles are an important link in ecosystem processes including nutrient fluxes and food web regulation.

In several studies, ground beetles have been used as indicators (Rainio & Niemelä 2003), because they reflect changes in their environment – especially disturbances caused by human actions – in short period of time. The effects of different land use on carabids have been studied widely in different kinds of environments around the world (Beaudry et al. 1997, Jukes et al. 2001, Plath et al. 2012). Most of these studies have concentrated on effects of forest management (Beaudry et al. 1997, Koivula 2002a, Toigo et al. 2013) and habitat fragmentation (Koivula & Vermeulen 2005).

Forest management seems to have several impacts on carabid community composition. Species richness can increase (Toigo et al. 2013), decrease (Magura et al. 2003) or stay constant (Koivula et al. 2002b) after forest management. Usually, as a result of clear cut, the dramatic changes in carabid community composition (Niemelä et al. 2007) appear to benefit open land and generalist species, at least temporally.

These different study results indicate that forest management is not the only factor influencing to species richness in carabid community. Dominant tree species, age of trees and their structure affects also (du Bus de Warnaffe & Dufrene 2004, Janssen et al. 2009, Taboada et al. 2010). Especially the canopy seems to be important structural factor influencing the light conditions of the ground layer (Jukes et al. 2001, Vanbergen et al. 2005). Open land and generalist species prefer more intensive light and drier conditions (Niemelä et al. 2007). The dominant tree species affect naturally litter quality and depth (Guillemain et al. 1997, Antvogel & Bonn 2001, Stroka & Finch 2006). The litter in turn, has influence on the established microclimates (Stroka & Finch 2006) and small-scale heterogeneity (Niemelä et al. 1996). Furthermore, many of the ground beetles are predators and their prey like springtails prefer litter as their habitat (Loranger et al. 2001). It has been demonstrated that abundant leaf litter has positive impact on carabid species richness (Magura et al. 2000 but see Guillemain et al. 1997). In addition, arising litter layer affects soil pH. Species richness has been shown to correlate positively with pH in studies focused on forests (Magura et al. 2003, Stroka & Finch 2006). This was believed to be a result from the absence of sensitive stages of development like eggs and larvae and species preferring acid conditions (Lindroth 1997). In conclusion, the identity of structural species with great biomass (e.g. trees) has significant effect on ground floor predators.

There has been only few research focused on ground beetles of afforested fields (Lindgren 2000), although research has been extensive in other kinds of environments (Antvogel & Bonn 2001, Jukes et al. 2001, Plath et al. 2012). Furthermore, the research made in afforested fields is usually considered on the forestry point of view. However, afforested fields offer different types of habitats because the variation of understory vegetation is considerable and different from any other forest types. Novel ecosystems may also contain ground beetle species in combinations and relative abundances differing from any other habitat. Already, the importance of novel ecosystems for biodiversity may be significant and their importance will probably still increase in near future as the expansion of human land use escalates.

5. RESEARCH QUESTIONS AND HYPOTHESIS

The overall aim of this study was to achieve knowledge about what kind of ground beetle species afforested fields maintain in Finland and what is their abundance and composition in these habitats. Furthermore, I studied the importance of tree species in determining carabid community. The hypothesis was that because afforested field is a mixture of agricultural legacy and current vegetation, there would be both forest and generalist species in these habitats. It was also hypothesized that the abundance and composition of ground beetles would be higher in birch plots compared to conifer plots because it has been shown that abundant leaf litter has positive impact on carabid species richness (Magura et al. 2000). The results of this study help in understanding if these habitats could function as novel ecosystems or suitable compensatory habitats for rare or endangered species. The research questions of this work were: (1) What kind of ground beetle species are there at afforested fields and what is their abundance? (2) Are there any rare or endangered species present? (3) What is the effect of tree species to ground beetle species composition and community structure? (4) Does the carabid community of afforested field differ between study sites?

6. MATERIALS AND METHODS

6.1. Study sites

I sampled ground beetles from forested fields that were wooded about 25 years ago. The study was carried out in the summer 2013 in 8 afforested field sites in Central Finland and Ostrobothnia. One of the study sites was located in Central Finland and the rest in Ostrobothnia (map: see Fig.1). Biogeographically these sites belong to middle boreal zone and the sites are at following biogeographical provinces: Tavastia borealis, Ostrobottnia australis and Ostrobottnia media (Hämet-Ahti et al. 1998). All sites were second growth stands that originated from planting following cultivation. These sites were part of a larger project of Finnish Forest Research Institute METLA, which was established to evaluate the growth of different tree species on afforested former agricultural peat soils. The study sites have been afforested during years 1990-92 using three different tree species: Silver birch (*Betula pendula*), Norway spruce (*Picea abies*) and Scots pine (Pinus sylvestris) (Ferm et al. 1993). (Hereafter referred to as birch, spruce and pine). Most sites had dense understory vegetation dominated by smallreeds (*Deschampsia cespitosa*, *Calamagrostis arundinacea*, *Calamagrostis purpurea ssp. phragmitoides*), meadowsweet (*Filipendula ulmaria*), marsh thistle (*Cirsium palustre*), common nettle (*Urtica dioica*) and raspberry (*Rubus idaeus*). There were also arctic raspberry (*Rubus arcticus*) and goutweed (*Aegopodium podagraria*) in the bottom layer of all study sites except Lappajärvi and Sarkala (Kyyjärvi). Furthermore, there was wood horsetail (*Equisetum sylvaticum*) in Alajärvi site. Some study sites had experienced silvicultural thinnings which continued at some sites during the sampling (Table 1). Unfortunately, it was not possible to control that. At sites with recent thinning practices, the coverage of the understory vegetation was lower.

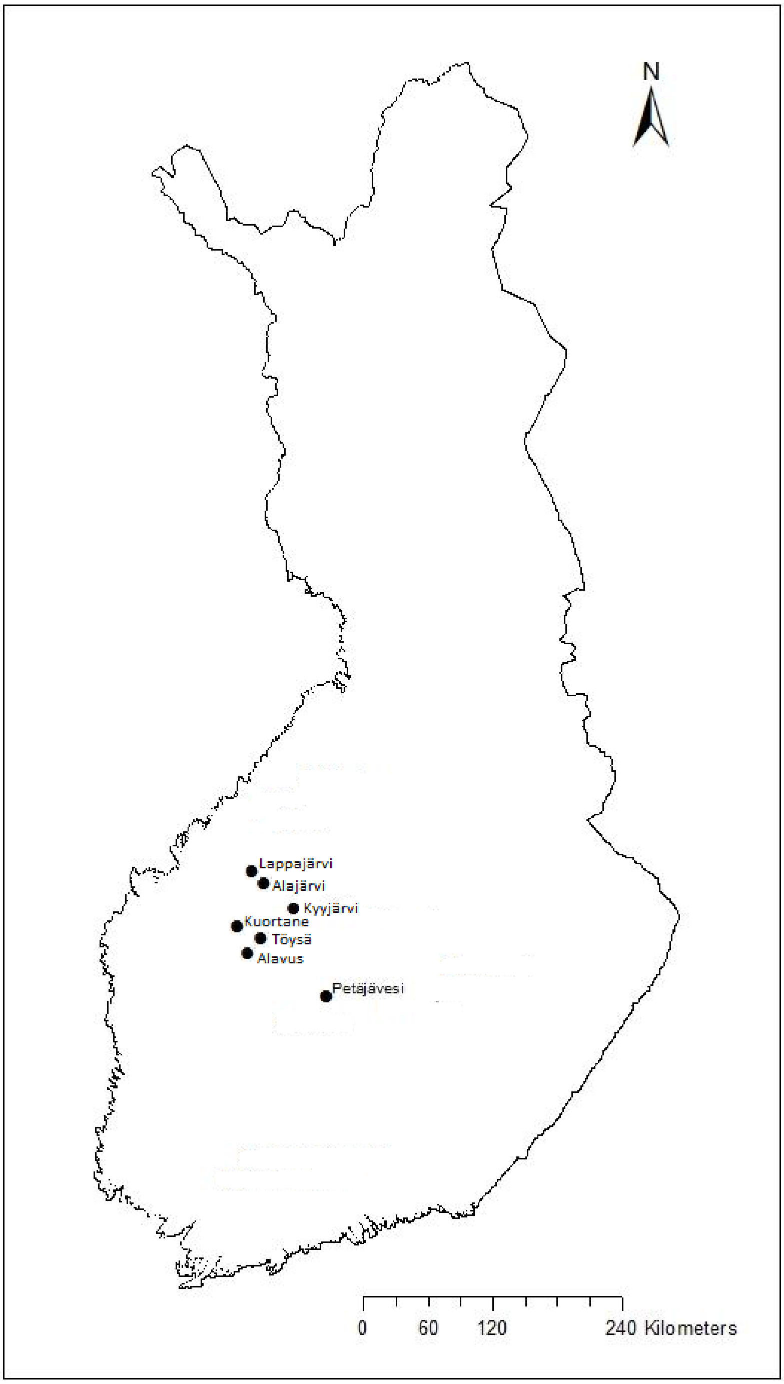

Figure 1. Geographical locations of the study sites in Finland. Two of the study sites were located in Kyyjärvi (Sarkala and Suosaari). Maanmittauslaitos 2013.

6.2. Experimental design

Each study site was divided to square shaped plots that were dominated by birch, spruce or pine. The length of plots varied somewhat but the average length of squares was about 30 meters. In every study site, I chose 6 plots which included two plots of each tree species. In the middle of each plot I put 4 pitfall traps in a line, where each trap was located 3 meters apart from the next one. There was no pitfall trap in the central point of the study plot. Pitfall traps were also at least 1 m apart from the edge of another tree species' plantation. In most cases the distance was much more but in some study sites (for example in Sarkala) the squares were quite narrow (about 12 m) and therefore, I turned the pitfall trap line little bit sideways. This was also done if there were thinning traces left behind by the machine (the effect of gap would be minimized). It was not possible to survey all the six plots from all of the study sites, because in some of them the afforestation had failed. In these sites only four (in Lappajärvi, Sarkala and Kuortane) to five (in Petäjävesi) plots could be included to the study. Altogether I had 41 study plots: 16 birch, 15 spruce and 10 pine plots. Afforestation of pine plots seemed to be least successful.

Table 1. The occurrence of recent thinning practices at the study sites. Symbol (x) indicates thinning, symbol (0) that there was no thinning and symbol (-) expresses study plots where afforestation had failed and therefore were left out of this study. Only in birch plots of Alajärvi thinning took place during sampling period and the thinning date could be estimated.

Study site	**Birch 1**	**Birch 2**	**Spruce 1**	**Spruce 2**	**Pine 1**	**Pine 2**
Alajärvi	just before 25.6.	soon after 25.6.	0	0	x	x
Alavus	x	x	0	0	x	x
Kuortane	x	x	0	0	-	-
Lappajärvi	x	x	x	x	-	-
Petäjävesi	0	0	0	-	0	0
Kyyjärvi (Sarkala)	x	x	x	x	-	-
Kyyjärvi (Suosaari)	x	-	x	x	x	x
Töysä	x	x	x	x	x	x

6.3 Ground beetle sampling

Ground beetles were collected with pitfall traps (200 ml capacity with a 6,5 cm diameter) in the 41 study plots. The study plots were measured with tape measure and the central point of the square was marked with fiber ribbon. Pitfall traps were set into ground in such a way that the top of the cup was leveled with the ground surface. There were 16 to 24 pitfall traps depending on afforestation success of the study site (164 traps in total). All traps were charged with approximately 100 ml solution of water with salt and a few drops of dishwashing liquid. To avoid flooding, the traps were covered with elevated plywood roofs (10 cm x 10 cm). The traps were placed to study sites during 14.-16.5.2013. Sampling was carried out approximately every three weeks, altogether 4 times: 4.6., 25.6., 16.7. and 6.8. in 2013. Only occasionally traps were disturbed during the trapping period (5 traps of spruce plots). Pitfall trapping is an invaluable and generally applied sampling method for studying surface dwelling arthropods, especially carabid beetles (e.g. Koivula et al. 2002). During the preliminary sorting of samples, non-arthropod debris was separated, while Carabidae were identified, and the residue stored in 70 % alcohol solution. In total I had 656 samples. The carabid beetles were identified to species level based on Lindroth (1997). Specimens were stored either in a 70 % alcohol solution or in personal dry collections.

6.4 Statistical analysis

I counted the total number of individuals and species for each study site and also for different tree species in each study site. In addition, I calculated the total number and percentages of forest, generalist, hygrophilic and open habitat species.

I analyzed the dependency between the number of carabid species and study plots with paired sample t-test and independent sample t-test (birch-pine and spruce-pine) using SPSS Statistics 20. I did both t-tests because in same study site plots can be thought to be dependent of each other and at different sites plots are independent of each other because of the geographical variation. There were also fewer pine plots than birch and spruce plots and independent sample t-test takes this into account.

To study if the number of carabid species differs between study plots and to evaluate has the sampling been sufficient to describe the actual ground beetle diversity of these study sites, I calculated species accumulation curve (SAC) for the data using EstimateS 9.1.0 (Colwell 2011). Species accumulation curve illustrates the cumulative number of species recorded as a function of sampling effort. If the sampling has been sufficient, results are more reliable. This can be interpreted from the shape of the curves: If curve is heading towards horizontal plane, all possible species are more or less found, but if the curve is still heading upwards, new species are found as the sampling continues. Therefore, curve also describes how well collected ground beetle data represents the actual number of species in the study sites and shows the rate at which new species are found within a community. Other reason for the choice of this curve was that the number of study plots was not equal between tree species and SAC takes this into account although the number of n differs between compared groups. Adding of the samples to the species accumulation curve was made randomly and then plotting the mean of these permutations. The test was replicated 1000 times. I did the test twice: For the number of species and for the number of individuals.

To make comparisons between carabid communities, I calculated Chao-Jaccard abundance-based similarity indices (Chao et al. 2005), which is a non-parametric approach. In contrast to the classic indices, which are based on the presence-absence of species in paired assemblages, the abundance-based similarity indices handle incidence counts in level of individuals and take account the relative abundance of species. Therefore Chao-Jaccard abundance-based similarity indices is resistant to undersampling, not sensitive to sample size and better suited for samples that are likely to contain numerous rare species. The boostrap was calculated 1000 times. I used this index to describe the variation between pairs of pitfalls belonging to four different categories (same tree species and same study site, different tree species and same study site, same tree species and different study site, different tree species and different study site). The indexes were calculated by using the program EstimateS 9.1.0 (Colwell 2011).

To study the similarity patterns between communities (Quinn & Keough 2002), I made Mantel´s test (Mantel 1967) using the same Chao-Jaccard similarity index data. Mantel’s test calculates the correlation between two distance matrices (here the matrix of pairwise similarities of pitfall communities and a categorized matrix) summarizing pairwise similarities among sample locations. However, the values in similarity matrices are not independent (Nekola & White 2004), but the test take this into account that the same sites are included in the analysis several times. I executed three separate tests. First, I tested whether similarities between pitfall pairs were different for same tree species and same study site pairs compared to different tree species and same study site pairs. Second, I tested whether the similarity of different tree species and same study site pairs was different from the similarity of the same tree species and different study site pairs. Third, I tested whether the similarity of same tree species and different study site pairs differs statistically from the similarity of different tree species and different study site pairs.

7. RESULTS

7.1. General aspects about species composition

A total of 4018 individuals representing 40 species from 18 genera were recorded during the sampling (Table 2). The four most numerous species were *Agonum fuliginosum* (40% of total), *Trechus secalis* (11%), *Pterostichus oblongopunctatus* (10%) and *Calathus micropterus* (6%). These four species represented 66% of the total catch. 9 species (22.5%) were considered forest or woodland species, 15 (37.5%) as generalist species with a wide distribution, 11 (27.5%) were hygrophilic species and 5 (12.5%) characteristic of open land habitats. It came out that one species numerically dominates diversity distribution of communities.

Table 2: List of species from the most abundant to the rarest.

	Species	Individual	Habitat preference
1.	*Agonum fuliginosum*	1597	hygrophilic
2.	*Trechus secalis*	436	generalist
3.	*Pterostichus oblongopunctatus*	383	forest
4.	*Calathus micropterus*	250	forest
5.	*Trichocellus placidus*	205	forest
6.	*Patrobus atrorufus*	181	hygrophilic
7.	*Carabus glabratus*	163	forest
8.	*Pterostichus sternuus*	148	generalist
9.	*Amara lunicollis*	145	generalist
10.	*Pterostichus niger*	107	forest
11.	*Trechus rivularis*	105	forest
12.	*Carabus cancellatus*	60	open land
13.	*Harpalus luteicornis*	44	generalist
14.	*Amara communis*	20	generalist
15.	*Loricera pilicornis*	20	generalist
16.	*Patrobus assimilis*	19	generalist
17.	*Cychrus caraboides*	18	forest
18.	*Pterostichus diligens*	15	hygrophilic
19.	*Trechus rubens*	14	generalist
20.	*Amara famelica*	13	generalist
21.	*Leistus terminatus*	10	hygrophilic
22.	*Clivina fossor*	8	open land
23.	*Amara nitida*	7	open land
24.	*Carabus nemoralis*	7	generalist
25.	*Pterostichus melanarius*	5	generalist
26.	*Amara brunnea*	4	generalist
27.	*Carabus hortensis*	4	forest

28.	*Harpalus quadripunctatus*	4	forest
29.	*Harpalus latus*	4	generalist
30.	*Philorhizus sigma*	4	hygrophilic
31.	*Bradycellus caucasicus*	3	open land
32.	*Notiophilus palustris*	3	hygrophilic
33.	*Pterostichus crenatus*	3	hygrophilic
34.	*Pterostichus nigrita*	2	hygrophilic
35.	*Pterostichus rhaeticus*	2	hygrophilic
36.	*Bembidion guttula*	1	generalist
37.	*Bembidion lampros*	1	open land
38.	*Carabus granulatus*	1	hygrophilic
39.	*Platynus mannerheimii*	1	hygrophilic
40.	*Pterostichus adstrictus*	1	generalist
	Total	4018	

7.2 Species richness between tree species

There were no significant differences in the carabid species richness between any study plots (for all P > 0.05). Differences in carabid species richness between tree species pairs were not significant (paired sample t-test for birch-spruce t = 0.588, df = 7, P = 0.575, birch-pine t = -1.087, df = 4, P = 0.338 and spruce-pine t = -1.165, df = 4, P = 0.309). I examined the same dependency also with independent samples t-test and carabid species richness did not differ between any of study plots (for all P > 0.05). Differences in carabid species richness between tree species pairs were not significant (independent samples t-test for birch-pine F = 1.865, df = 11, P = 0.482 and spruce-pine F = 1.045, df = 11, P = 0.412).

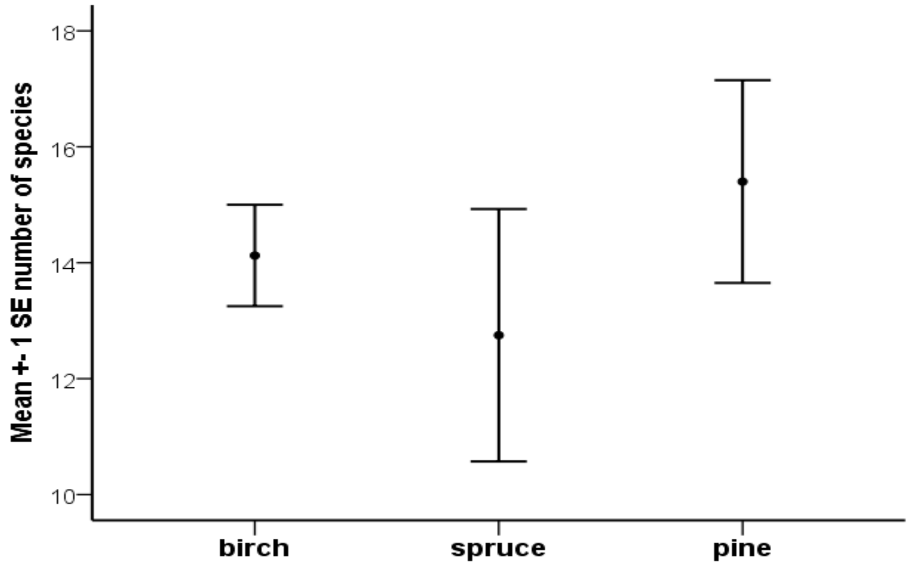

Figure 2. Ground beetle species richness and its standard error for study plots with different tree species.

Furthermore, to study carabid species richness between study plots, I made species accumulation curve (Fig. 3). Carabid species richness did not differ between any of the study plots since the 95 % upper and lower bounds overlap between all tree species. From the shape of curves it can be concluded that almost all possible species have been found. The curve of spruce plots is arising most steeply. Curves differ in their length since there were different number of study plots depending on the study site and therefore different total number of pitfalls per tree species.

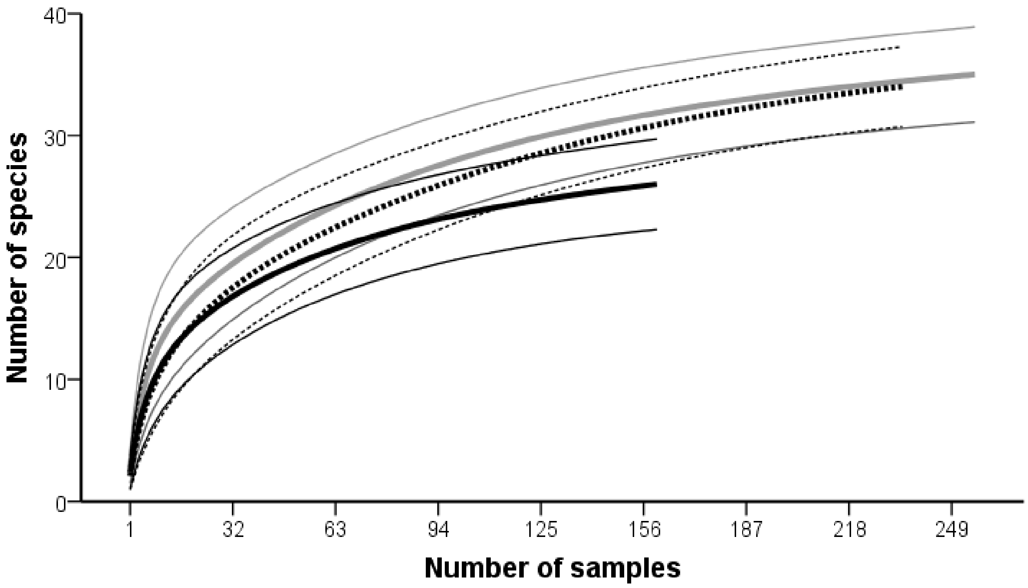

Figure 3.The rate at which new species are found as a function of sampling effort. Grey lines represent birch, dashed lines spruce and black lines pine plots. Bold lines are the average number of new species found in each random permutation of samples and thin lines their 95% upper and lower bounds. Altogether there were 656 samples.

7.3. Number of individuals between tree species

I studied also if the number of ground beetle individuals differs statistically between study plots (Fig. 4). There was no difference in the number of carabid individuals between any study plots (t-test for all P > 0.05). Paired comparisons between the study plots for the number of carabid individuals were not significant (paired sample t-test for birch-spruce t = 0.856, df = 7, P = 0.420, birch-pine t = 0.527, df = 4, P = 0.626 and spruce-pine t = -1.943, df = 4, P = 0.124). I examined the same dependency also with independent samples t-test and there were no significant differences in the number of individuals between any study plots (for all P > 0.05). Paired comparisons between the study plots for the number of carabid individuals were not significant (independent samples t-test for birch-pine F = 0.162, df = 11, P = 0.901 and spruce-pine F = 0.861, df = 11, P = 0.701).

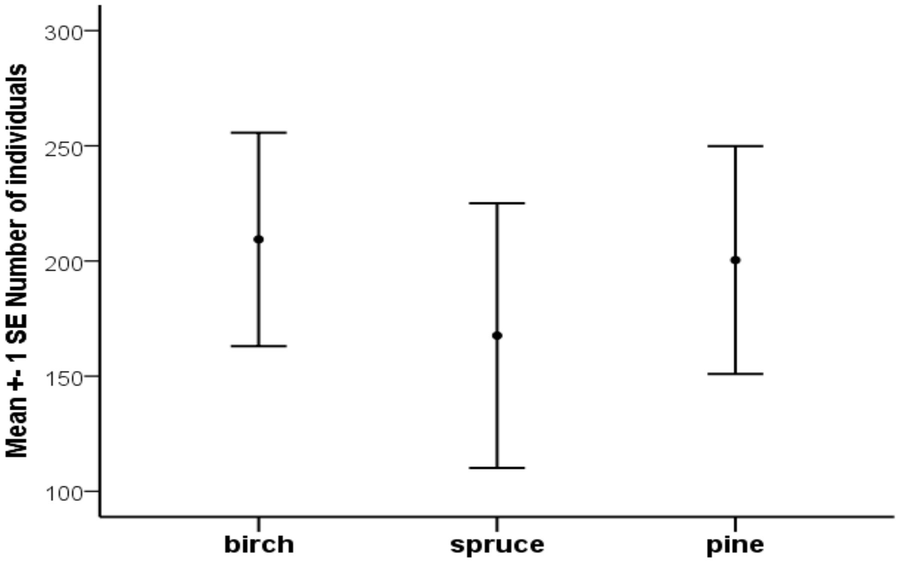

Figure 4. Number of ground beetle individuals and their standard error of the mean for study plots with different tree species.

I did species accumulation curve also for the number of ground beetle individuals between study plots (Fig. 4). The result was the same as in species richness: The number of carabid individuals did not differ between any of the study plots. Furthermore, the more individuals were sampled the more species were found. Curves of birch and spruce plots are still heading a little bit upwards but the curve of pine plots is almost in horizontal plane although there were fewer individuals.

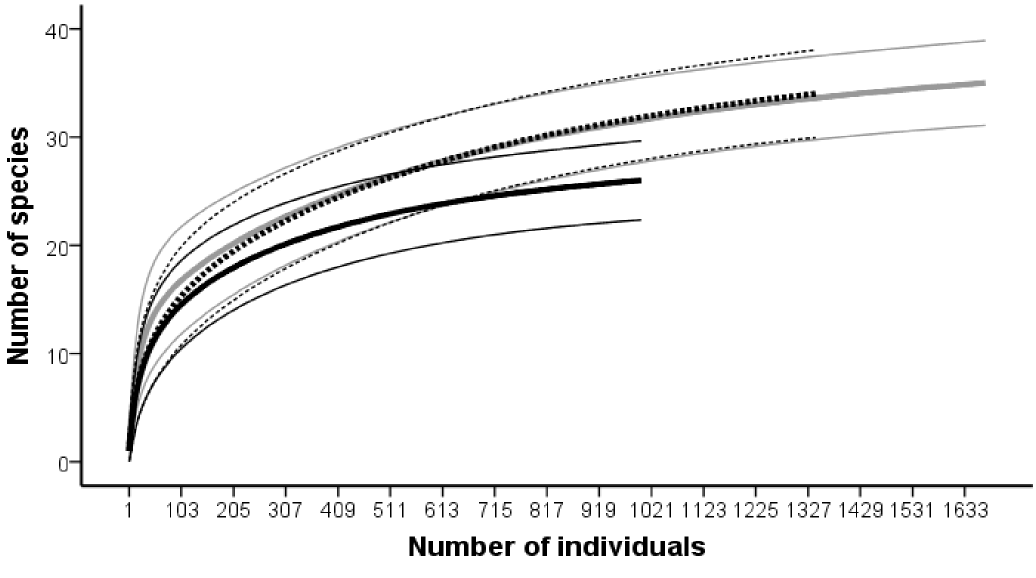

Figure 5. The rate at which new species are found as the random adding of individuals continues. Grey lines represent birch, dashed lines spruce and black lines pine plots. Bold lines are the average number of new species found in each random permutation of individuals and thin lines their 95% upper and lower bounds. Altogether 4018 individuals were identified.

7.4. Community similarity

Mantel´s test showed that the similarity of carabid community was significantly higher within same tree species and same study site than between different tree species and same study site (r = 0.037, P < 0.01) (Fig. 6). Also, the similarity was significantly higher within different tree species and same study site than between same tree species and different study sites (r = 0.08, P < 0.01). Furthermore, the similarity was significantly higher within same tree species and different study sites than between different tree species and different study sites (r = 0.015, P < 0.01).

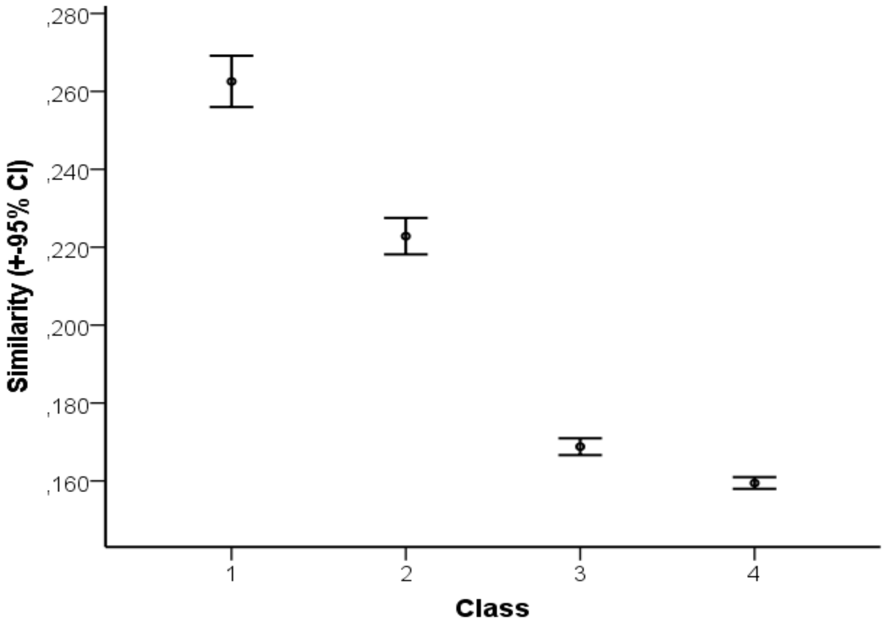

Figure 6. Chao-Jaccard-estimated abundance-based similarity indices and their 95% confidence intervals in four different category. Numbered categories are 1 = same tree species and same study site, 2 = different tree species and same study site, 3 = same tree species and different study site, 4 = different tree species and different study site.

8. DISCUSSION

Afforested fields are considered as novel ecosystems, and therefore it was crucial to achieve knowledge about what kind of ground beetle species they maintain in Finland and what is their abundance and community composition in these habitats. In addition, research of ground beetles of afforested fields has been scarce (Lindgren 2000). The hypothesis was that there would be both forest and generalist species in these habitats. I also studied the effect of tree species to ground beetle species composition and community structure. The hypothesis was that the abundance and composition of ground beetles would be higher in birch plots compared to conifer plots because it has been shown that abundant leaf litter has positive impact on carabid species richness (Magura et al. 2000). The answer to these questions will help to understand the importance of afforested fields for ground beetle species and what wooded species would be the best for them or whether it is relevant at all.

8.1. Carabid species of afforested fields

Afforested fields were inhabited by a species rich ground beetle fauna. Altogether 40 carabid species accept afforested fields as suitable compensatory habitats. This means that species living in certain habitats accept some other sufficient habitat as their environment established elsewhere (Gibbons & Lindenmayer 2007). From all four categories the most frequent group was generalist species. This could be due to the mixture of agricultural legacy and current second growth stands that originated from planting and were not yet considered as old forest with closed canopy. Exceptionally *Agonum fuliginosum* was the numerically dominant species in this study. This may be explained by the fact that the soil of study sites was initially peat and this species is strongly hygrophilous and very common in wetlands and moist sites of spruce forests. However, it is not usually considered to be the dominant species of managed forests. Species composition and abundance were particularly interesting when considered together. *Calathus micropterus* and *Pterostichus oblongopunctatus* are the most common carabids in Finnish spruce forests, (e.g. Koivula 2002a, b) and also *Trechus secalis* is abundant (Koivula et al. 2002). In addition to these, *Amara brunnea* is typical in managed forests (PhD Olof Biström, Finnish Museum of Natural History, personal communication). From these species, *T. secalis*, *P. oblongopunctatus* and *C. micropterus* were the three most abundant species after *A. fuliginosum* in my study. Suprisingly, only four individuals of *A. brunnea* were found. This is less than 1 % of the whole data. However, this species is considered as specialized forest species and because afforested fields in this study were young and their canopy closure was still in progress, they were probably not suitable habitat for *A. brunnea*. However, *P. oblongopunctatus* and *C. micropterus* are also considered as forest species but their numbers were abundant in contrast to *A. brunnea*. This indicate that they have not as strict habitat requirements as *A. brunnea* or other competition advantages which enable them occur in study sites. It is suggested that many forest species become slowly more abundant when the forest grows older and that the radical assemblage level change happens together with canopy closure, about 20-30 years after clear-cutting (Koivula et al. 2002). Probably the canopy closure would have already taken place without thinning practices. Silvicultural thinning is also likely reason for the low abundance of *A. brunnea*. Also in other studies (Jukes et al. 2001, Vanbergen et al. 2005) canopy has proven to be an important structural factor affecting the lighting conditions of ground layer. After canopy closure, the conditions of ground floor become more appropriate for forest species (shadier and moister).

Any rare or endangered species were not found in this study. This may be due to the fact that many endangered ground beetle species are heliophilous; occuring in open and dry sun-exposed ground such as meadows, heaths and dunes or other sandy soil habitats (Lindroth 1997). Meadows are nutrient poor and dry habitats and therefore afforested fields do not compensate these habitats even when tree stands are young due to decades of fertilization. Instead, afforested fields may be compensatory habitats for old forest species if they are allowed to grow old and the canopy closure. Although any rare species were not found, there was one interesting discovery: *Platynus mannerheimii* which was lately thought to be species of spruce-mires with closed canopy (Niemelä et al. 2007). However, it seems that *P. mannerheimii* is more dependent of moist microclimates such as *Sphagnum* depressions than canopy closure because one individual of this species was found in Sarkala, Kyyjärvi. Koivula et al. (2002) have settled on the same conclusion earlier.

8.2. Variation in carabid communities

The carabid species richness did not differ between study plots. Therefore, the assumption of more species rich birch plots was not fulfilled. The same was true for the number of individuals. Actually, for the number of individuals, the differences between study plots were even smaller.

It seems that the data represents quite well the actual number of ground beetle species to be found in these particular study sites (see Fig. 3). Curves are heading toward horizontal plane and therefore sampling has been sufficient and results are reliable. Even if the sampling was extended for example by one month, more new species were probably not found apart from the late summer and autumn occurring species. Curves for the number of individuals suggest the same as curves for the number of species: Sampling has been sufficient and all possible species are mainly found (Fig. 5).

There were statistical differences in the similarities of ground beetle communities between four different categories. First, the similarity of carabid community was significantly higher within same tree species and same study sites than between different tree species and same study sites (Fig. 6). This suggests that carabids found the identity of tree species important. It has been observed that the identity of tree species effects on arboreal beetle assemblage in tropical pasture afforestation (Plath et al. 2012). My results support this observation. However, the comparison is difficult because these two studies were made at totally different vegetation zones (tropical versus boreal), in different habitats and with different study organisms. Nevertheless, other important factors for carabids like canopy closure (Jukes et al. 2001, Vanbergen et al. 2005), microclimate (Stroka & Finch 2006) and small scale heterogeneity (Niemelä et al. 1996) naturally depend on the identity of tree species. It has been studied that the spatial distribution of ground beetles varies with progressing vegetation succession (Antvogel & Bonn 2001), which creates different kinds of microclimates and small-scale heterogeneity.

Furthermore, since the ground beetle communities were more similar within the plots with same tree species than between plots with different tree species in same study sites, it can be interpreted that the carabids move between study plots (Fig. 6). Studies focused on the moving distances of carabids have shown variable results. Baars (1979) studied the moving of ground beetles by using radioactive isotopes. He found that a mean distance that *Pterostichus versicolor* covered within 1 year was 160 meters. In contrast, Vermeulen and Opdam (1995) studied a comparable species, *Pterostichus lepidus*, and showed that a mean distance for that species within 1 year was 76 meters. However, Vermeulen and Opdam used mark-recapture as a method which probably underestimates the moved distance because the dispersal is interrupted by repeated catching of marked beetles in pitfalls. Other significant distinction is that *P. versicolor* is eurytopic (geographically widespread) whereas *P. lepidus* is stenotopic (occurring in a small area) species. According to Nève de Mévergies and Baguette (1990), the direction in which stenotopic species walk tends to be more random and this is why these species move shorter distances than eurytopic ones. In addition to the method, this may explain the differences in the results between these two studies. In the end of article Vermeulen and Opdam (1995) suggest that corridors for carabids with poor dispersal abilities are only effective up to about 100–500 meters. Therefore, the moved distance can be even more for effectively moving ground beetles. Anyway, it seems that there is no problem for widely moving surface active predators to move between square shaped study plots with average side length about 30 meters.

Secondly, similarity was higher within different tree species and same study sites than between same tree species and different study sites. This result indicates that geographical variation (depending on study site) can change community composition of ground beetles. Similar results have been found before (Niemelä et al. 1994). Niemelä and colleagues studied the variation in ground beetle assemblages on mature taiga among 8 geographical areas in southern and central Finland and found that significantly more species were captured in the southern study areas than in the more northern ones. This could be even more important if the study sites were further from each other, for example in southern and northern Finland. Geographical variation probably originates from the gradual change in climate across country. Also, according to this result, the study plots with same tree species are different between study sites. Silvicultural thinning may be an explanation for the variation within study plots with same tree species. It brought undesirable variation to the data which further reflected to results. Therefore, interpretation is troublesome although all the other factors were standardized. In addition to geographical location, there may also be some unrecognized difference between study sites.

Finally, the similarity was significantly higher within same tree species and different study sites than between different tree species and different study sites. This mainly indicates the same as the first significant difference: Within the plots with same tree species, the carabid species composition is more similar than between plots with different tree species. Therefore, although ground beetles may see study sites as one large mosaic of environments after disturbance, they found the identity of tree species important. All in all, both tree species and geographical location are important for ground beetles when considering them together.

8.3. Conclusions

The number of ground beetle species is impressive and diverse in afforested fields included in this research compared to managed forests. Species composition and abundance are also special although any rare or endangered species were not found. One species numerically dominates the community. Tree species seems to be an important factor for carabids along with geographical variation but not alone. Therefore, it seems that afforested fields in this study really are novel ecosystems at least in regard to carabids due to their exceptional composition and abundance. Furthermore, afforested fields seem to be suitable compensatory habitats for many species. In future, the importance of novel ecosystems for biodiversity will continue to increase as human land use expands and escalates. For these reasons, more research is needed from the importance of afforested fields and their importance as novel ecosystems also for other group of species.

ACKNOWLEDGEMENTS

I thank my supervisors Atte Komonen and Panu Halme for excellent guidance and support. I am grateful to Jaakko Mattila for identification help. I really appreciate your expertise. Thank you Lotta Sundström for interesting discussions, materials and enthusiasm. I thank my father, Helena Siirtola, Kaisa Mustonen, Sonja Saine and Tinja Pitkämäki for helping to collect the carabid samples and Neea Heinonen for helping with preliminary sorting of samples. Thank you Anssi Lensu for statistical guidance. I owe thanks also to Mikko Hietaranta for being liaise between me and Excel program in times when we did not get along. I am grateful to my family for their support over the whole time of my studies and this project. Thank you Liisa Hämäläinen for helpful comments on this manuscript. I owe thanks also to Metsäntutkimuslaitos for cooperation and Societas Entomologica Fennica and Societas pro Fauna et Flora Fennica for funding this interesting work.

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APPENDIX 1

Study site	Alajärvi			Alavus			Kuortane		Lappajärvi		Petäjävesi			Sarkala		Suosaari			Töysä			Total
	birch	spruce	pine	birch	spruce	pine	birch	spruce	birch	spruce	birch	spruce	pine	birch	spruce	birch	spruce	pine	birch	spruce	pine	
Number of individuals	67	34	59	201	197	244	208	97	97	64	85	5	190	227	484	359	140	152	431	320	357	4018
Number of species	13	6	10	13	15	13	13	13	13	15	17	3	19	19	19	13	21	16	12	10	19	40
Agonum fuliginosum	16	4	19	36	37	116	61	10	26	5	26	0	118	83	302	55	53	44	212	152	222	1597
Amara brunnea	0	0	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	0	0	0	0	4
Amara communis	7	0	0	0	0	0	3	0	0	0	1	0	2	0	4	2	0	1	0	0	0	20
Amara famelica	0	0	0	1	4	0	0	0	0	0	0	0	0	0	5	3	0	0	0	0	0	13
Amara lunicollis	2	0	0	28	4	0	2	0	2	1	4	0	2	13	3	56	6	0	21	0	1	145
Amara nitida	0	0	0	0	0	0	0	0	0	0	0	0	2	1	4	0	0	0	0	0	0	7
Bembidion guttula	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
Bembidion lampros	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Bradycellus caucasicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3
Calathus micropterus	2	14	7	9	50	13	22	21	0	1	8	3	8	6	6	22	19	14	1	21	3	250
Carabus cancellatus	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	54	1	3	60
Carabus glabratus	1	0	1	8	7	16	18	5	4	3	4	0	3	19	11	14	2	17	10	10	10	163
Carabus granulatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Carabus hortensis	0	0	0	0	0	0	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	4
Carabus nemoralis	0	0	0	0	0	0	0	0	0	0	2	0	5	0	0	0	0	0	0	0	0	7
Clivina fossor	2	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	2	1	8
Cychrus caraboides	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	2	13	0	18
Harpalus quadripunctatus	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Harpalus latus	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
Harpalus luteicornis	3	0	1	2	1	7	17	1	1	1	0	0	0	0	0	0	0	0	2	1	7	44
Leistus terminatus	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	4	0	1	10
Loricera pilicornis	0	0	0	3	2	4	0	2	0	1	0	0	0	0	5	0	1	0	1	0	1	20
Notiophilus palustris	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	3
Patrobus atrorufus	2	0	2	0	0	0	0	0	0	0	5	0	11	0	1	22	6	4	47	22	59	181
Patrobus assimilis	0	0	0	0	0	0	0	0	0	0	0	0	3	0	1	1	0	0	6	2	6	19
Philorhizus sigma	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	4
Platynus mannerheimii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Pterostichus adstrictus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Pterostichus crenatus	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Pterostichus diligens	2	0	0	0	1	0	0	0	2	1	0	0	0	0	0	4	0	0	2	0	3	15
Pterostichus melanarius	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	1	0	5
Pterostichus niger	0	0	0	0	0	0	0	0	11	17	2	0	5	9	12	24	2	7	8	6	4	107

Study site	Alajärvi			Alavus			Kuortane		Lappajärvi		Petäjävesi			Sarkala		Suosaari			Töysä			**Total**
	birch	spruce	pine	birch	spruce	pine	birch	spruce	birch	spruce	birch	spruce	pine	birch	spruce	birch	spruce	pine	birch	spruce	pine	
Number of individuals	67	34	59	201	197	244	208	97	97	64	85	5	190	227	484	359	140	152	431	320	357	4018
Number of species	13	6	10	13	15	13	13	13	13	15	17	3	19	19	19	13	21	16	12	10	19	40
Pterostichus nigrita	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2
P. oblongopunctatus	4	0	4	56	31	46	33	11	16	6	8	1	4	26	21	20	1	10	7	68	10	383
Pterostichus rhaeticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	2
Pterostichus sternuus	14	0	7	9	12	9	8	0	11	2	7	0	4	2	5	33	1	6	16	1	1	148
Trechus rivularis	0	0	0	0	0	1	0	0	0	0	1	0	4	29	34	0	0	0	12	13	11	105
Trechus rubens	0	1	1	0	0	2	0	1	0	0	1	0	0	0	1	0	0	0	2	2	3	14
Trechus secalis	6	12	11	32	19	22	34	38	15	19	2	0	7	25	58	49	35	35	6	5	6	436
Trichocellus placidus	6	2	6	15	26	5	6	1	3	4	10	0	7	12	6	48	13	14	16	0	5	205