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Ground beetles of Lauzelle Forest (Belgium, Walloon Region): community characterization and study on mean individual biomass as an indicator of forest ecological state

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Thesis presented for the Master's degree in Biology of Organisms and Ecology

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II. Résumé

Le monde actuel fait face à une sixième extinction de masse principalement causée par les activités humaines. Cette crise de biodiversité affecte de nombreux organismes dont certains s’avèrent particulièrement utiles en raison de leur statut de bioindicateur. C’est le cas des carabes en raison de leurs nombreuses qualités qui en font un modèle d’étude simple et sensiblement efficace. Les carabes sont reconnus comme de bons bioindicateurs permettant de réaliser le suivi d’une succession écologique et ce particulièrement en milieu forestier à la suite des activités sylvicoles.

Cette étude fait suite au dernier inventaire de carabes réalisé dans le bois il y a plus de 40 ans. Elle a pour objectif de réévaluer la diversité de carabes au sein du Bois de Lauzelle (une forêt tempérée en Belgique) et cela en caractérisant la distribution des communautés et de la biomasse de carabes au moyen de différentes variables environnementales biotiques et abiotiques. Les carabes ont été piégés avec des pièges à fosse disposés à travers le bois dans huit différents types d’habitats forestiers (boulaie, hêtraie, chênaie, chênaie-hêtraie, lande à callune, lisières, pinèdes, zone protégée). Ils ont ensuite été pesés pour obtenir une valeur de biomasse moyenne individuelle (MIB) par station. Les résultats obtenus ont démontré qu’il existait trois communautés de carabes au sein du bois et que leur distribution dépend des gradients d’humidité et d’ouverture de l’habitat. Les mesures d’abondance, de richesse spécifique et MIB sont influencées par des variables environnementales différentes. La MIB a également permis de dévoiler un effet positif des mesures de conservation entreprises au sein d’une parcelle sur les carabes et la succession écologique. Une attention particulière à certaines caractéristiques propres aux différentes espèces démontre que les espèces spécialistes de milieux forestiers sont moins abondantes que les espèces généralistes et spécialistes de milieux ouverts. Bien que la plupart des résultats obtenus sont en accord avec la littérature, des contradictions permettent de mettre en évidence l’impact de la gestion forestière sur les carabes et sur la succession écologique au sein du bois.

Mots-clés : Carabidae, forêts, communautés, humidité, biomasse, gestion

III. Abstract

The world is currently facing a sixth mass extinction caused mainly by human activities. This biodiversity crisis is affecting many organisms, some of which are particularly useful because of their status as bioindicators. This is the case of carabid beetles, whose many qualities make them a simple and highly effective study model. Carabid beetles are recognized as good bioindicators for monitoring ecological succession, particularly in forest environments following wood production activities.

This study follows on from the last carabid inventory carried out in the wood over 40 years ago. It aims to reassess the diversity of carabid beetles in the Lauzelle Forest (temperate woodland in Belgium) by characterizing the distribution of carabid communities and biomass using different biotic and abiotic environmental variables. Carabid beetles were trapped with pitfall traps laid out across the wood in eight different forest habitat types (birch, beech, oak, mixed oak and beech plots, heathland, forest edges, pine tree plots and protected area). They were then weighed to obtain an individual mean biomass value (MIB) per trapping station. The results showed that there were three communities of carabid beetles within the wood and that their distribution depended on the gradients of humidity and openness of the habitat. The measures of abundance, species richness and MIB are influenced by different environmental variables. The MIB also revealed a positive effect of conservation measures undertaken within a plot on carabid beetles and ecological succession. A closer look at certain characteristics of the different species shows that forest specialist species are less abundant than generalist species and open habitat species. Although most of the results obtained are in line with the literature, some contradictions highlight the impact of forest management on carabid beetles and on ecological succession within the wood.

Keywords: Carabidae, forests, communities, humidity, openness, biomass

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1. Introduction

1.1 Context of the study

Although the insects are a very diversified group of organisms (1 013 825 described species and potentially 5.5 million in total), they are particularly affected by the current biodiversity crisis (Stork, 2018). It has been reported that the total flying insects biomass has decreased by more than 75% in 27 years in protected areas of Germany (Hallmann *et al*, 2017). Some of those threatened species are useful for humans because they provide ecosystem services like pollination or bioindication. Total pollination value in the world is estimated at 153 billion € and 5-8% of agricultural production are directly dependant of this service (Khalifa *et al*, 2021). The current context of the sixth mass extinction is directly attributable to human activities and essentially due to overexploitation of natural resources (Ceballos *et al*, 2010; Cardoso *et al*, 2020). Agriculture, pesticide use, urbanisation and deforestation are responsible of the decline in insect number counting respectively for 23.9%, 12.6%, 10.7% and 8.8% (Sánchez-Bayo and Wyckhuys, 2019). In forests, the management methods have a huge impact on biodiversity and it is thus important to consider management methods for conservation purposes in addition to wood production (Lindenmayer, 2009; Kosewska *et al*, 2018) while avoiding ecological trap creation (Hollander *et al*, 2017). In that context, the identification and study of bioindicators is a tool to better analyse the consequences of management practices on insect conservation (Brown and Matthews, 2016; Khalifa *et al*, 2021).

1.2 Ground beetles as bioindicators

For a long time now, humans have used natural indicators present in their environment to detect resources like food or to avoid potential risks (Rainio and Niemelä, 2003; van der Wal *et al*, 2022). Bioindicators are defined as species truly reflecting the biotic or abiotic state of an environment, representing consequences of environmental change in a habitat, a community or an ecosystem, or that constitutes an index of a part or the total diversity in a zone (McGeoch, 1998). It is notably the case of ground-beetles or carabid beetles that are ubiquitous terrestrial animals. The ground-beetles are part of the largest insect order, the Coleoptera (359 000 - 386 000 described species), and are grouped inside the Carabidae family that contains around 39 000 species (Condamine *et al*, 2016; Stork, 2018). It is the most successful family of the Adephaga sub-order in terms of species number. Adephaga are recognizable because their hind hips cover the first abdominal segment and partially the second segment. The name of this suborder refers to the voracious appetite of its members like Dytiscidae and Carabidae (Beutel and Leschen, 2016). Adults ground beetles are quiet easily identifiable thanks to their striated elytra and prominent mouth parts (prognathes). Their antennae and tarsi are respectively constituted by 11 and 5 articles (Jeannel, 1941; Roger *et al*, 2010). The length of adult individuals varies between 0.7 and 90.2mm around the World and between 1.8 and 14mm in Belgium (Kotze and O'Hara, 2003). Most of carabid species have functional wings allowing them to fly and disperse (Erwin *et al*, 2015) while some species do not have wings, some others show wing dimorphism. This feature helps to maintain their populations. The presence of wings requires maintenance and therefore the sacrifice of some of the resources taken from the environment, especially if the wings do not have sufficiently developed muscles for flight. The presence within the same species of winged individuals capable of dispersing or fleeing from disturbance, and of flightless individuals able to invest more resources and energy in reproduction, enables the species to respond to the various environmental stresses that could threaten it. (Kotze and O'Hara, 2003). In Belgium, 379 species were recorded (Desender, 1985) and the population of 46% of those species are decreasing while only 20% are increasing (Kotze and O'Hara, 2003). In Europe, ground beetles are grouped in two main categories according to their life cycle : autumn or spring reproducers that respectively overwinter as larvae or adults (Loreau, 1984, 1985, 1988). Ground beetles communities shows a higher activity peak in summer between July and August (Loreau, 1984).

Ground beetles can be considered as bioindicator because they have several interesting characteristics. They are widely distributed probably thanks to the ability of some species to fly. They can be found on every continent except Antarctica. Ground beetle species can be specific of various habitats like intertidal environments, beaches, caves, moors, meadows, forests, tropical canopies or on the edge of mountain glaciers (Erwin *et al*, 2015). Carabid beetles are patchy distributed in microhabitats showing different biotic and abiotic characteristic (*e.g.* pH, humidity, soil compaction) promoting the establishment of various specific organisms. Then, the high concentration of those specific organisms attracts their own specific or generalist predators (Thiele, 1977). This specificity makes different species sensitive to different changes in their environment (Ings and Hartley, 1999; Pocock and Jennings, 2007; Jouveau *et al*, 2019). It has been observed that carabid beetles respond like some other macroinvertebrates to habitat fragmentation (Cameron and Leather, 2012). They are very diversified and well known. Every year, European experts gather to share their knowledge on this insect family (Pizzolotto, 2019). They are easy to study and have potential economic values. Carabid beetles can be used as biological control agents because of their food habits. Granivorous carabids restrict weeds proliferation while carnivorous control insect pests (Hance, 1987; Lundgren, 2005; Woodcock *et al*, 2010; Erwin *et al*, 2015; Nourmohammadpour-Amiri *et al*, 2022). Carnivorous species can be generalist (feeding on other arthropods no matter which species) or specialist (feeding on specific type of prey like molluscs, insects or myriapods). Predatory carabid beetles prefer to attack soft parts of their prey first. The larvae of certain species can even take advantage of ants as nest parasites (Shough, 1940; Erwin, 1979; Erwin *et al*, 2015). The potential use of carabid beetles in biological control and the economic value that would be linked to this encourages research. All of these characteristics make them good bioindicators (Rainio and Niemelä, 2003). It is partly with these insects that the metapopulation theory has been developed (Kotze *et al*, 2011). Nevertheless, it is important to keep in mind that a bioindicator perfectly reflecting the response of other organisms does not exist. Thus it is sometimes better to rely on several kinds of bioindicators (Pearce and Venier, 2006). Ground beetles activity is also influenced by abiotic factors like humidity, pH, temperature, soil type and precipitations (Tsafack *et al*, 2020; Fülöp *et al*, 2021).

It has been 40 years since the last inventory of ground beetles in the Lauzelle Forest. The wood management has changed and the communities of ground-beetles possibly too. The total forested area is decreasing around the world. Forests and tree covers are slowly replaced by expanding agricultural fields or cities and the ecosystem services they provide are slowly lost. However, Belgium does make an exception. For 150 years, forest areas increased by 25% and now cover 23% of the Belgian territory ("Les forêts de Belgique — Société Royale Forestière de Belgique," n.d.). Peri-urban forests like the Lauzelle Forest still offer various advantages for urban dwellers and shelters for biodiversity far from the urban unrest (Williams and Harvey, 2001; Nowak and Dwyer, 2007; Barron *et al*, 2016; Bottalico *et al*, 2016).

In forests, ground beetle communities are impacted by clear cutting. Indeed, clear cuts increase openness and forest border. This promotes forest colonisation by habitat generalists that may outcompete larger specialist carabid beetles and lead to their local extinction if forest patches are smaller or more isolated (Spence *et al*, 1996). In the other hand, heathland converted in wooded area (by natural regeneration) is colonised by larger and forest specialist species of ground beetles if other forests patches of sufficient size are at proximity (Ings and Hartley, 1999). Canopy closure may coincide with forest specialists establishment (Butterfield, 1997). Henceforth, large specialist carabid species can be considered as a clue of good ecological succession in regenerated plots (Kędzior *et al*, 2020). Large species are more threatened than small ones because most of them have a more restricted dispersion ability since not being able to fly and thus to flee a perturbation in the environment (Kotze and O'Hara, 2003). Macropterous species are more abundant in open areas than in forests (Riley and Browne, 2011). However, large species tend to be more resilient (Beissinger, 2000). In order to increase forest diversity in ground beetles, forests managers should arrange a diversified habitat mosaic to promote generalists and specialists (Ings and Hartley, 1999). Tree species have also an impact on ground beetles communities since they influence soils pH, litter quality and necromass notably (Finér *et al*, 2007; Vician *et al*, 2018).

1.3 Objectives and hypotheses

The aim of this study was to analyse ground beetle communities across different tree stands in the peri-urban wood of Lauzelle Forest with a particular focus on biomass in addition to abundance and species richness. Biomass measurements allow numerical comparisons between sample groups. It has been useful to determine what forest type can act as carbon sinks and thus help forests owners to sustainably manage their forest (Salunkhe *et al*, 2018). Fluctuations in the biomass of an ecosystem can be used to highlight variations in the food resources available over time (Hollander *et al*, 2017). The mean individual biomass (MIB) is often used to quantify ground beetle biomass. It is a unique value allowing comparisons between ecosystems without taking into account species. If one ecosystem shows a higher MIB it is because more individuals of larger and heavier species have been found. It is particularly useful to study forest management since large species are expected to live in forest or more closed habitats. Over long time periods, an increase in ground-beetles MIB can thus be considered as a good indicator of successful ecological succession in forests and a good tool to evaluate the change in wooded areas and management practices (Cárdenas and Hidalgo, 2007; Schwerk and Szyszko, 2007; Kędzior *et al*, 2018). MIB can also be useful to compare regularly tree stands in forests and help managers to identify plots needing a better management since higher MIB is correlated with (Hallmann *et al*, 2017). However, study on biomass should be analysed in the same time than abundances and species richness, since MIB can be low while a high diversity or abundance can be observed. MIB has been reported to be positively correlated to beech stands age (Jelaska *et al*, 2011).

Three main hypotheses were tested during this experiment. I) The diversity in ground beetles is expected to be higher in forest border due to edge effect (Molnár *et al*, 2001). II) Abundance of open habitat specialists and habitat generalists species should also increase in more open areas since they should be more accessible for those flying beetles (Gaublomme *et al*, 2008; Cvetkovska-Gjorgjievska *et al*, 2017; Riley and Browne, 2011). III) MIB should increase in older tree stands since they are more heterogenous, provide more resources and thus sustain greater ground beetle species. Higher deadwood volumes should also promote higher MIB (Jelaska *et al*, 2011; Kacprzyk *et al*, 2021).

2. Material and methods

2.1 Sampling site: Lauzelle Forest

The studied site is the Lauzelle Forest, a forested area of the Walloon Brabant province (Belgium) situated in a very densely populated area between the communes of Ottignies-Louvain-la-Neuve, Chaumont-Gistoux and Wavre (**Figure 1**). The wood covers a total area of 203.17 ha from which 181 ha constitute the main forest massif isolated by several major public roads. The site is owned by the University of Louvain-la-Neuve (UCL) and has to fulfil several roles : sylviculture (mainly), conservation of biodiversity, scientific research and public education (Baudry, 2015).

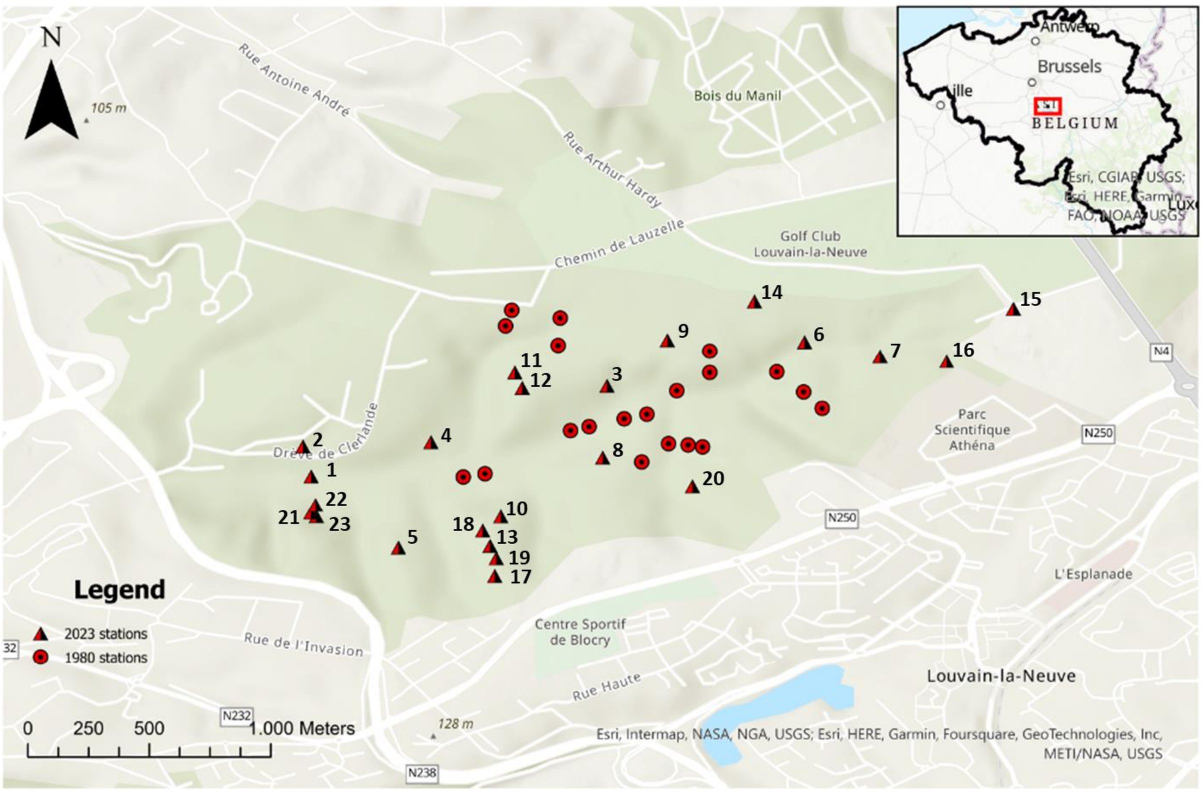

Figure 1: Lauzelle Forest location in Belgium. This map shows slightly the relief of the wood (in green) and its proximity with the urban network of Louvain-la-Neuve town in the south east. The red triangles (numbered from 1 to 23) represent the sampling stations for ground beetles catching of this study, while the red circles are those used in the study of Nedergedaelt published in 1981.

This forest is under an oceanic climate with an annual mean temperature of 10.5°C and total precipitations of 750 to 800mm. The Lauzelle Forest is mainly composed by the Blanc-Ry valley which is also constituted of five small dales with several water sources. The lowest point is situated at 63 m of altitude while the highest peaks at 130m. In the most recent inventory of

2013, 35 tree species have been identified and 75% of the inventory sites presented at least 3 different species. The sandy plateaus represent 75.9 ha and host coniferous trees on podzolic soils (mainly *Pinus sylvestris* and *Pseudotusga menziesii*). This type of soil is acidic and has significant drainage that makes it unsuitable for cultivation. The rest of the area is wooded by deciduous trees on luvisols (clay soils with high drainage). The main encountered species are sycamore maple (*Acer pseudoplatanus*), white birch (*Betula pendula*), common beech (*Fagus sylvatica*) and pedunculate oak (*Quercus robur*). The bottoms valleys (20.1 ha) are more wet and thus not suitable for timber harvesting. However, they constitute areas of special biological interest since that type of sites is rare in the region. A great portion of the wood remains part of Natura 2000, program whose purpose is to create a web of protected areas across all European Union taking into account socio-economic constraints. An area of 5.48 ha inside the Natura 2000 zone is strictly protected to ensure serenity for biodiversity. It is the biological area. Restauration of forest edges are underway. Those transition sites should not be neglected, since they provide links between different sites while limiting the entry of invasive species (Baudry, 2015).

2.2 Sampled tree stands description

In order to constitute a global view of the ground beetle communities in the Lauzelle Forest, we selected 23 sampling stations representative of the different plots found in the wood. They were chosen on basis of maps reading (***Appendices A***) and on sites observations. They were then grouped in 8 habitats types according to the dominant vegetation. One station is located in a birch plot; 3 stations in oak plots; 3 stations in plots where oak and beech are the main tree species; 3 stations in beech plots; 3 stations in moorlands; 3 stations in forest edges; 4 stations were located in coniferous plots; and 3 stations in the biological area.

1: The birch plot (Bf) is localised at the bottom of the valley near the pound and thus on peaty soil with very low drainage and a small leaf layer. Peaty soils have a thick layer of organic matter. The plot is under soft forestry management to conserve this part of the alluvial forest. It is a slightly open area and thus promote a very different vegetation from the other stations. The main tree species is white birch and the herbaceous layer is well developed. There is also one or two ant hills in the plot (probably *Formica polyctena*).

2: The first oak plot (Cm) is isolated from the rest of the wood by two small roads but is a slightly more open area than the two other oak plots. It lays on a south-facing slope of luvisols and thus with a high drainage. This plot undergoes a hardwood regeneration on the contrary of the two others but is still intended for hard wood production. The main tree species is pedunculate oak and the ground level is covered by small oak plants.

3: The second oak plot (Cp) is situated on a south-facing steep slope of luvisols at the limit of the high slopes. It has then a high drainage. Despite those characteristics, the plot is under hardwood management for production purposes. It is probably the less open oak plot of the three sampled. The main tree species is pedunculate oak and the ground level is covered with a thick leaf layer and small oak plants.

4: The third oak plot (Ct) is on a south-facing low slope constituted by luvisols with a high drainage. The plot is under hardwood management for production purposes. The ground level very densely covered by high young oak and beech. A large fallen oak is also present inside the plot. On the contrary of the other plots, some areas are monitored by the university to study the impact of climate change on oak growth and regeneration. Those small areas are fenced with wide mesh to exclude large mammals like roe deer that are very presents in the wood.

5: The first beech and oak plot (HCc) is located on a gentle north-facing slope constituted by luvisols with high drainage and is near the biological area. Despite the main tree species (oak and beech), there is a large fallen white birch in the middle of the plot. The ground is covered by a small leaf layer. This plot is undergoing a hardwood regeneration for production purposes.

6: The second beech and oak plot (HCs) is located on a south-facing slope on luvisols with high drainage. It is under hardwood management for production. The main tree species is beech and its cover allows little light to reach the ground covered with a thin leaf layer.

7: The third beech and oak plot (HCt) is located near the top of a south-facing slope constituted by luvisols and presenting thus a high drainage. It is under hardwood management for wood production but the trees are still young plants. The main species is the common beech and sycamore maple. The ground is covered with a thin leaf layer. A fallen tree is also found inside the plot.

8: The first common beech plot (Hc) is located near the top of a north-facing slope constituted by luvisols and presenting high drainage. It is undergoing a hardwood regeneration for production purposes. The plot can be described as a rather open area with a bare soil. The main tree species is beech but there are also some small black cherry trees.

9: The second beech plot (Hm) is located on luvisol plateau with high drainage. It is under hardwood management for wood production. There is a small coniferous plot and a fenced study area on beech regeneration near to it. The main tree species is common birch. The ground is mainly covered with a small leaf layer but there is also some young birch plants and eagle ferns. Some piles of relatively small dead wood are also present.

10: The third beech plot (Hp) is located on a north-facing slope constituted by luvisols and presenting high drainage like the first beech station (8) but the slope is steeper. The plot is undergoing a hardwood regeneration thus many young beech plants are present. The main tree species is common birch. The ground is covered by a thin leaf layer and some small deadwood pieces are present. A huge heap of wood is also present in the plot.

11: The first heathland plot (Laa) is located on a sandy plateau constituted by podzol and presenting a very high drainage. It is an open forest habitat in creation in order to offer new habitat types in the Lauzelle Forest. However, this plot is the most wooded among the three heathland plots studied. There is a large Scots pine in the middle of it and several birches. Young trees are also growing in the periphery of the plot while birches are mostly growing inside the plot. The ground is mainly covered by heather and mosses. There is a dead tree stump and a decaying wood pile in the plot.

12: The second heathland plot (Lab) is located near the first one (11) and thus on the same sandy plateau and showing the same drainage. It is undergoing the same management method but it is less wooded. These two plots are surrounded by coniferous and hardwood stands. The tree cover is exclusively constituted by white birches and lets more light reach the ground. The herbaceous layer is mainly constituted by heather. The ground is mainly covered by mosses and there are also two small birch piles inside the plot.

13: The third heathland plot (Lag) is located on a sandy plateau constituted by podzolic soils with a very high drainage. It is the greatest open area of the Lauzelle Forest and is under management for conservation purposes. There are only a few young trees scattered inside the site as well as dead tree trunks. The ground is covered by heather and mosses but there are also some patches of bare ground letting the podzolic soil appear. The heathland is mainly surrounded by coniferous plots.

14: The first forest edge (Lim) is located on sandy plateau near a golf course grass. The soil is constituted by luvisols and presenting a high drainage. The wood border is under protection and managed to promote a mix of tree species. Several tree species are found in this plot and the ground is covered by a small leaf layer. It can be considered as a transition site between forest outer border and inner forest since it is a very closed area. In addition, the site possesses a great volume of dead wood.

15: The second forest edge (Lip) is located on sandy plateau near roads and footpaths. It is on luvisols with high drainage. It can be considered as an outer forest border between inner forest and the grassland or orchards. The site presents several tree species, a very developed herbaceous layer in addition to a great volume of dead woods from different sizes. There is probably an ant hill inside the plot too.

16: The third forest edge (Liv) is located in a wet dale on the sandy plateau of gleysolic soils showing a low drainage. This edge can be considered as an inner forest border undergoing hardwood regeneration. This very unique site in the wood is the wettest site of this study and is protected. The soggy bottom of the dale is covered by a small layer of leaves and patchy distributed mosses. Some dead wood pieces can also be found (branches, small dead trees). The slopes of the dale feature young trees at the bottom and larger trees on top.

17: The first coniferous plot (Pfd) is situated on the same sandy plateau that the third heathland (with podzolic soil and very high drainage). It is under maintenance for wood production. There is a rather big pile of dead wood on the plot. The site is densely wooded by *Tsuga canadensis* and *Thuja plicata*. The ground is only covered by a layer of conifer needles and can be considered as a very closed only allowing little light to reach the ground.

18: The second coniferous plot (Pfo) is situated on the same sandy plateau that the first coniferous plot but on the other side of the third heathland. It is under maintenance for wood production. The site is very different from the first coniferous plot. It is more open site since Scots pines (*Pinus sylvestris*) are less densely grown but the ground is covered by a high herbaceous layer of eagle ferns.

19: The third coniferous plot (Po) is situated on the same sandy plateau that the two other coniferous plots studied. It is also under maintenance for wood production. The plot is a more open area than the first coniferous plot because it is less densely wooded by *Pseudotsuga menziesii* and located on the border between the heathland and the coniferous plot. The ground is covered with needles and small branches. A dead tree trunk and stump can also be found on the site.

20: The fourth coniferous plot (Cp) is located on a sandy plateau of podzolic soil with very high drainage and a gentle slope. It is under management for wood production. The main tree species is Scots pines and the ground is covered by a needle layer and patchy distributed eagle fern.

21: The first station in the biological area (Zb) is located at the bottoms of a north-facing slope of luvisols with high drainage. The site is dedicated to biodiversity conservation and thus no management is applied. The main tree species is oak but there are many young trees growing that makes the station a very closed area. Tree fallen dead trees (one in an advanced stage of decomposition) are a bit buried under the thick leaf layer.

22: The second station in the biological area (Ze) is located on the same slope bottoms that the first biological area station (Zb). It is situated near the pond and is a slightly more open area than the two other station in the biological zone. The main tree species is oak but many young trees are growing (oak and hornbeam). The ground level is covered by a small leaf layer and a big dead tree trunk can be found in the station and many branches.

23: The third station in the biological area (Zh) is the second wettest site studied. It is located near a small stream on a gleysolic soil with a low drainage. The main tree species is birch and some young trees are growing (oak and hazel). The wet ground is covered by a leaf layer and there are two dead trees in the station (rooted and fallen).

2.3 Stations measurements

After selection of the 23 tree stands, the sampling station area was chosen and then characterized by measuring altitude, tree circumference, herbaceous ground cover, tree density, tree species richness, deadwood quantity and habitat openness on a small part of the plot. Altitude and stations coordinates were obtained with My GPS Coordinates° app (Andrew, 2023) and adjusted with WallOnMap soil type also used to determine soil type and drainage as an estimation for humidity. Tree circumference was measured at breast height (CBH) and maximal and mean circumference were then calculated. Maximal circumference will be used as an estimation for tree stands age. Tree density (number of trees divided by tree stand area) was calculated at the tree stand scale. Herbaceous ground cover was measured approximately by sight. The measure represents the total area covered by small vegetation (mosses, heather, horsetail, brambles and very small trees). Deadwood quantity and habitat openness description was inspired by the score grid of the IBP (Indice de Biodiversité Potentielle). IBP is a simple index firstly used in French forests to estimate biodiversity inside different tree stands and help forest managers in their decisions to promote biodiversity (Larrieu and Gonnin, 2010). The attractiveness of forests for biodiversity are evaluated in each tree stands following 10 characteristics like deadwood volume and habitat openness (Larrieu and Gonnin, 2010; Emberger *et al*, 2016; “Réaliser des relevés IBP,” n.d.). Concerning dead wood, the evaluation grid has been slightly adapted by considering the circumference instead of the diameter since we did not have the tools to measure the diameter (**Table 1**). However, the circumference benchmarks were calculated on basis of diameter benchmarks used in IBP. A score was attributed according to the number of fallen or rooted big and medium deadwoods (bDW and mDW) measuring at least 1m in length that were present inside the sampling station. A score was also attributed for small dead wood on the ground (sDW) like branches by visual estimation.

Table 1: score grid for dead wood measurements inspired from IBP where bDW stands for big size dead wood, mDW for medium sized dead wood and C for circumference. Small dead wood on ground measurements are based on visual appreciation.

Measures	Criteria	Scores
Fallen dead wood	bDW if **C > 1.18m** mDW if **0.55 < C < 1.18m**	**0** : bDW<1 & mDW<1 **1** : bDW < 1 & mDW ≥ 1 **2** : 1 ≤ bDW < 3 **5** : bDW ≥ 3
Rooted dead wood	bDW if **C > 1.18m** mDW if **0.55 < C < 1.18m**	**0** : bDW<1 & mDW<1 **1** : bDW < 1 & mDW ≥ 1 **2** : 1 ≤ bDW < 3 **5** : bDW ≥ 3
Small dead wood on ground	**Small** and **medium branches**	**0** : no branches **1** : few small branches **2** : pile of small branches **3** : medium branches **4** : pile of medium branches **5** : large pile of medium branches or small timber(s)

Concerning habitat openness, a score of 0 was attributed to the stations that have a total canopy hole inferior to 1% of the station area. A score of 2 was attributed if the canopy hole was >5% and a score 5 if the hole represented 1 to 5% of the total area of the station. This scoring methods is assumed to be representative of habitat attractiveness for biodiversity according to IBP.

2.4 Ground beetles trapping and biomass measurements

Concerning ground beetle samplings, pitfall traps were used since it is frequently used in literature for this kind of experiment because of its advantages. This trap can generate easily a big quantity of data while being cost-saving. This catching method measure activity-density and thus represents more local abundance than species richness since different ground beetles species live in different microhabitats that cannot all be sampled (Jouveau *et al*, 2019). Moreover, all ground beetle species are not active at the same time of the day (Loreau, 1984). Thus, passive trapping avoids days long of active catching. However, the traps can influence sampling by their own characteristics like the size, material, colour, complexity or preservative/killing solution (Luff, 1975; Lange *et al*, 2011; Brown and Matthews, 2016). For this study, we used pitfall traps constituted by a transparent plastic pot (height = 14.5cm, upper diameter = 10cm) buried just under the ground surface, and partly filled (4cm from the trap bottom) with a liquid solution able to kill and preserve the captured organisms. The killing solution was made with salt water (200g/L) and a drop of TWEEN®20 detergent (Sigma-Aldrich, USA). A grid was put just on top of the trap and anchored to the ground with wooden sticks to prevent little vertebrate animal captures (*e.g.* little rodents, amphibians or slow-worms). In practice, 2 traps were buried at 5m from each other on every station site (**Figure 2**).

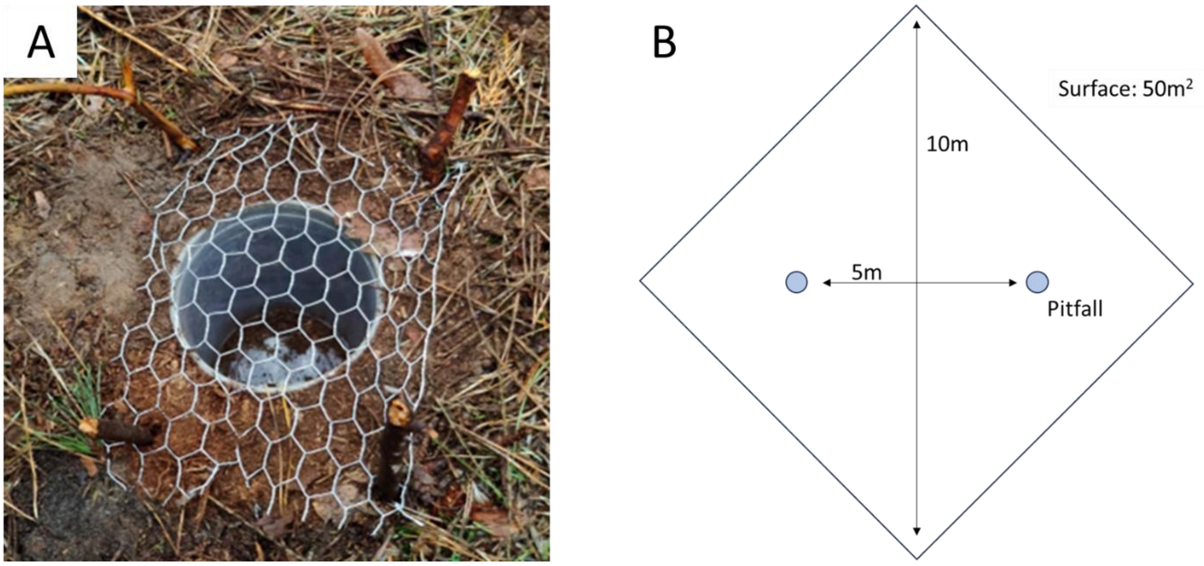

Figure 2: Pitfall trap used (A) and sampling station plan (B) used for ground beetles catching and environmental factors measurements.

Each sampling station was defined by a square of 50m^2 with its centre equidistant from the two pitfalls and one of its diagonals is aligned with the line joining the pitfalls. During this study, 46 traps were placed during 4 catching sessions of five days (late April, early July, mid-August and mid-September) thus a total of 184 traps were retrieved during this study. The traps were set for only 5 days because a longer period was not suitable with the killing solution and we tried to avoid catching too many ground beetles or little vertebrates. Between each session, the traps were emptied and the organisms of interest were collected. No minimum or maximum time limit was set for searching for organisms in the traps. Collected organisms were then sorted or put aside in addition to ground beetles for further studies (spiders and dung beetles) or to constitute an insect collection. Carabid beetles were then identified to species using the identification keys written by (Jeannel, 1941, 1942) or Roger *et al* (2010). To determine their dry biomass, they were dried at 60°C during 7 days. This period was assessed after preliminary trials aiming to determine the minimal time needed before no more decrease in weight is measured for all size categories of ground beetles. The insects were then weighted with an accuracy of 10^{-5}g to obtain the dry weight.

2.5 Data management

For this study, the maps of the Lauzelle Forest were created on ArcGis and QGIS. All statistical analyses were conducted on RStudio with the collected data and compared to data of (Nedergedaelt, 1981) when it was possible. The quality of sampling was estimated with accumulation curves and Chao equation. Collected data were first described using illustrative graphs. Stations were clustered according to their similarity of ground beetle diversity using Jaccard index. In order to find links between stations characteristics and ground beetle assembly, several multivariate analyses were conducted. PCA is used to visualize stations characteristics, FCA for ground beetle species repartition in the different stations according to their abundance or biomass and CCA to show the repartition in the different stations and according to the environmental characteristics. Generalized linear mixed models were performed to identify which quantitative environmental variable have a significant effect on abundance, species richness or MIB. They were then tested with Anova function in R. Concerning categorical variables (openness, management methods or objectives), their effects were visualized using bar plots and tested by performing ANOVA and Tukey multiple pairwise-comparisons when normally distributed or Kruskal-Wallice when not.

3. Results

3.1 Stations characteristics

Stations environmental characteristics that were measured are shown in **Table 2**. The highest amounts of small dead wood were found on stations 12, 5, 16, 22. Large rooted dead trees were rather rare since only four were found over the 23 stations while only 4 stations did not possess at least one large dead tree on the ground. However, the station 8 (beech plot) had no dead tree at all but it was the only station presenting an optimal canopy hole (1-5%) according to IPB scoring method. The highest maximum circumferences were observed in stations of oak, beech and oak and beech. The large Scots pine inside station 11 (heathland) was the fifth greatest tree measured. Herbaceous layer was the denser in more open areas like heathlands (stations 11, 12, 13), forest edges (stations 14, 15, 16) but also in one pine tree plot and in the birch plot near the pond (station 1). Mean circumference and tree density showed a high correlation with maximal circumference. Four types of drainage were identified and were linked with the four different soil types identified.

Table 2: sampled stations environmental characteristics. Station – identification number of the station ; smallDW.ground – quantity of small dead wood on the ground ; DW.rooted – quantity of large rooted dead wood ; dW.ground ; quantity of large deadwood on the ground ; Cmax – maximum tree circumference in centimeters; Cmean – mean tree circumference in centimeters; Tdensity – tree density ; Tspecies – number of tree species ; Area.Type – openness according to IPB ; Altitude_m – altitude in meters ; Sol – soil type ; drainage intensity categories ; Herbaceous – herbaceous layer density ; Tree dom – dominant tree species.

Station	smallDW.ground	DW.rooted	DW.ground	Cmax	Cmean	Tdensity	Tspecies	Area.Type	Altitude_m	Sol	Drainage	Herbaceous	Tree.dom
1	2	0	1	110.0	68.80	0.14	2	2	92	NC/tourbe	1	1.20	Birch
2	2	0	1	173.0	168.50	0.06	3	2	92	Luvisol	3	0.80	Oak
3	1	0	1	264.0	190.70	0.06	4	0	107	Luvisol	3	0.85	Oak
4	0	1	2	339.5	211.00	0.06	1	0	86	Luvisol	3	0.95	Oak
5	2	0	2	348.0	160.50	0.10	2	0	108	Luvisol	3	0.00	Oak and beech
6	1	0	1	209.0	144.00	0.06	3	0	125	Luvisol	3	0.10	Oak and beech
7	1	0	2	113.0	58.00	0.06	2	0	126	Luvisol	3	0.20	Oak and beech
8	0	0	0	189.0	167.40	0.08	2	5	107	Luvisol	3	0.00	Beech
9	2	0	1	199.0	197.50	0.06	1	2	134	Luvisol	3	0.20	Beech
10	1	0	2	293.4	240.10	0.04	2	0	112	Luvisol	3	0.30	Beech
11	2	0	1	239.0	105.40	0.10	5	2	117	Podsol	4	0.50	Heathland
12	3	0	0	67.5	64.60	0.08	2	2	117	Podsol	4	1.40	Heathland
13	0	0	1	0.0	0.00	0.00	0	2	118	Podsol	4	1.70	Heathland
14	2	1	1	149.0	54.80	0.20	5	0	123	Luvisol	3	0.05	Forest edge
15	5	1	2	130.0	83.75	0.08	4	2	129	Luvisol	3	1.10	Forest edge
16	3	0	1	35.0	32.00	0.04	2	0	127	Gleysol	2	1.00	Forest edge
17	1	0	0	120.0	80.20	0.20	3	0	118	Podsol	4	0.00	Pine trees
18	0	0	0	153.0	122.80	0.10	1	2	112	Podsol	4	0.95	Pine trees
19	2	0	2	147.5	117.50	0.06	1	0	118	Podsol	4	0.00	Pine trees
20	1	0	1	199.5	155.20	0.10	2	0	124	Podsol	4	0.00	Pine trees
21	4	0	1	113.0	113.00	0.02	4	0	92	Luvisol	3	0.00	Biological area
22	2	0	1	246.0	91.50	0.08	3	0	92	Luvisol	3	0.15	Biological area
23	1	1	1	47.0	37.00	0.04	3	0	92	Gleysol	2	0.55	Biological area

3.2 Sampling description

3.2.1 Trapped ground beetle in 2023 and 1981

During this study, 226 adult ground beetles of 26 species belonging to 16 genera were caught in 184 traps (trapping ratio per day: 0.2456 beetles per trap). Trapping results are presented in **Table 3**. It is much less than in 1980, where 3013 carabids of 19 species were caught in 1400 traps (trapping ratio per day: 0.2152 carabids per trap per day). Only eight species from 1980 have been trapped in this study (*Abax parallelepipedus*, *Carabus problematicus*, *Nebria brevicollis*, *Notiophilus substriatus*, *Pterostichus madidus* and *Pterostichus strenuus*) and two of which were considered rare (*Cychrus caraboides* and *Leistus rufomarginatus*). More species have been identified during this study than in 1980 but more stations were sampled (23 against 20). In addition, open areas and forest edges were not sampled in 1980. The seven most trapped species in the wood are *Cicindela campestris* (n=88), *P. madidus* (n=29), *C. problematicus* (n=22), *A. parallelepipedus* (n=20), *Pterostichus melanarius* (n=11), *Notiophilus rufipes* (n=10) and *N. brevicollis* (n=8). *C. problematicus* is the heaviest trapped species (0.1720g in average). In total, *C. problematicus* individuals constitute 32.26% of the total ground beetle biomass, followed by *C. campestris* (24.08%) and *A. parallelepipedus* (17.47%). Total abundance of ground beetle species during each sampling session are presented in **Appendix B.1**.

Table 3: Ground beetle sampling summary per species. Number of stations of occurrence (Stations), total abundance (Ab.), relative abundance in whole sample (Rel.Ab), total biomass (B.), relative biomass in whole sample (Rel. B.) and mean biomass (B.). Marginal species are those having only one individual trapped.

Abr.	Species	Stations	Ab.	Rel. Ab. (%)	B. (g)	Rel. B. (%)	B. mean (g)
App	*Abax parallelepipedus*	8	20	8.85	2.0486	17.47	0.1024
Ap	*Abax parallelus*	2	2	0.88	0.2139	1.82	0.1069
Am	*Amara montivaga*	1	2	0.88	0.0241	0.21	0.0120
Bd	*Bembidium deletum*	1	2	0.88	0.0029	0.02	0.0014
Cp	*Carabus problematicus*	10	22	9.73	3.7836	32.26	0.1720
CIc	*Cicindela campestris*	3	88	38.94	2.8239	24.08	0.0371
CYc	*Cychrus caraboides*	2	2	0.88	0.1994	1.70	0.0997
La	*Limodromus assimilis*	1	2	0.88	0.0373	0.32	0.0186
Nb	*Nebria brevicollis*	5	8	3.54	0.2935	2.50	0.0367
Nr	*Notiophilus rufipes*	5	10	4.42	0.0292	0.25	0.0029
Ns	*Notiophilus substriatus*	1	5	2.21	0.0066	0.06	0.0013
Pc	*Poecilus cupreus*	1	2	0.88	0.0410	0.35	0.0205
Pmc	*Pterostichus macer*	3	7	3.10	0.0306	2.61	0.0438
Pmd	*Pterostichus madidus*	12	29	12.83	1.3567	11.57	0.0468
Pme	*Pterostichus melanarius*	2	11	4.87	0.3780	3.22	0.0344
Po	*Pterostichus ovoideus*	2	3	1.33	0.0124	0.11	0.0041
Ps	*Pterostichus strenuus*	1	2	0.88	0.0079	0.07	0.0039
	Marginal species						
Af	*Amara familiaris*	1	1	0.44	0.0056	0.05	0.0056
Cm	*Calathus melanocephalus*	1	1	0.44	0.0789	0.07	0.0789
Er	*Elaphrus riparius*	1	1	0.44	0.0051	0.04	0.0051
Lr	*Leistus rufomarginatus*	1	1	0.44	0.0061	0.05	0.0051
Oo	*Oxypselaphus obscurus*	1	1	0.44	0.0033	0.03	0.0033
Pa	*Paranchus albipes*	1	1	0.44	0.0053	0.05	0.0053
Pk	*Poecilus kugelanni*	1	1	0.44	0.0239	0.20	0.0239
Pnr	*Pterostichus niger*	1	1	0.44	0.0815	0.69	0.0815
Pna	*Pterostichus nigrita*	1	1	0.44	0.0233	0.20	0.0233
Total			226	100	11.7274	100	

Further data analyses compare the results obtained with and without marginal species. Even though marginal species could be removed since they are only represented by one individual, their use can also help to precise the results. All trapped ground beetle life history traits are presented in the **Appendix D.1**. Only six trapped species are considered as forest specialists while 10 are open habitat specialists and the 10 others are generalists. Concerning ground beetle size, more large species (11) were trapped than medium (5) or small (10).

3.2.2 Accumulation curves and sampling quality

The sampling quality in different sampling subsets (forest plot type or sampling session) is represented by the accumulation curves. They seem to indicate a low quality of sampling even though the general accumulation curve is near a plateau phase. While sampling session accumulation curves increase similarly to the general curve (**Figure 3.A**), those concerning sampling in different forest covers are different (**Figure 3.B**). Species accumulation curves tend more to a plateau phase in coniferous, heathland and deciduous, but concerning forest edge, the situation is quite different as the curve seems really far from the plateau.

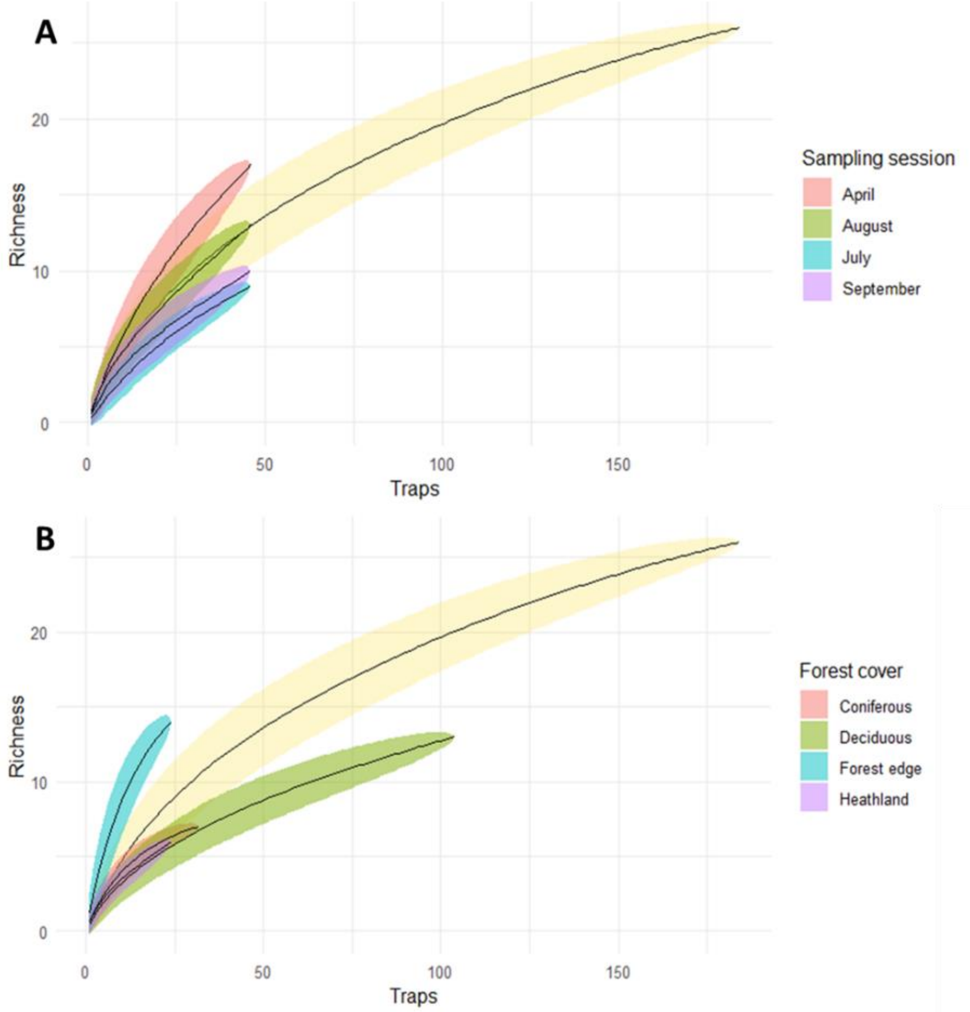

Figure 3: accumulation curves of ground beetle abundance in function of the number of traps set during the different sampling sessions (A) and in the different types of forest plots (B). The yellow curve represents the species accumulation during the whole study. Each accumulation curve is surrounded by a coloured halo that represents the standard deviation obtained by random permutations in the trap retrieving order.

Minimal species richness for the different subsamples are estimated using Chao equation (Chao, 1987) and presented in **table 4**. Chao has determined a way to evaluate the minimal species richness on basis of observed species richness, number of species occurring only in one or two stations and are thus considered as rare. Species richness across the wood is estimated to at least 32 ± 5 species. Estimations for deciduous plots and all sampling stations indicates that more samplings should be made in these conditions since richness observed are quiet under the estimations given by Chao's equation.

Table 4: Estimated species richness and standard error (SE) using Chao equation on basis of all samplings (All), forest cover (Coniferous, Deciduous, Heathland, Forest edges) and sampling date (April, July, August, September).

Sampling pool	Observed richness	Estimated richness	SE
All	26	32.216	5.148
Coniferous	7	7.646	1.272
Deciduous	13	37.264	30.81
Heathland	6	11.750	6.764
Forest edges	14	18.313	4.622
April	17	46.592	28.034
July	9	23.674	13.24
August	13	52.620	48.031
September	10	30.543	16.875

3.2.3 Station clustering

The different stations were clustered in a dendrogram using the Jaccard distance which measures dissimilarity between samples (**Figure 4**). With the dendrogram, we could potentially observe similarities between groups of tree stands and thus assume similarities between ground beetle communities. Stations situated in the same type of tree stands were expected to show similarity. However, stations of the same type are rather clustered in different sub-groups except stations 8 and 10 (two beech plots) but they still show a dissimilarity of 65% while being exposed to the same drainage and management methods. The two most similar stations are 4 (oak plot on slope) and 23 (more humid part of biological) area that shows a biodiversity dissimilarity of approximately 25% but only share the same openness score. Station 13 is dissimilar to every other station (dissimilarity =1.0). This station had 2 ground beetle species that were only sampled there (*Poecilus cupreus* and *Poecilus kugelanni*) or almost only (*C. campestris*). Other stations are pooled in 4 sub-groups. The first sub-group (8,10,17,20) seems to gather forest stations with very high drainage and production objectives. The second sub-group is more difficult to describe. Station 11 is quite similar to pine tree plots (18 and 19) and it is not so surprising since it is situated near a pine tree plot and presents a large Scots pine in its centre and several small ones at its border.

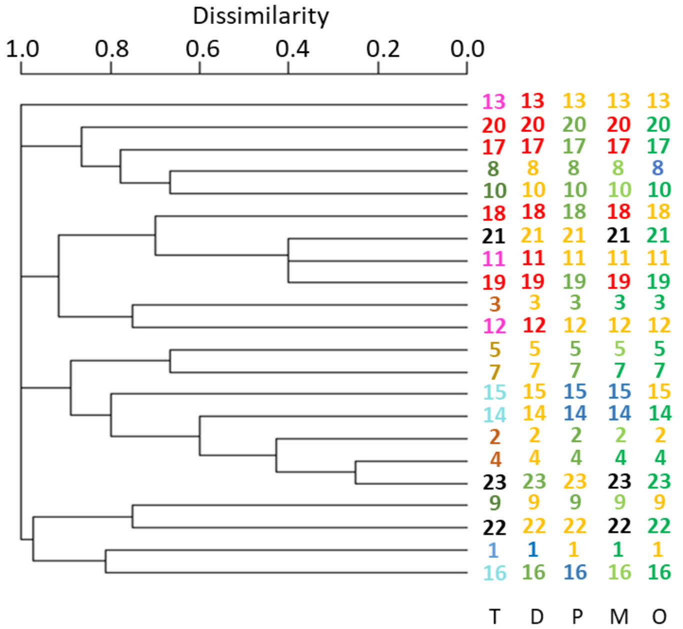

Figure 4: Stations clustering by similarity of ground beetle diversity according to Jaccard index. Dissimilarity between stations is represented by the latest shared node. Numbers on the right identify the station. Colours refer to the different levels of the following variables. T – station types ; D – drainage ; P – management purposes ; M – management method; O – habitat openness. 1 – birch plot ; 2,3,4 – oak plots ; 5,7 – oak and beech plots ; 8,9,10 – beech plots ; 11,12,13 – heathlands ; 14,15,16 – forest edges ; 17,18,19,20 – pine trees plots ; 20,21,22 – biological area.

The stations of third sub-group (5,7,15,14,2,4) are all dominated by deciduous trees and show a rather high drainage. In the fourth sub-group, stations 1(birch plot) and 16 (forest edge) are the most humid plots sampled while 9 (beech plot) and 22 (biological area) are dominated by beech. Station 11 (heathland) and 1 (birch plot) both present birch trees but are completely dissimilar. All of these results suggest that similarities between stations are difficult to explain thanks to these qualitative variables.

3.2.4 Ground beetle abundance and biomass

In this study, *P. madidus* is the most ubiquitous species (**Figure 5**). It is found in 12 stations and nearly exclusively in stations dominated by deciduous trees. The second most ubiquitous is *C. problematicus* that is found in 10 stations but is more abundant in heathlands near pine trees (stations 11 and 12) or in pine trees (stations 17, 18 and 19). It can also be found in biological area (station 21 and 23). Stations 6, 13 and 16 appear to be very different from the 20 others. In station 6, no ground beetles were trapped. Station 13 cannot really be considered as a forest area since it is a great heathland without any trees. *C. campestris* was almost only found there in high abundance but only during the two first sampling sessions (**Appendix B.1**).

Station 16 (wettest and forest edge station) shows the highest species richness and was dominated by *Pterostichus macer* (n=5), *P. melanarius* (n=10) and *A. parallelepipedus* (n =5).

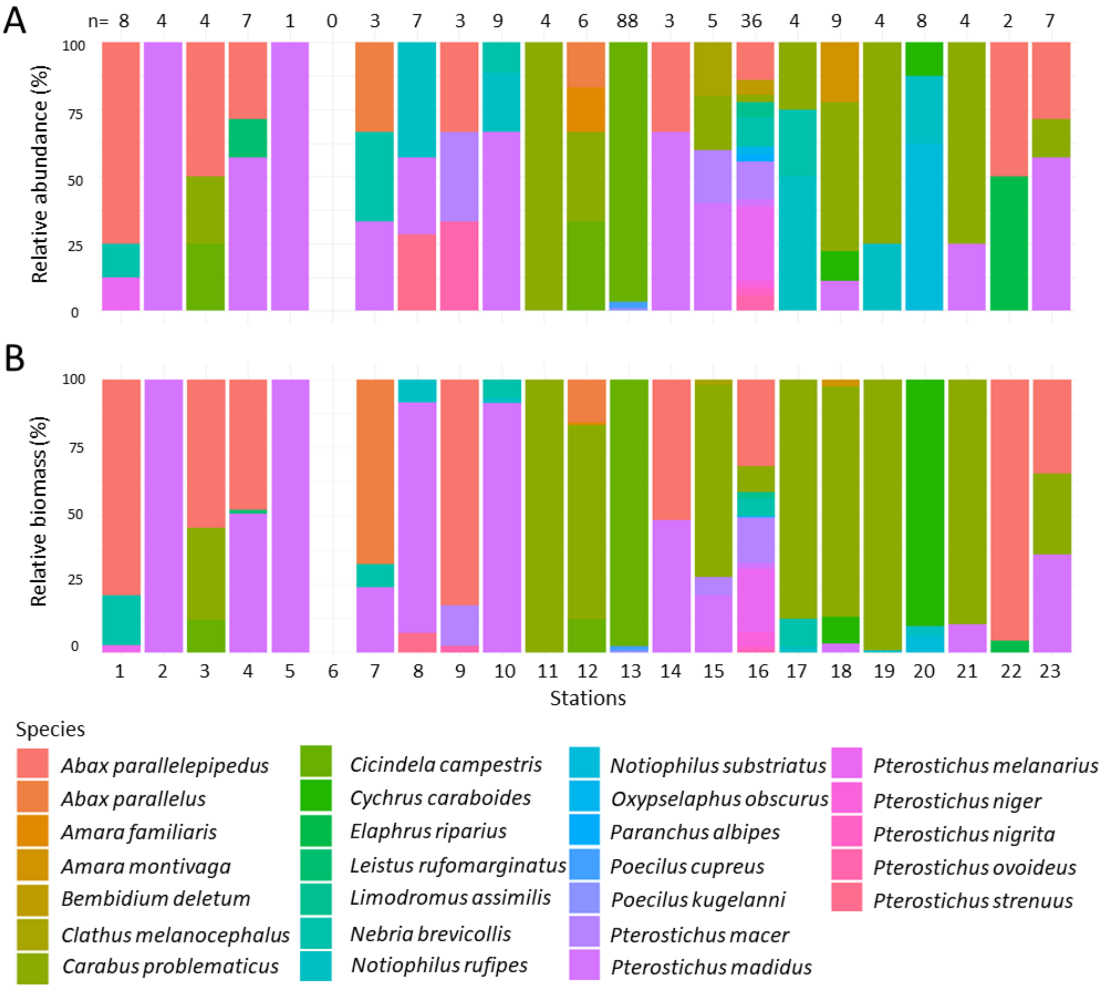

Figure 5: Ground beetle species relative abundance (A) and biomass (B) in the 23 sampling stations. The numbers on top of the bars (n) are the total number of ground beetles trapped in the different stations.

Ground beetles were not the only trapped invertebrates, dung beetles and spiders were also trapped in great number across the different stations (**Figure 6**). A total of 905 dung beetles and 249 spiders were trapped with ground beetles. While ground beetle abundance is quite similar throughout the wood except in station 13 and 16, spiders and dung beetles show a rather high variability. Dung beetles are more present in deciduous plots (stations 1 to 10) especially in the biological area (stations 21 to 23). However, no dung beetles were trapped in stations 1 (birch plot with high humidity) and 15 (forest edge near roads). They are also highly abundant in station 14, which is a densely wooded deciduous forest edge. Spiders are most abundant in oak plots (stations 2 to 4) compared to oak and beech plots (stations 5 to 7). Dung beetle abundance increase during sampling season on the contrary of spiders and ground beetles that shows a decrease but dung beetles abundance was not recorded during the first sampling session. In addition, the second sampling session shows a lower abundance of ground beetles.

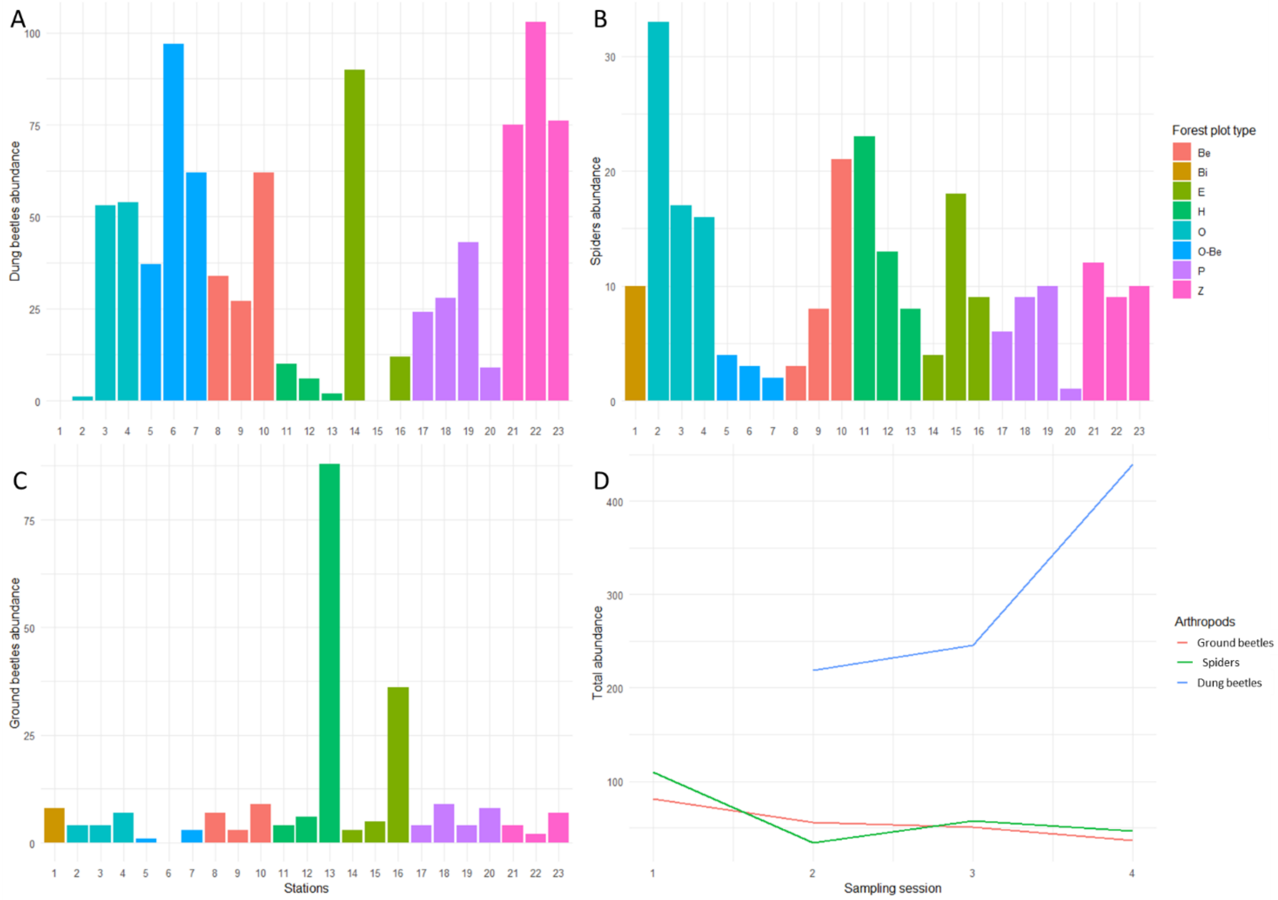

Figure 6: Total abundance of dung beetles(A), spiders (B) and ground beetles (C) in the 23 stations and at each sampling session (D). E – forest edges ; Be – beech plots ; P – pine tree plots ; H – heathlands ; O – oak plots ; Z – biological area ; Bi – birch plot : O-Be ; oak and beech plots ; D – deciduous tree stands.

Among all station types (on basis of plot types), forest edges showed the greatest diversity of ground beetles with 14 species (**Figure 7**), accounting for more than half of encountered species. Moreover, 13 species were found in only one station (station 16) while the species number on other stations was on average 2.54. In comparison with Nedergedaelt (1981), 15 species were trapped in the same type of tree stands and 8 are in common with sampling of 1981. Altogether, stations from unsampled type in 1981 (forest edges, heathlands and biological area) represented 20 species and 5 in common with 1981 sampling. Stations in deciduous plots showed a total of 13 ground beetle species which is more than pine trees (7 species) and heathlands (6 species). Among deciduous tree stands, beech plots showed the highest diversity (7 species) which is more than oak plots (5 species) and even more than mix plots of oak and beech (3 species).

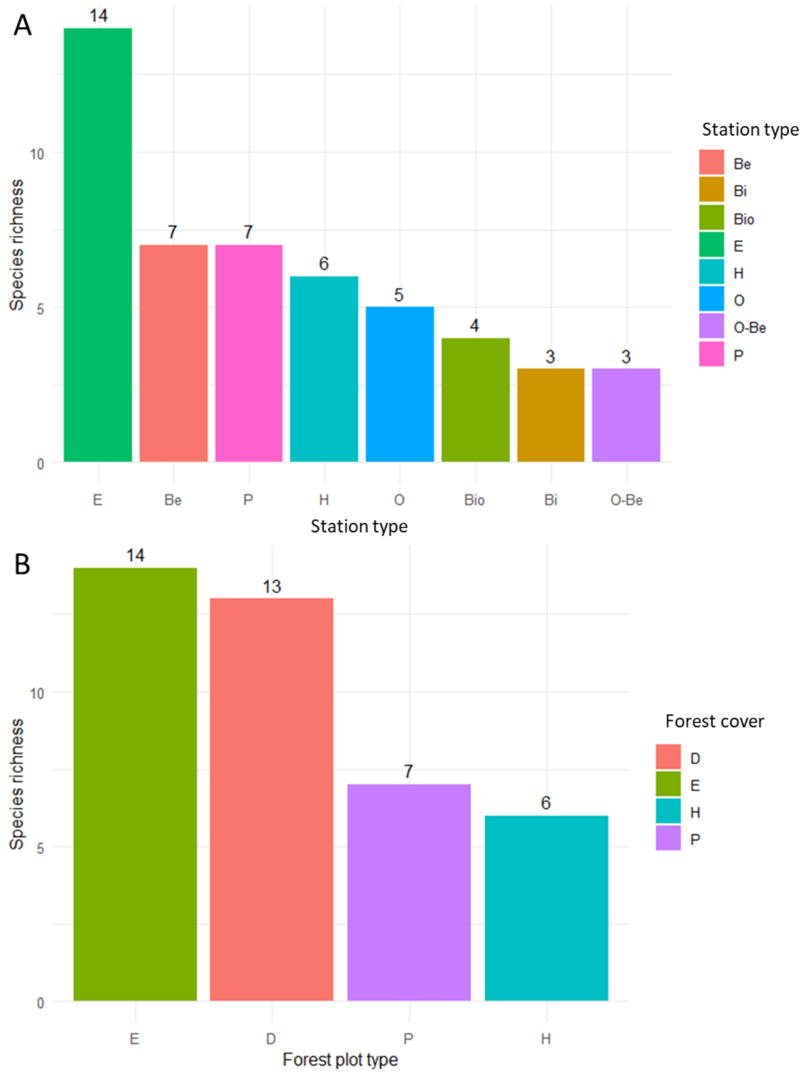

Figure 7: Total species richness inside the different stations types (a) and forest cover (b). E – forest edges ; Be – beech plots ; P – pine tree plots ; H – heathlands ; O – oak plots ; Z – biological area ; Bi – birch plot : O-Be ; oak and beech plots ; D – deciduous tree stands.

Total ground beetle biomass (**Figure 8 A**) inside the different stations is linked to ground beetle abundance. Indeed, stations 13 and 16 shows the highest ground beetle total biomass since they are the stations with the highest abundance. The third station with the highest total biomass is a pine tree plot where most of *C. problematicus* were found. However, results are completely different regarding mean individual biomass in each station. Among the ten stations with the highest MIB, 9 stations presented at least one *C. problematicus*. Highest MIB is found in station 11 (heathland with large Scots pine). Pine trees stations 18 and 19 shows the second highest MIB on a par with station 3 (oak plot) and 21 (biological area). The sixth higher MIB is found inside the birch plot (station 1) due to the high abundance of *A. parallelelpipedus*. Lowest MIB are in station 8 (beech plot) and 20 (pine tree plots with high abundance of *Notiophilus*).

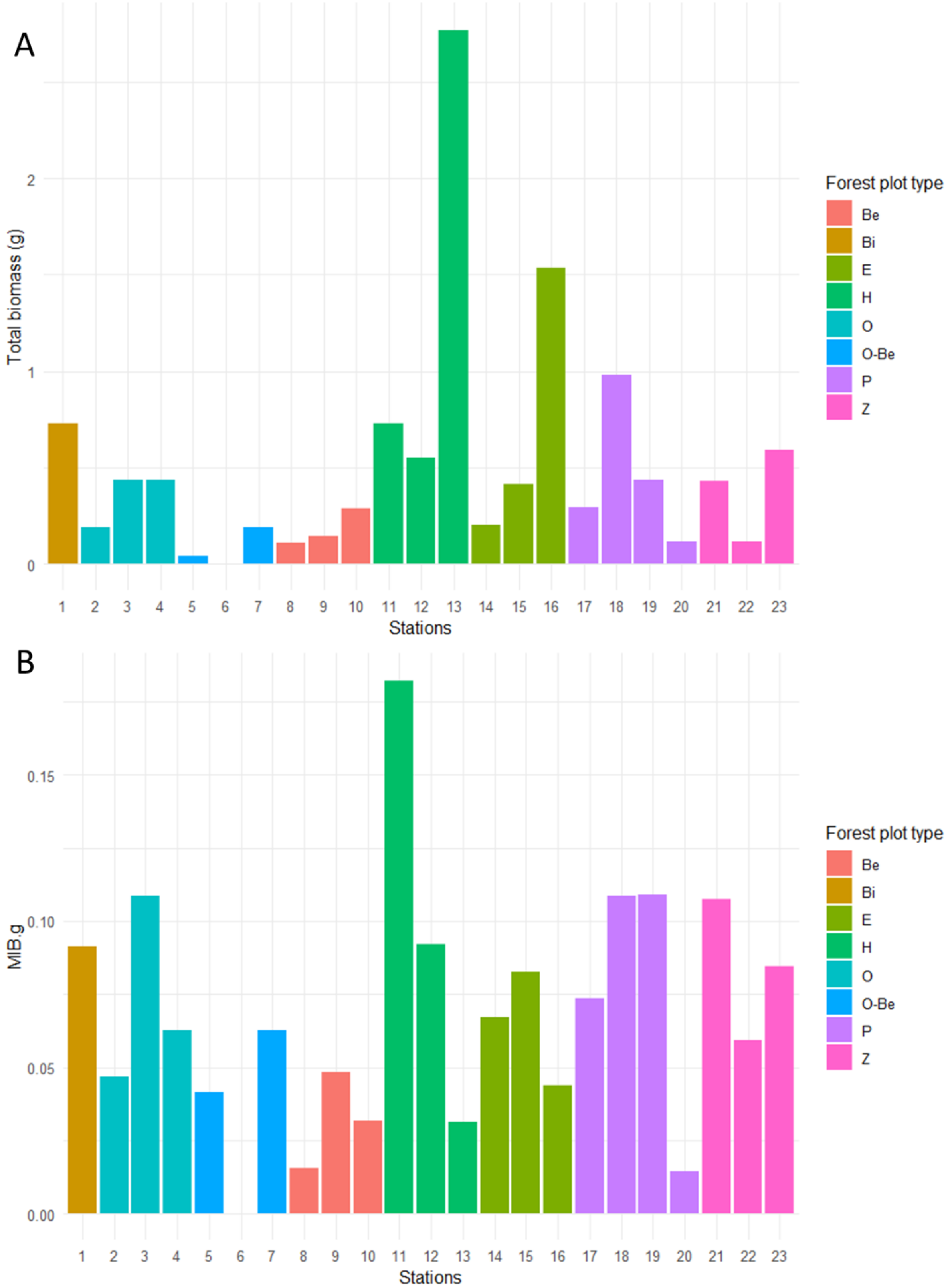

Figure 8: Ground beetles total biomass (A) and mean individual biomass (B) in the different stations. E – forest edges ; Be – beech plots ; P – pine tree plots ; H – heathlands ; O – oak plots ; Z – biological area ; Bi – birch plot : O-Be ; oak and beech plots ; D – deciduous tree stands.

3.3 Multivariate analyses

3.3.1 Principal Component Analysis (PCA)

The principal component analysis (PCA) performed with the characteristics of the 23 stations (**Appendix C.**1) after removing too correlated ones (Tree density and mean tree circumference) is presented in the **Figure 9**. The observed variability is explained at 42.4% by the two first dimensions.

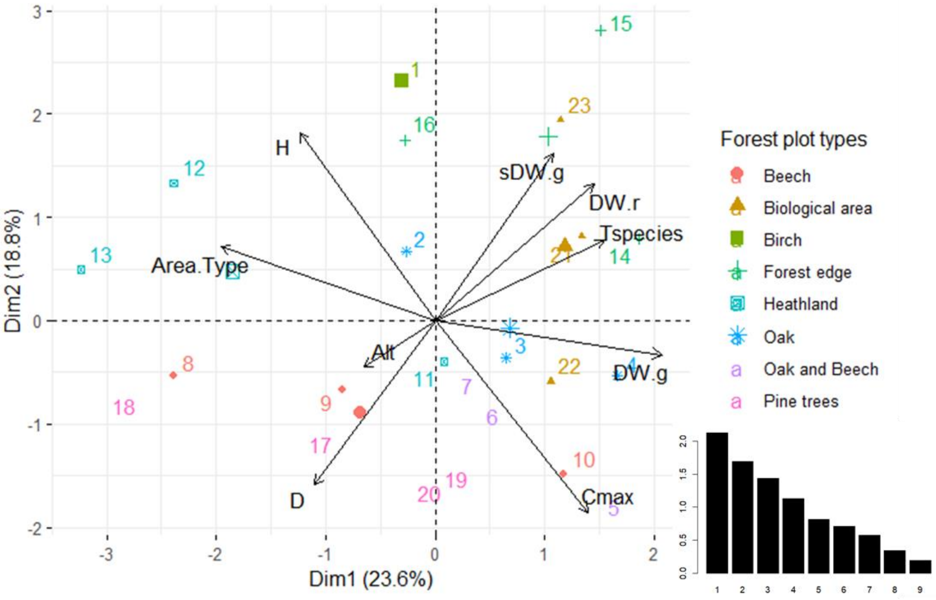

Figure 9: Principal Component Analysis (PCA) of the 23 sampling stations grouped by forest plot types. Each forest plot type was attributed a colour and a big symbol to indicate their mean position in the 1-2 dimensions. Area.Type – Openness attractivity according to IPB ; H – density of the herbaceous layer ; sDW.g – small dead wood quantity on the ground ; DW.r – rooted dead wood quantity ; DW.g – large dead wood quantity on the ground ; Tspecies – number of tree species ; Cmax – maximum circumference ; D – drainage ; Alt – altitude in meters. Arrow length indicates the representation quality of the different environmental characteristics. Inertia of the different axis are represented in to bottom right graph.

The horizontal axis (Dim1 = 23.6%) seems to be defined by a gradient from open areas to closed forest (from left to right). It can be described by denser herbaceous layer (H) or openness (Area.type) and trees with higher maximal circumference (Cmax) since the two first variables seem to be anticorrelated with the last one. Every forest plot type seems to follow this gradient with heathlands as open habitats and deciduous tree stands as closed areas with higher Cmax. The vertical axis (Dim2 = 18.8%) seems characterized by drainage intensity (D) or dead wood quantity (DW). Drainage and dead wood quantity seems uncorrelated and it is possibly because tree stands with higher drainage are mainly used for wood production thus contain less dead wood. Drainage gradient and habitat openness gradient seems to be independent.

3.3.2 Factorial Correspondence Analyses (FCA)

Several factorial correspondence analyses (FCA) were performed to compare ground beetle abundance and biomass repartition across the different sampling stations. The **Figure 10** shows station distribution according to ground beetle abundance without marginal species (only one individual trapped). Dimension 1 (explain 17.9% of inertia) seems to represent an openness gradient, from open areas (on the left) to forests areas (on the right). The Ground beetle communities of deciduous and coniferous tree stands seems slightly different regarding station dots distribution. However, the deciduous ellipse is mainly overlapping the coniferous ellipse thus the communities are rather similar. Dimension 2 (15.0% inertia) seems to represent a drainage gradient from top (high drainage) to bottom (low drainage). High drainage is represented by pine tree plots and high slop tree stands (stations 8 and 10) and low drainage is represented by stations 22, 16 and 1. The horizontal axis explains well the difference between station 13 and the others.

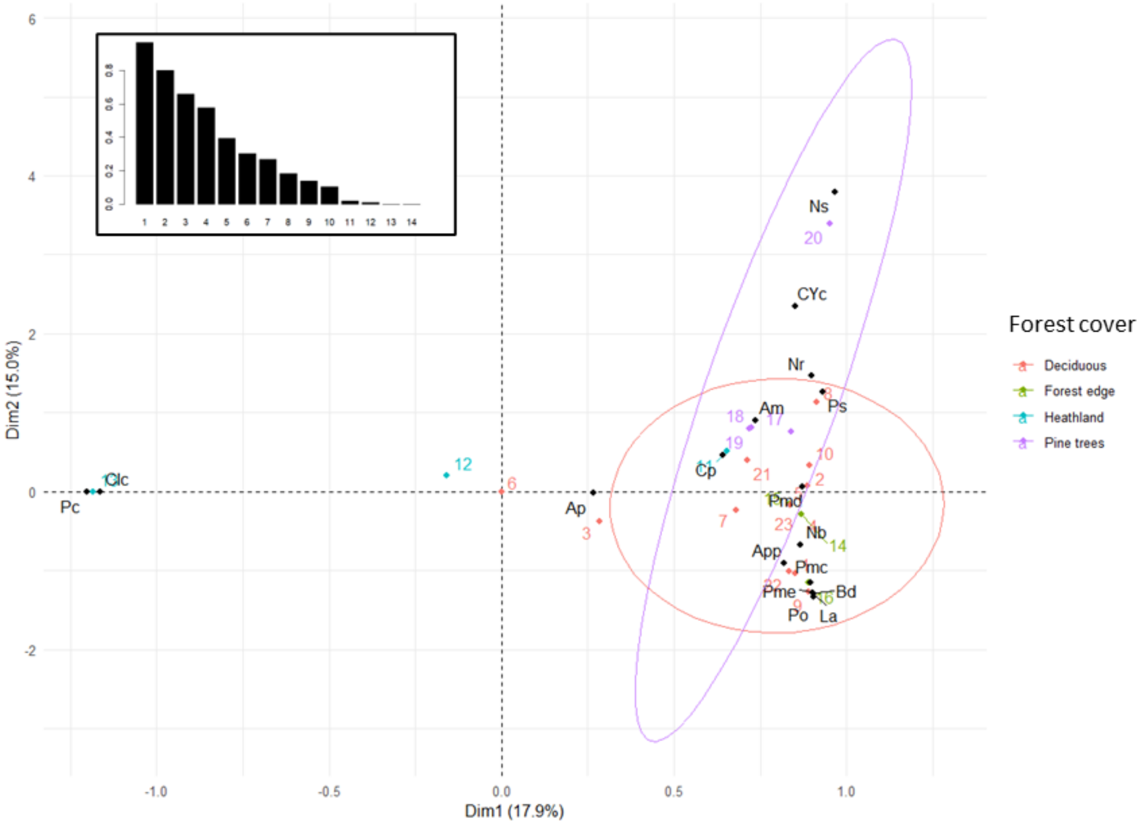

Figure 10: Factorial Correspondence Analysis (FCA) of the 23 sampling stations according to ground beetles species abundance after removing marginal species and empty stations. Black dots are ground beetle species and are identifiable thanks to abbreviation given in table 2Coloured dots are the stations, the coloured numbers help to identify them thanks to the sampled tree stands description. Inertia of the different axis are represented in the top left frame.

The **Figure 11** shows the stations and species distribution according to their abundance on dimensions 1 (20.6% inertia) and 2 (18.0%) after removing extreme stations (13 and 16). It is quite similar to their distribution in dimensions 2 and 3 before removing them (**Appendix C.2**). Drainage gradient can still be observed from bottom left to top right. The ellipses of deciduous and pine trees plots are less overlapping than in **Figure 10**. It suggests that the two plot types communities could be different. *Notiophilus substriatus* (Ns) and *C. caraboides* (Cyc) appear to be specialists of pine trees. It is less the case of *N. rufipes* (Nr) and *Pterostichus strenuus* (Ps) which are quite near deciduous ellipse. *C. problematicus* appears more like a habitat generalist since it is situated near pine trees plots, deciduous plots and heathlands but with a preference for dry habitats. While *A. parallelepipedus* (App) shows a preference for deciduous tree stands and humid habitats. *P. madidus* (Pmd) and *N. brevicollis* (Nb) seems to be more habitat generalists and preference for dryer habitats.

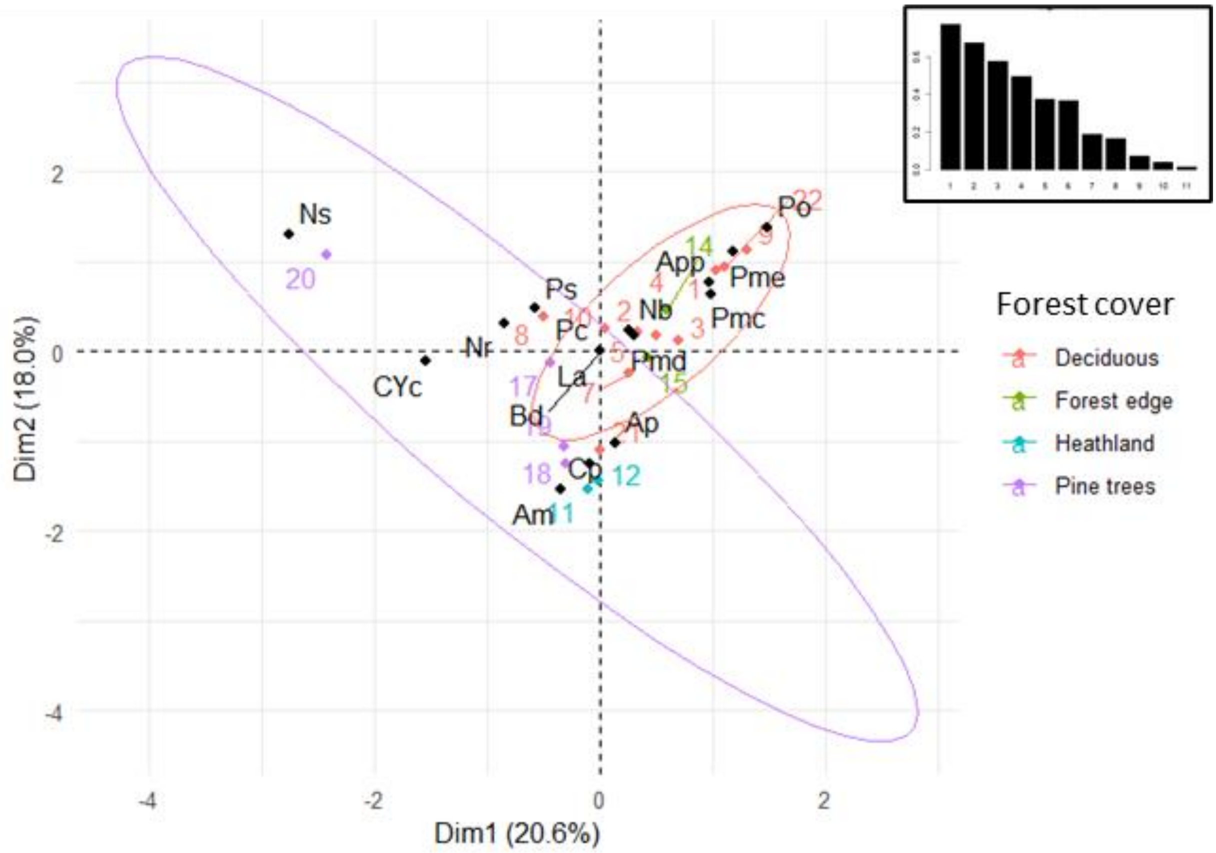

Figure 11: Factorial Correspondence Analysis (FCA) of the 23 sampling stations according to ground beetle species abundance after removing marginal species and extreme stations. Black dots are ground beetle species and are identifiable thanks to the **Appendix D.1**. Coloured dots are the stations, the coloured numbers help to identify them thanks to the sampled tree stands description. Inertia of the different axis are represented in the top right frame.

FCA can also be done using ground beetle biomass instead of abundance. According to biomass (**Figure 12**), the habitat openness and drainage gradients are still present along respectively dimension 1 and 2. The ellipsis are even less overlapping. This suggests that the communities can be more different according to biomass repartition. In addition, this second FCA shows a higher representativity on the two first axis (26.6% against 20.6%). Dimension 1 is still strongly affected by station 13

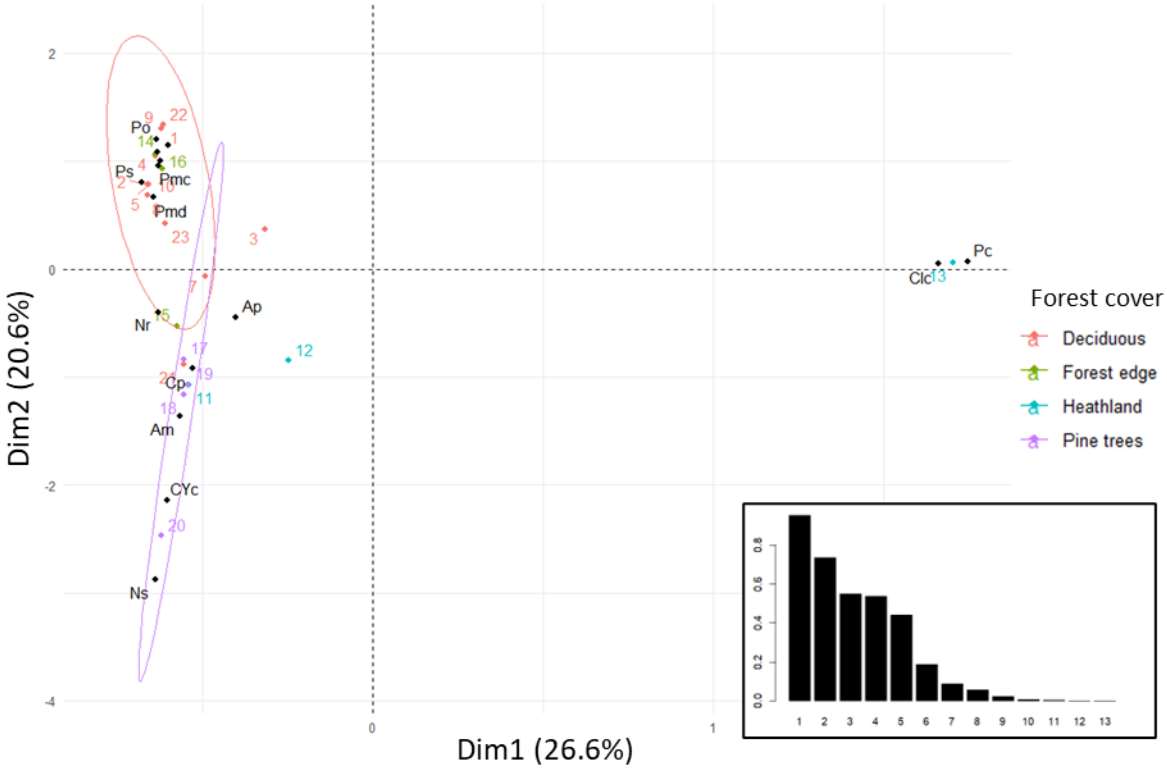

Figure 12: Factorial Correspondence Analysis (FCA) of the 23 sampling stations according to ground beetle species total biomass after removing marginal species and empty stations. Black dots are ground beetle species and are identifiable thanks to the **Appendix D.1**. Coloured dots are the stations, the coloured numbers help to identify them thanks to the sampled tree stands description. Inertia of the different axis are represented in the botttom righ frame.

After removing extreme stations, the remaining stations distribution in dimensions 1-2 (**Figure 13**) is similar to their distribution in dimensions 2-3 before removal (**Appendix C.3**). The ellipsis of deciduous tree stands and pine trees plots are still slightly overlapping and suggests that coniferous and deciduous ground beetle communities can be slightly similar. The drainage gradient is still present from top left (hugh drainage) to bottom right (low drainage). According to this new representation, *P. madidus* (Pmd) appears to have a higher biomass in deciduous forests dry forests while *N. brevicollis* (Nb) has a higher biomass in more humid areas. The distribution of *A. parallelepipedus* (App), *C. problematicus* (Cp), *C. caraboides* (Cyc) and N. substriatus (Ns) seem to confirm the preferences identified according to abundance.

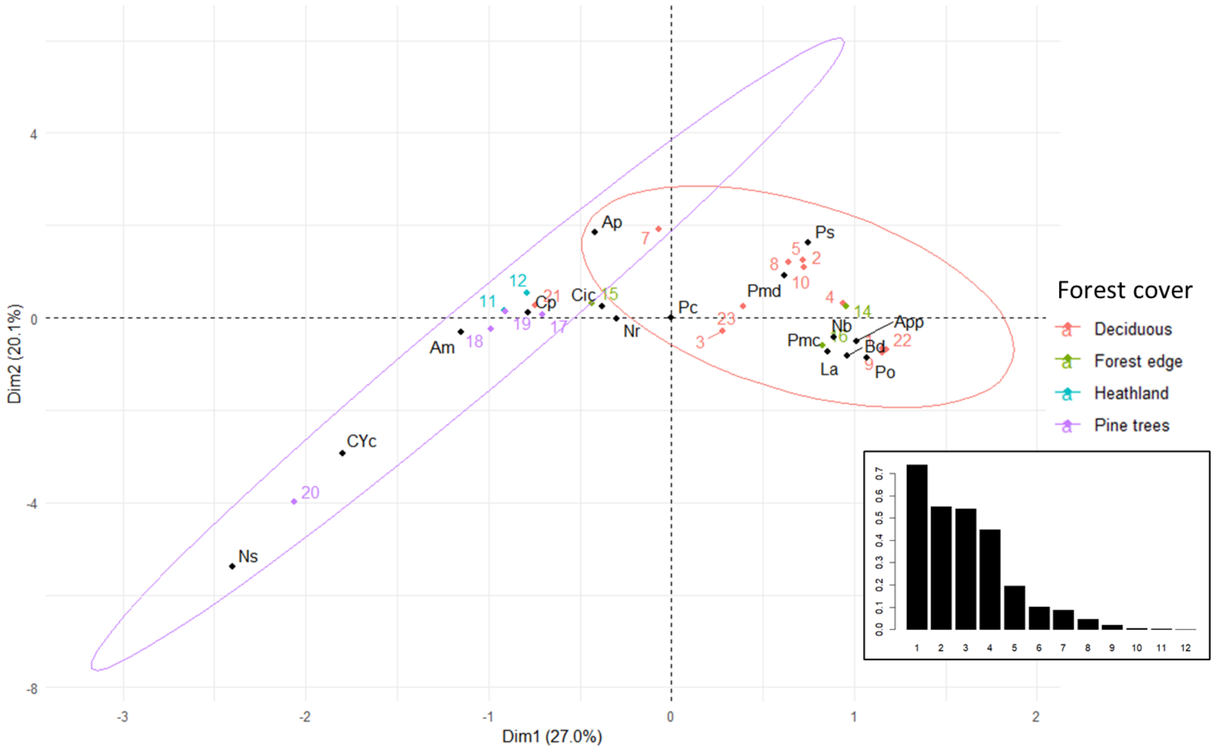

Figure 13: Factorial Correspondence Analysis (FCA) of the 23 sampling stations according to ground beetle species total biomass after removing marginal species and extreme stations. Black dots are ground beetle species and are identifiable thanks to the **Appendix D.1**. Coloured dots are the stations, the coloured numbers help to identify them thanks to the sampled tree stands description. Inertia of the different axis are represented in the botttom righ frame.

3.3.3 Canonical-Correlation Analyses (CCA)

In order to summarize PCA and FCA results Canonical-Correlation Analyses (CCA) were performed for abundance and biomass of ground beetles. CCA gather sites and species distribution according to environmental characteristics and ground beetle abundance or biomass. However, only CCA according to biomass are shown in this section since biomass repartition seems to be more explained by few axes. With only environmental characteristics and after removing marginal species, coniferous and deciduous ellipses are mainly overlapping according to biomass (**Figure 14**). The ellipses still seem to follow drainage intensity. Denser herbaceous layer seems to be anticorrelated with denser forest cover (maximal circumference, number of tree species) and correlated with drainage and open habitat. The horizontal axis (Dim1 = 44.9%) still seems to represent the habitat openness gradient while the vertical axis (Dim2 = 29.1%) is more representative of tree stands types and may be drainage. However, station 13 still strongly impacts dimension 1.

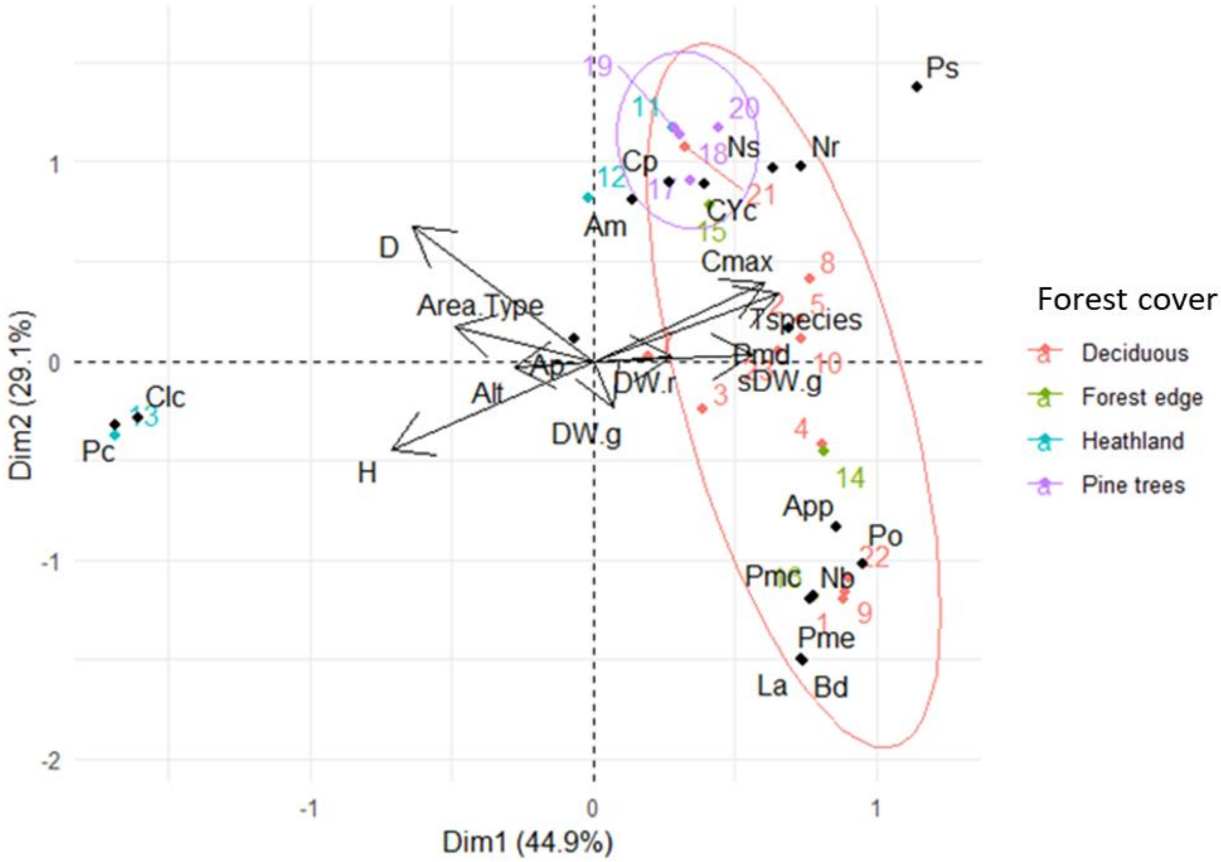

Figure 14: Canonical-Correlation Analysis (CCA) of the ground beetles distribution according to their total biomass in the different stations and following the environmental characteristics (after removing marginal species and empty station). D - Drainage ; A.t - Area type according to openness ; Alt - Altitude ; DWg - dead wood on ground ; DWr = standing dead wood ; sDW = small dead wood on ground ; Ts = number of tree species ; Cmax = maximum tree circumference ; Herbaceous = station cover by herbaceous layer and small trees.

After removing station 13, ellipses are still overlapping (**Figure 15**) but dimension 1 (50.2%) seems to be associated with drainage intensity (from right to left). *Amara montivaga* (Am), *C. caraboides* (Cyc), *C. problematicus* (Cp), *C. campestris* (CIc), *N. substriatus* (Ns), *N. rufipes* (Nr), and *A. parallelus* (Ab) seem to be xerophilous species while *A. parallelepipedus* (App), *N. brevicollis* (Nb), *P. ovoideus* (Po), *P. macer* (Pmc), *P. melanarius* (Pme), *Limodromus assimili*s (La) and *Bembidium deletum* (Bd) are more likely to be hygrophilous and prefer denser herbaceous layer. Dimension 2 (26.8%) seems more related to maximal circumference and dead wood amounts.

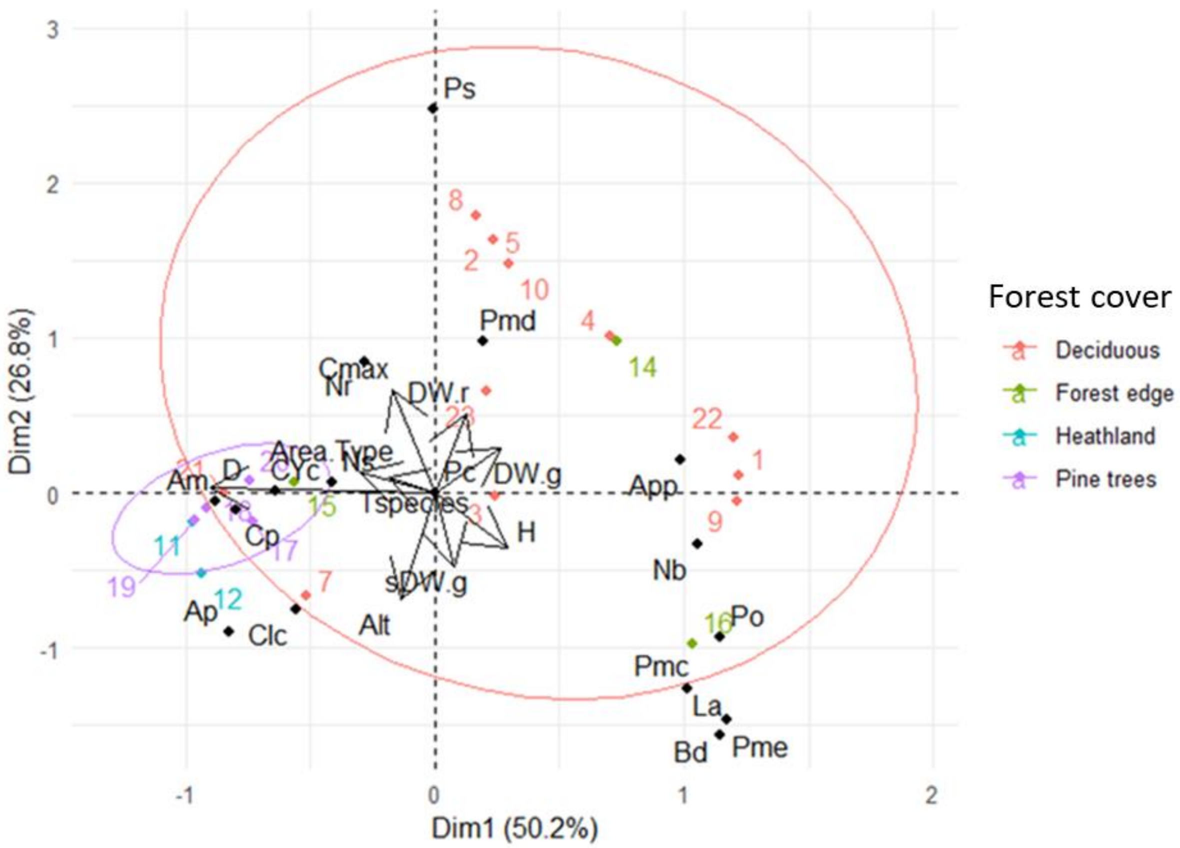

Figure 15: Canonical-Correlation Analysis (CCA) of the ground beetles distribution according to their total biomass in the different stations and following the environmental characteristics (after removing marginal species and stations 6 and 13). D - Drainage ; A.t - Area type according to openness ; Alt - Altitude ; DWg - dead wood on ground ; DWr = standing dead wood ; sDW = small dead wood on ground ; Ts = number of tree species ; Cmax = maximum tree circumference ; Herbaceous = station cover by herbaceous layer and small trees.

The **Figure 16** shows CCA according to biomass but with variables dependant of ground beetles (abundance, species richness and MIB). Dimension 1 (34.1%) seems to represent the habitat openness gradient (from left to right) while dimension 2 (24.6%) is more related to drainage. MIB seems correlated to maximal circumference and thus to wooded areas. It is pointing towards Pine trees plots presenting larger ground beetle species (Cyc, Cp, Ap). Species richness (R.sp) is pointing towards more humid stations but surely because of the station 16. Ground beetle abundance (Ab) seems correlated to herbaceous layer density (H) but it is surely strongly influenced by station 13.

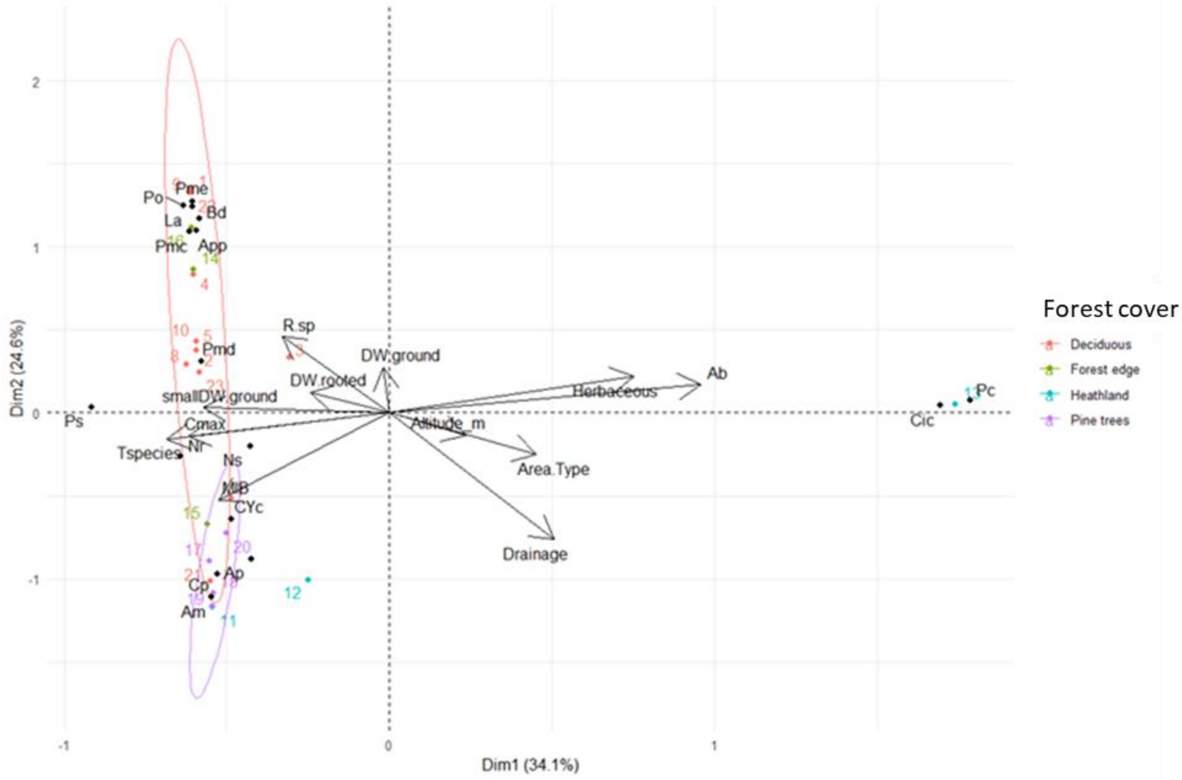

Figure 16: Canonical-Correlation Analysis (CCA) of the ground beetles distribution according to their total biomass in the different stations and following the environmental characteristics (after removing marginal species and stations 6). D - Drainage ; A.t - Area type according to openness ; Alt - Altitude ; DWg - dead wood on ground ; DWr = standing dead wood ; sDW = small dead wood on ground ; Ts = number of tree species ; Cmax = maximum tree circumference ; Herbaceous = station cover by herbaceous layer and small trees ; R.sp – species richness ; Ab – abundance ; MIB – mean individual biomass.

The **Figure 17** shows the distribution of ground beetles and stations after removing stations 13 and 16. Dimension 1 (37.9%) seems still explained by drainage gradient but dimension 2 (26.0%) is poorly explained by studied variables. MIB is still pointing towards pine trees plots but is now anticorrelated to maximal circumference and species richness and abundance which seems correlated with large dead wood amounts. Abundance is also still pointing towards deciduous tree stands and seems correlated with large dead wood amounts.

Additional CCA presenting dung beetles and spiders abundances are presented in **Appendices C.4** and **C.5**.

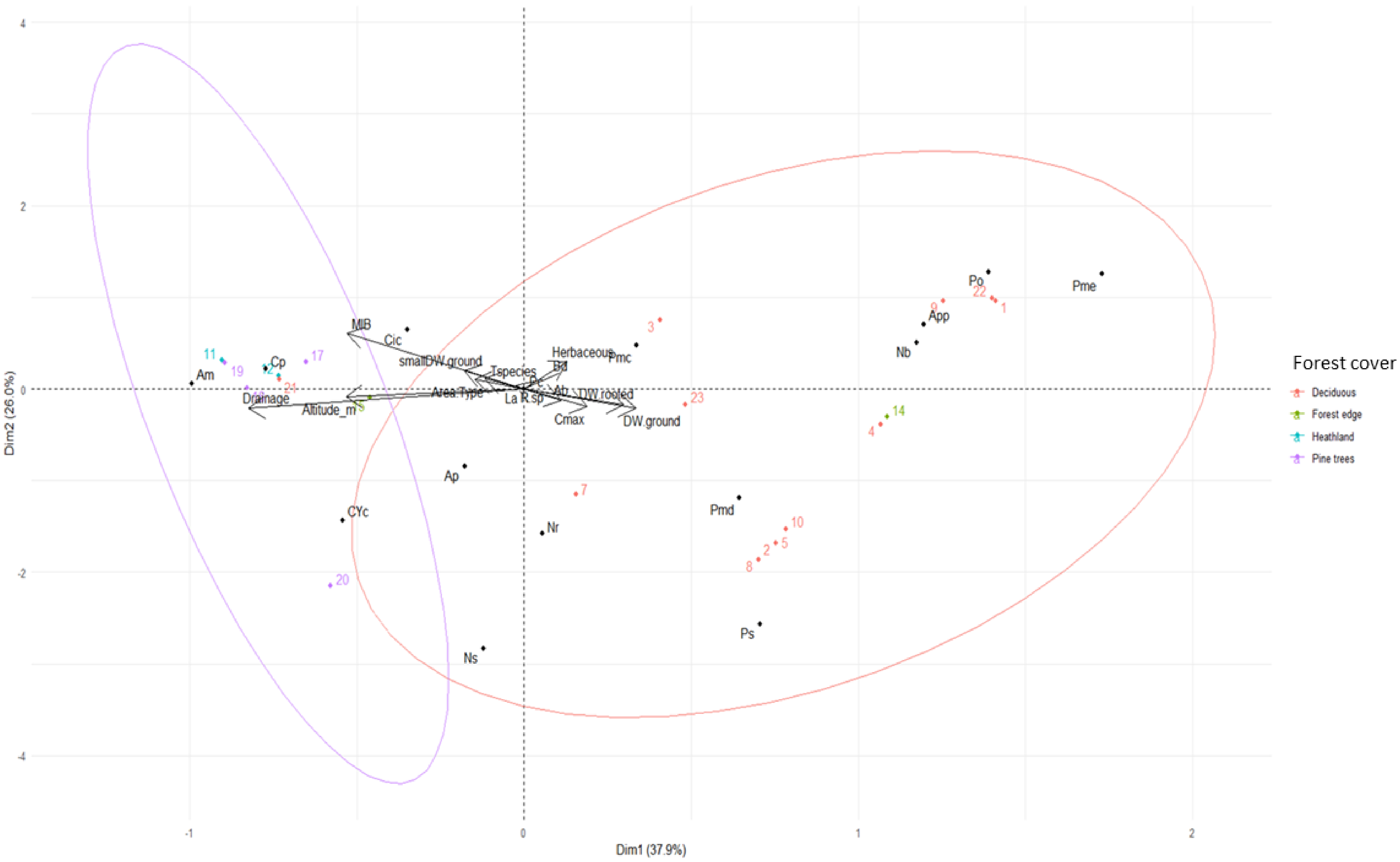

Figure 16: Canonical-Correlation Analysis (CCA) of the ground beetles distribution according to their total biomass in the different stations and following the environmental characteristics (after removing marginal species and stations 6,13 and 16). D - Drainage ; A.t - Area type according to openness ; Alt - Altitude ; DWg - dead wood on ground ; DWr = standing dead wood ; sDW = small dead wood on ground ; Ts = number of tree species ; Cmax = maximum tree circumference ; Herbaceous = station cover by herbaceous layer and small trees ; R.sp – species richness ; Ab – abundance ; MIB – mean individual biomass.

3.4 Generalized linear models

Generalized linear models were performed in order to identify the quantitative environmental factors that have a significant effect on ground beetle abundance, species richness, and mean individual biomass. The following results were obtained after removing marginal species and extreme stations (6, 13 and 16).

3.4.1 Ground beetle abundance

The only environmental variable that had a significant effect on ground beetle abundance is the quantity of small deadwood on the ground (**Figure 18**). ANOVA test shows a p-value of 0.021. It appears that higher quantity of small dead wood decrease carabid beetle abundance. This is consistent with observation of the final CCA (**Figure 17**)

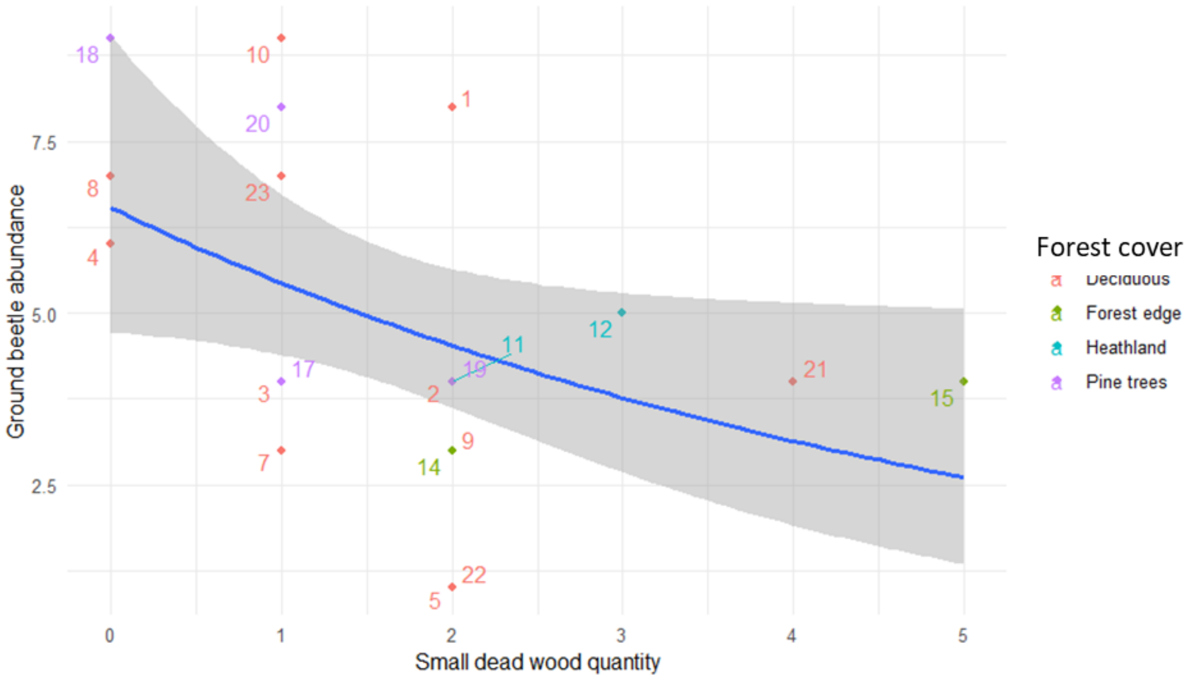

Figure 18: Poisson generalized linear model of ground beetle abundance in function of the quantity of small dead wood on ground.

Figure 19 shows the effect of herbaceous layer on ground beetle abundance. It seems there is a positive effect of herbaceous layer density on ground beetle abundance but according to ANOVA test, the effect is only nearly significant ($p = 0.079$). This result is consistent with **Figure 16** but it is less evident in **Figure 17**.

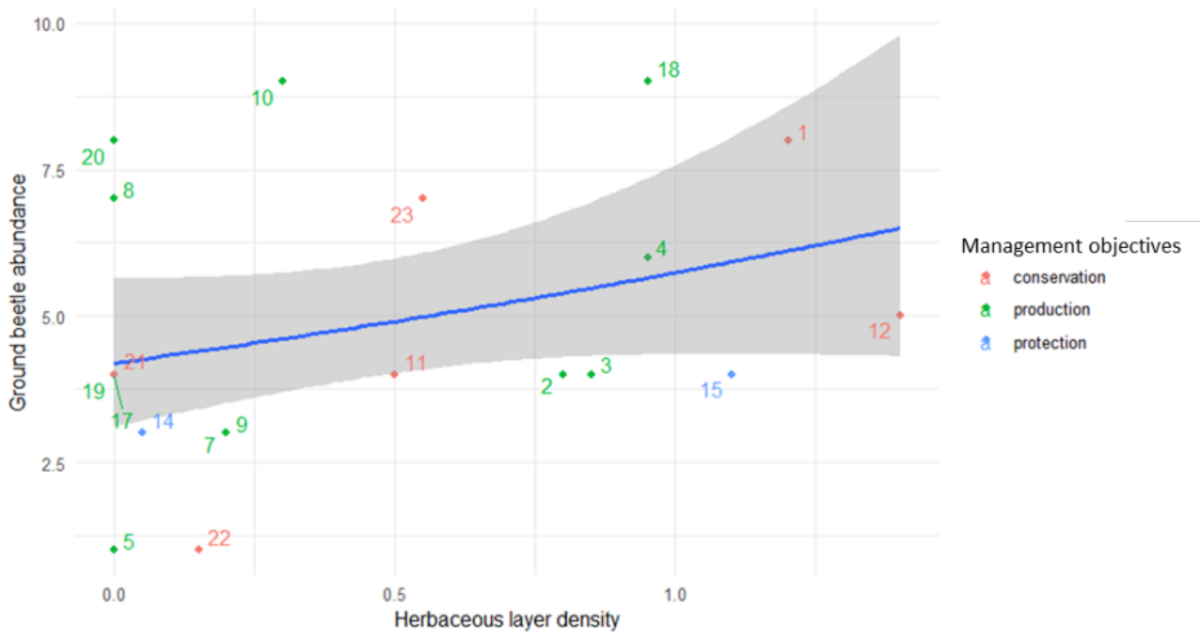

Figure 19: Poisson generalized linear model of ground beetle abundance in function of herbaceous layer density.

3.4.2 Ground beetle species richness

Regarding ground beetle species richness, maximal circumference is the only variable having a significant effect according to ANOVA test ($p = 0.0309$). The **Figure 20** shows that tree stands with higher maximal tree circumference have lower number of ground beetle species. This result is consistent with observations made from final CCA (**Figure 17**)

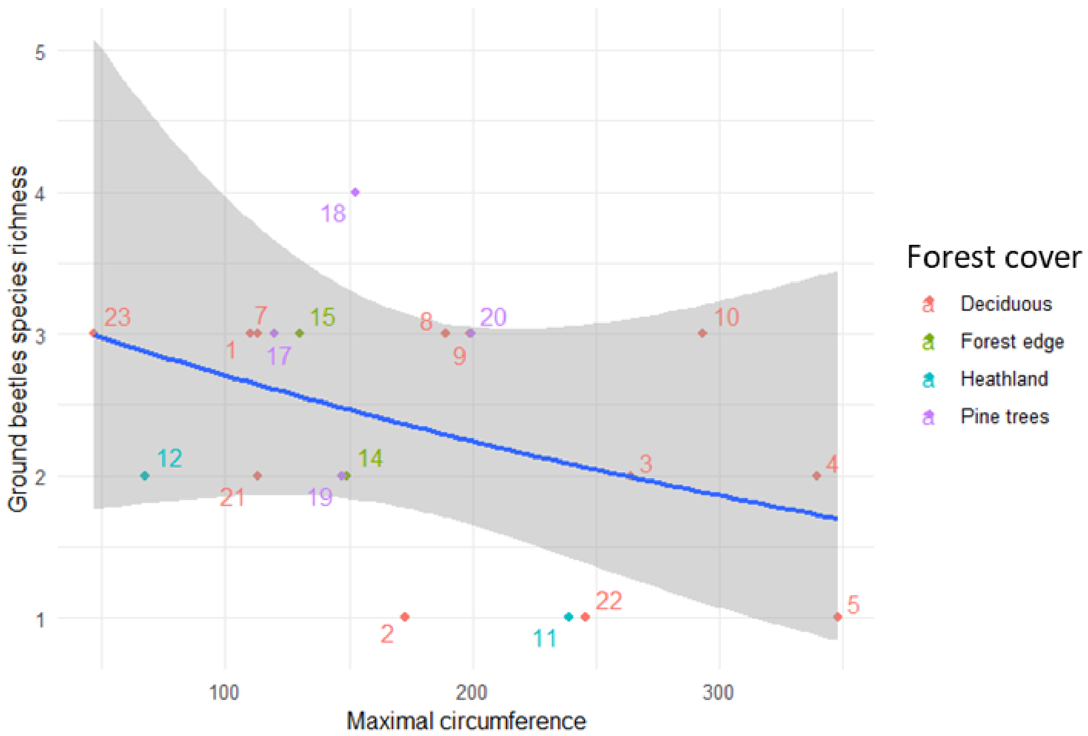

Figure 20: Poisson generalized linear model of ground beetle species richness in function of maximal tree circumference.

3.4.3 Ground beetles mean individual biomass

According to ANOVA test, ground beetle mean individual biomass is significantly impacted by the number of tree species ($p = 0.034$). Tree stands with higher tree diversity present a higher mean individual biomass of ground beetles (**Figure 21**). This is consistent with results observable in the final CCA (**Figure 17**).

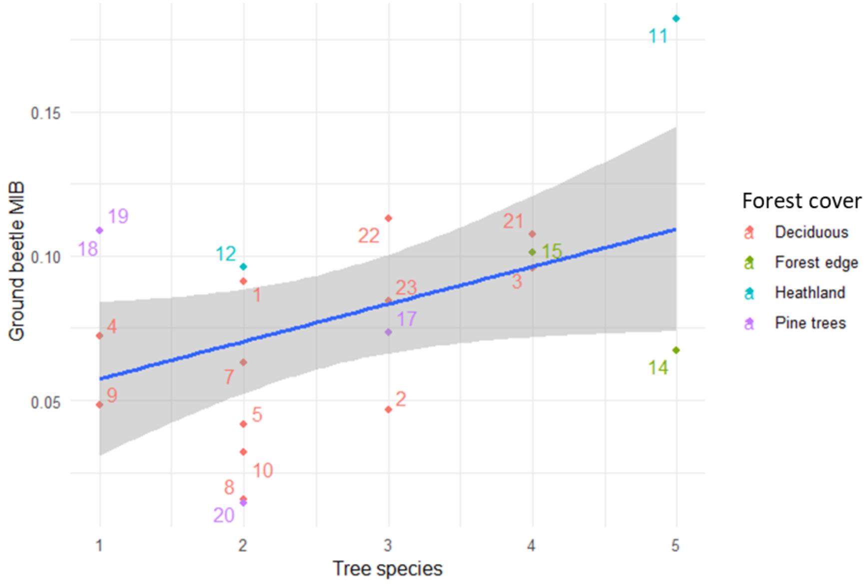

Figure 21: generalized linear model of ground beetle MIB in function of tree species number.

According to ANOVA test, herbaceous layer density has a nearly significant effect on ground beetles MIB ($p = 0.089$). In the **Figure 22**, it seems there is a positive effect of herbaceous layer density on MIB. However, this result is not evident in **Figure 17**, herbaceous layer density is poorly represented compared to MIB and it appears to be more anti correlated than correlated.

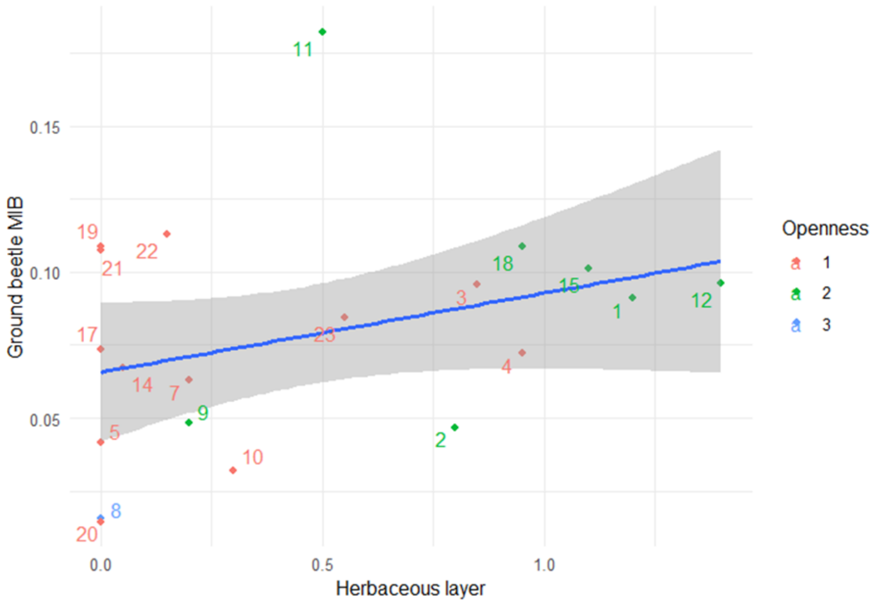

Figure 22: generalized linear model of ground beetle MIB in function of herbaceous layer density.

3.5 Hypotheses tests

3.5.1 Hypothesis 1: species richness

According to the first hypothesis, ground beetle species richness should increase in forest edges due to border effect. Kruskal-Wallis tests do not show any significant differences between median of the different groups of forest plot types whether all species and stations are taken into account ($p = 0.362$) or whether marginal species and extreme stations are removed ($p = 0.254$). However, it seems that forest edges can have a higher species richness than other forest plot types since only one station showed a diversity of 13 species it can also be due to particularly high humidity level recorded in that station.

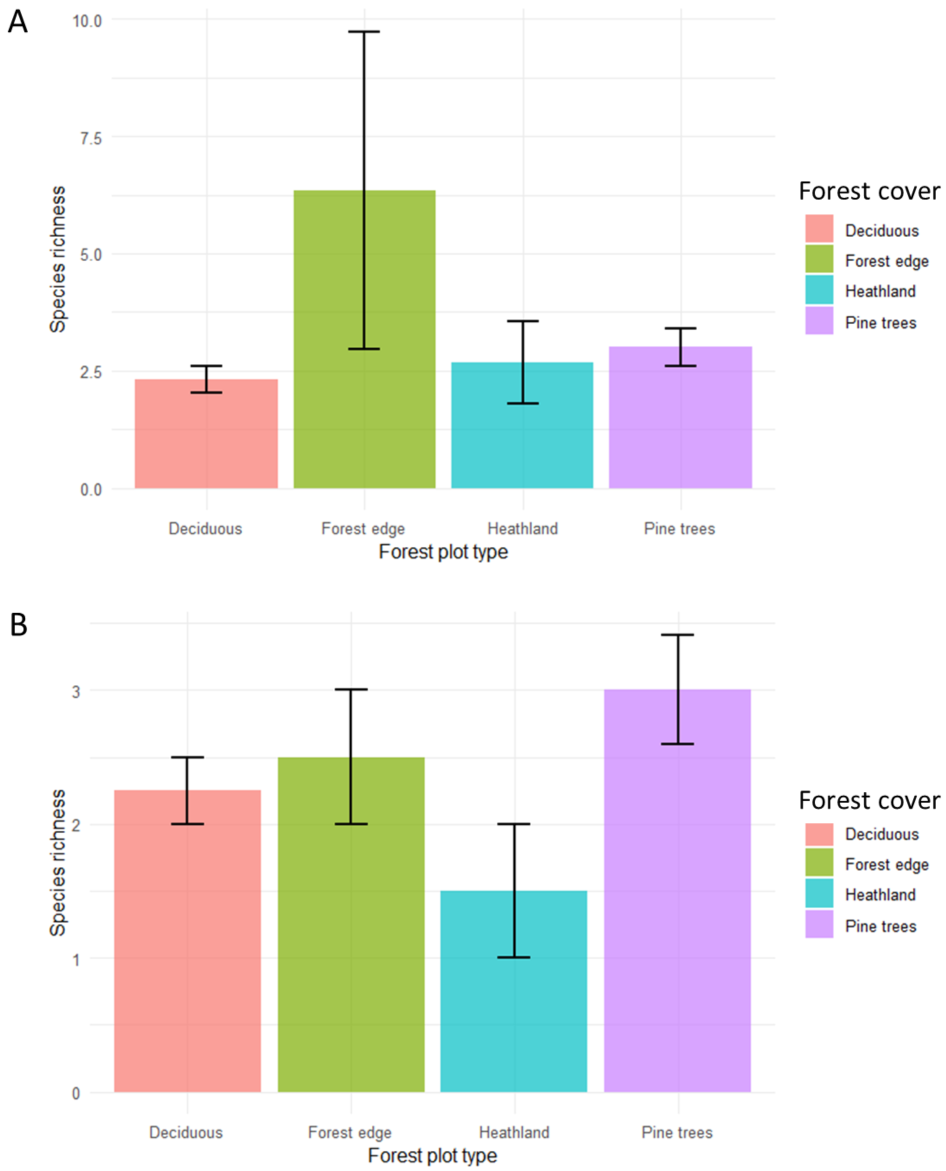

Figure 23: bar plot of the mean species richness (± SE) in the different forest cover with all species and stations (A) and without marginal species and extreme stations (B).

3.5.2 Hypothesis 2: abundance

According to the second hypothesis, the abundance of open habitat specialists and habitat generalists are expected to increase in more open areas since they should be more accessible for those flying beetles. No significant difference (p-values > 0.05) was observed between groups of habitats (type of area or habitat preference) but well between abundance of ground beetles according to their habitat preference (p-values < 0.05) inside the different groups (**Figure 24**). Indeed, it seems that generalists are more abundant than forest specialist in closed areas and deciduous, forest edges and heathlands. Open habitat specialists are more abundant than forest specialists in open areas. Generalists ground beetles seems to be similarly abundant along the habitat openness gradient described by the types of areas while they seem more abundant in forest edges.

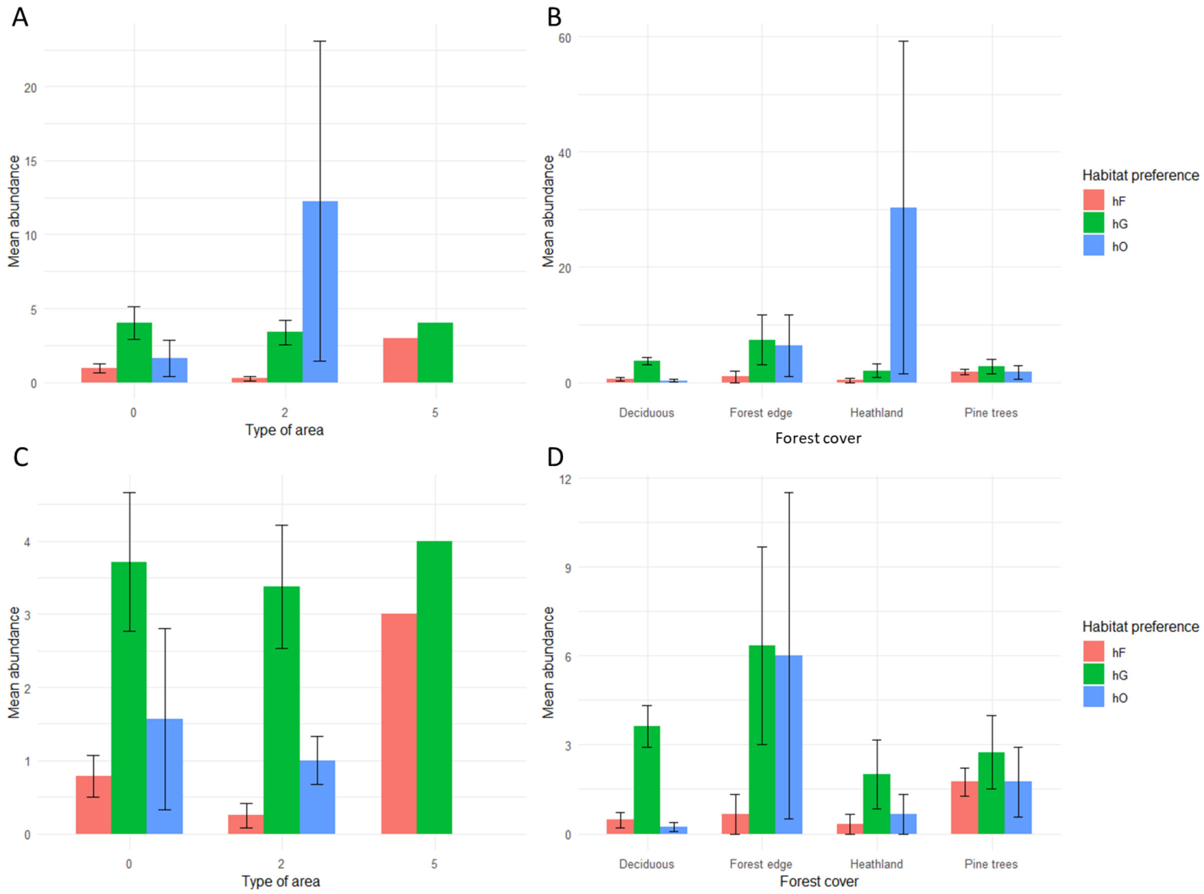

Figure 24: Mean abundances (± SE) of ground beetles according to their habitat preference inside the different types of areas and forest covers with marginal species (A and B) and without (C and D). Habitat preference: hF – forest specialists ; hG – habitat generalists ; hO – open habitat specialists. Type of area according to IPB: 0 – closed forest area (<1%) ; 2 – open area (>5%) ; 5 – slightly open wooded area (1-5%).

The **Figure 25** shows that after removing extreme stations and *C. campestris* there are still significant differences between abundance according to habitat preference (p-value < 0.05).

Forest specialists seem more abundant in closed areas than open habitat specialists which are more abundant in open areas.

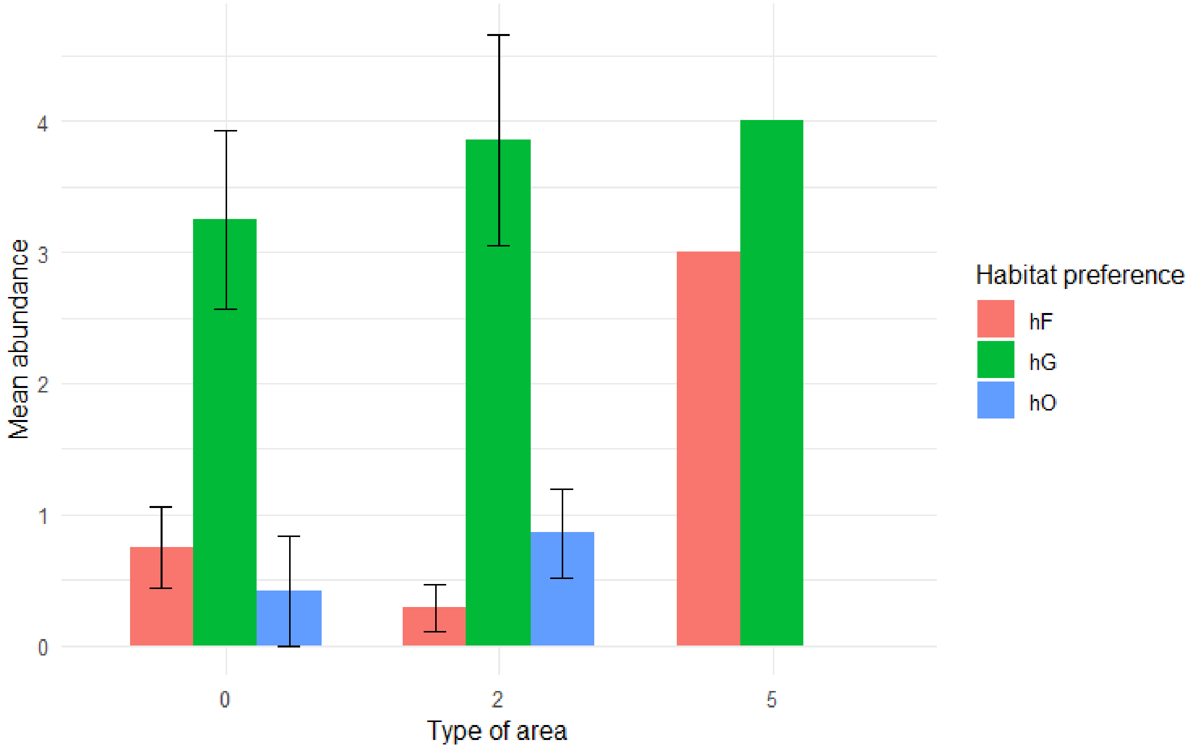

Figure 25: Mean abundances (± SE) of ground beetles according to their habitat preference inside the different types of areas without marginal species and *C. campestris* after removing extreme stations (6,13,16). Habitat preference: hF – forest specialists ; hG – habitat generalists ; hO – open habitat specialists. Type of area according to IPB: 0 – closed forest area (<1%) ; 2 – open area (>5%) ; 5 – slightly open wooded area (1-5%).

Flying beetles are also expected to be more abundant in open areas and forest edges since those habitats are more accessible for those beetles. **Figure 26**, shows no difference of abundance between habitats (p-values > 0.05) but well between flight ability groups in the different station groups (p- value < 0.05). Indeed, abundance of flying beetles seems to be higher than dimorphic in open areas but it is lower than apterous in forest edges. No evident difference can be observed in pine trees and deciduous plots. However, since most of macropterous ground beetles are represented by *C. campestris* (n=88) that are nearly exclusively found in station 13, the results are completely different when removing station 13 from the analyse. The samplings are now dominated by apterous species and the highest abundance of macropterous beetles are found in pine trees plots which is probably due to the presence of *N. rufipes* and *N. substriatus*.

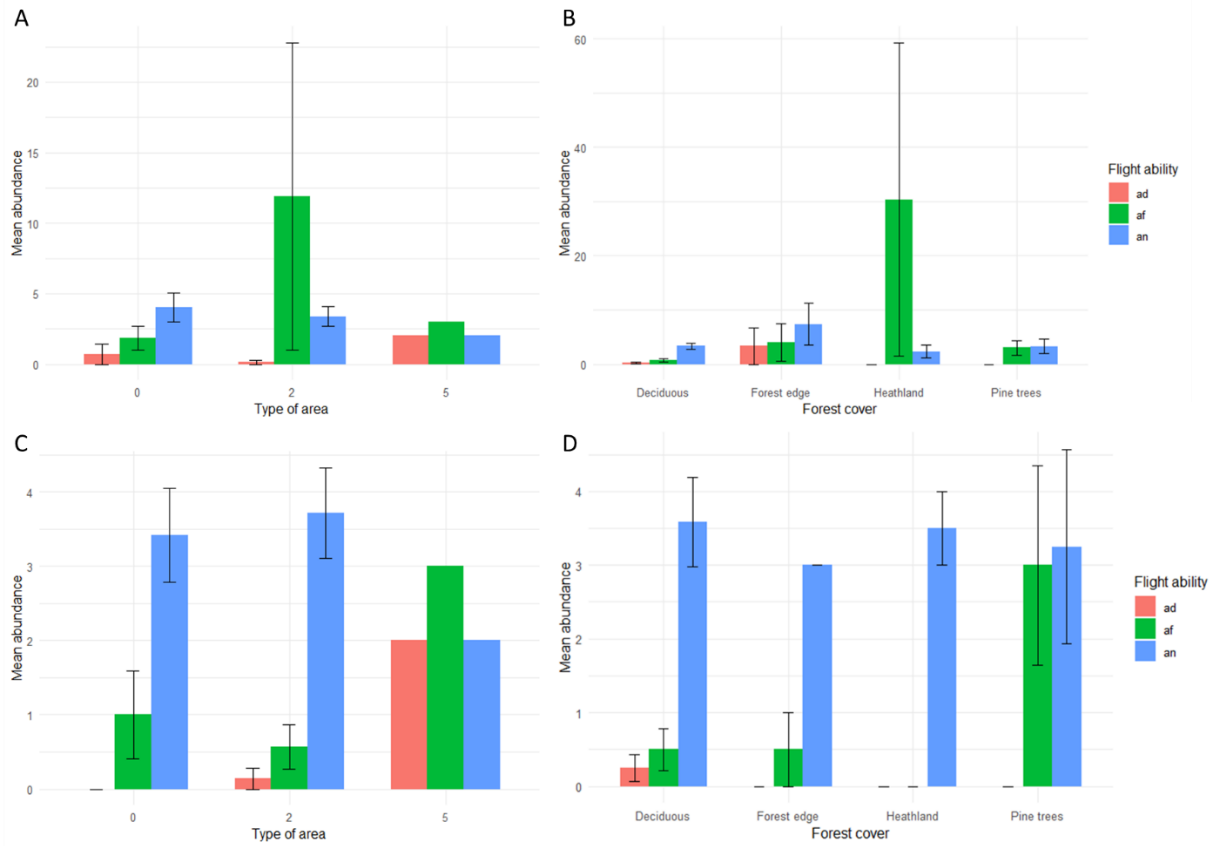

Figure 26: Mean abundances (± SE) of ground beetles according to their flight ability inside the different types of areas with all species and stations (A and B) or without marginal species, *C. campestris* and extreme stations (C and D). Flight ability: ad – dimorphic ; af – able to fly (macropterous) ; an – not able to fly (apterous). Type of area according to IPB: 0 – closed forest area (<1%) ; 2 – open area (>5%) ; 5 – slightly open wooded area (1-5%).

3.5.3 Hypothesis 3: mean individual biomass

According to the third hypothesis, ground beetles MIB is expected to increase in older tree stands (approximated in this study by maximum tree circumference). Even though no significant effect was found using Kruskal-Wallis test for the entire scatter plot (p = 0.466), a particular trend is observable among the different forest plot types. MIB seems to reach a maximal value in middle aged tree stands (**Figure 27**). Since no ground beetles were found in station 6, it has been removed. On every tree stands (excepted biological area), MIB seems to be lower in tree stands with low maximum circumference (young) and increase until an optimal maximum circumference (middle aged) before decreasing in tree stands presenting even more high maximal circumference (old). This observation can also be made in forest edges. Tree stands in the biological area and heathlands seems to make an exception. In the biological area, no decrease in MIB seems to be observed (after removing marginal species) may be thanks to the conservation purposes but we cannot reject the possibility that there is no optimal maximal tree circumference for ground beetles MIB between 110cm and 240cm of circumference. On the contrary, ground beetles MIB in heathlands seems to increase with maximal tree circumference but this result is strongly affected by the fact that only individuals of the heaviest ground beetle species (*C. problematicus*) were found.

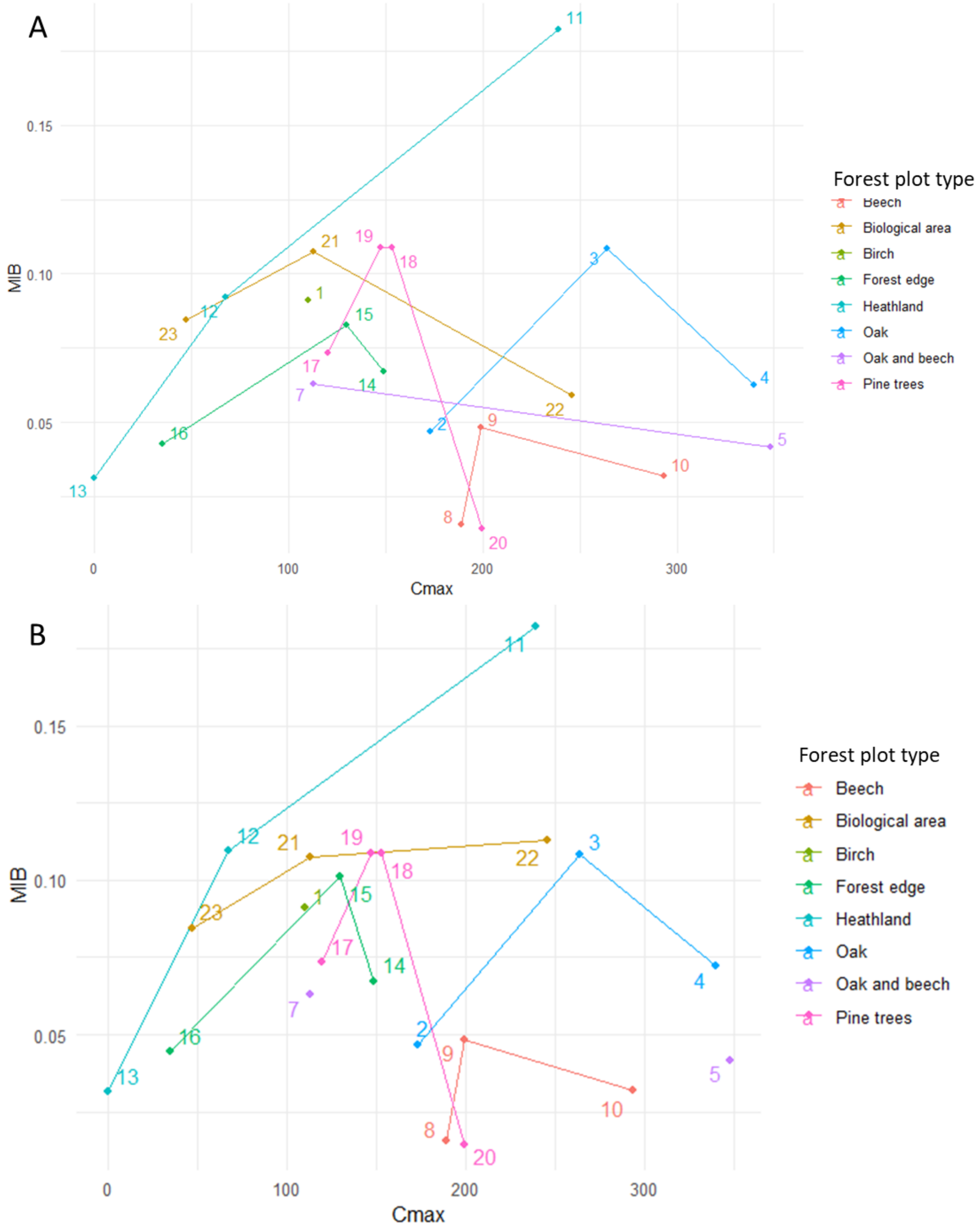

Figure 27: Ground beetle MIB in function of maximum tree circumference (Cmax) observed in each station with marginal species (A) and without (B). Dots are coloured according to forest plot type since we assume that different tree species have different growth speed.

4. Discussion

4.1 Particular stations

The main collected species was the common green ground beetle (*C. campestris*) and was almost only found in heathlands and particularly in the largest. which are in reality the most suitable habitat for them in Lauzelle Forest. The tiger beetles larvae lives in pits from which they ambush their preys (Jeannel, 1941). They thus need a soil in which they can easily dig like in the heathlands. In addition, adults are also xerophilous and prefer open habitats well exposed to sun. Since tiger beetles are mainly breeding in early spring (Luff, 1998), it explains why they were not trapped during the last two catching sessions. In fact, it has long been debated whether tiger beetles belong to the Carabidae family. Recently, it has been identified as a sister group of the Carabidae (Duran and Gough, 2020). As pitfall trapping measure activity-density (Luff, 1975), the very high abundance of *C. campestris* is representative of its large population or high activity. Adults tiger beetles are highly active predators since they are fast runners (Wilson, 1978).

The forest edge located at the bottom of a dale shows the second highest abundance and the highest species richness. It is consistent with the study of Sroka and Finch (2006) that showed a significant impact of moisture and distance from forest edges on carabid beetles species richness. Indeed, forest edges were expected to show higher species richness due to border effect (Molnár *et al*, 2001; Brigić *et al*, 2014; Caitano *et al*, 2020). The three dominant ground beetle species in this station (*P. melanarius*, *P.macer*, *A. parallelepipedus*) are known to be hygrophilous (Judas *et al*, 2002; Luff, 1998).

The birch plot presented a high density of ants but also the highest abundance of *A. parallelepipedus*. Hawes *et al* (2002) observed that ground beetle abundance are expected to decreases in the presence of wood ants. However, their results also seemed to present *A. parallelepipedus* as the least impacted species in high abundance of ants. Not a single ground beetle was found in one of the 23 stations while dung beetles were very abundant. The studied environmental variables were not sufficient to identify the possible reasons.

4.2 Ground beetle community distribution

FCA and CCA presented in this study showed the distribution of ground beetle species according to their total abundance or biomass in the different station. Although station clustering using Jaccard distance has shown high dissimilarities between stations (probably because of the low catching effort, 3 communities of ground beetles can be identified. Habitat openness and moisture appeared to be the two main factors influencing ground beetle community distribution even though no significant results were observed. Community differences between heathlands and wooded areas was increasing along the openness gradient. From *C. campestris* dominated heathland, communities tend to be dominated by *C. problematicus* in pine trees plots and by *P. madidus* in deciduous tree stands. Communities differences along openness gradient were also observed by Ings and Hartley (1999) and Zimmermann *et al* (2023). Even after removing tiger beetles from the FCA, openness gradient was still representative of the distribution. The humidity gradient seemed to be the main factor influencing ground beetle distribution in wooded areas of Lauzelle Forest. Dryer stations presented communities dominated by *C. problematicus* or *C. campestris* (xerophilous species) while the wetter stations were dominated by *A. parallelepipedus* or *P. melanarius* (hygrophilous species). This was also one of the conclusions in the previous study in Lauzelle Forest conducted by Nedergedaelt (1981). She identified two main communities: valley bottom and higher slopes communities. Ground beetles communities distribution following humidity gradient is relatively well supported in scientific literature (Baguette, 1993; Ings and Hartley, 1999; Bonn and Schröder, 2001; Sroka and Finch, 2006). Almost every ground beetle species distribution corresponded with current scientific knowledge **Appendix D.1**.

In addition to moisture and openness gradient impacting community distribution, 3 environmental factors showed significant impact on carabid beetles biodiversity measurements (abundance, species richness and MIB). Quantity of small dead wood on the ground was negatively correlated with ground beetle abundance. Species richness is negatively impacted by maximum tree circumference used as tree stands age indicator but it is in contradiction with the results of Jelaska *et al* (2011). Concerning dead wood, scientific literature reports only the impact of larger dead wood on ground beetles (Sroka and Finch, 2006; Jelaska *et al*, 2011; Kacprzyk *et al*, 2021; Klepzig *et al*, 2012). Large dead wood increase shelter number but also reduce mobility of forest specialist (Sroka and Finch, 2006) thus decreasing the trapping probability (Luff, 1975; Crist and Wiens, 1995). Since small dead wood quantity was measured at a very local scale around the traps ($50m^2$). The observed decrease in abundance may be due to a reduction of trapping probably because of a higher density of obstacles. In addition, a nearly significant positive correlation between abundance and herbaceous layer was also observed. And could indicate higher abundance in open areas but such conclusion would be against those of Ings and Hartley (1999). Open habitat specialist ground beetles were more abundant in open areas or forest edges as expected (Gaublomme *et al*, 2008; Cvetkovska-Gjorgjievska *et al*, 2017). Regarding, forest specialists, they were less abundant than open habitat and generalists in every forest cover type. This suggests that current management methods used in the sampled plots are not suitable with forest specialists (Spence *et al*, 1996). On the contrary, apterous species were similarly the most abundant ground beetle type in each forest cover (heathlands, forests edges, deciduous or pine trees plots) after removing tiger beetles.

4.3 Mean individual biomass as woodland ecological state indicator

This study has shown that MIB was significantly and positively correlated with increase in tree species number and nearly significantly with herbaceous layer density. These results were rather surprizing since MIB was expected to increase in relation with forest age and canopy closing (Skłodowski, 2006; Schwerk and Szyszko, 2007; Jelaska *et al*, 2011). However, another result of this study showed a tendency in the different forest tree stands even though no tests were performed to verify significant differences. In tree stands used for wood production, MIB increased until an optimum maximum circumference before drastically decreasing. This tendency was not observed in the biological area. MIB in the biological area seems to be slightly increasing with maximum tree circumference. It suggests that conservation actions are efficient for assemblages of large ground beetles in forests. Several studies have shown the impact of forest management on ground beetles (Ings and Hartley, 1999; Schwerk and Szyszko, 2007). Ground beetles MIB increase with ecological succession in forest habitats since larger species inhabits older forests areas. Nevertheless, all these results on mean individual biomass should be taken with caution since MIB was measured with less than 50 individuals in total per station (Schwerk and Szyszko, 2007).

4.4 Critical look and necessary improvements for further works

Accumulation curves have shown that collected ground beetles are probably not representative of the whole carabid community of Lauzelle Forest. In order to improve this, pitfall traps number in each station can be increased and the distance between them too in order to optimize trapping system (Luff, 1975). Increasing the number of trapping session by doubling the number or adding at least one catching session in late spring. A more balanced catching effort between forest plot types could also be made by adding samplings in pine trees and birch plots. The killing solution repellence has not been tested and might have possibly affected comparisons with results obtained by Nedergedaelt since some species could be more or less repelled by the detergent. Although all these improvements could help to identify more rare species and catch more individuals (necessary for MIB estimations), this could threaten their population in the wood.

Environmental variables measurements like maximum circumference, tree species number, dead wood amounts and herbaceous layer could have been made at a larger scale to be more representative of the whole plot. Others variables like drainage could have been more precisely measured. Station pH and leaf litter depth were not measured but several studies report their effect on ground beetle abundance and biodiversity (Koivula *et al*, 1999; Poole *et al*, 2003; Vician *et al*, 2018). IPB scores for dead wood and habitat openness are usually measured at the tree stands scale and thus the application of this scoring method for smaller area is may be not representative. Concerning MIB use as a bioindication for ecological succession, samplings in the grasslands around the forest, in clear cut areas or in other forests near the Lauzelle Forest could allow a more precise comparison of biomass changes across the wood.

4.5 Forest management propositions for the future

In the light of this work and scientific literature, three management objectives are recommended. Firstly, the conservation of areas presenting a high level of moisture in Lauzelle Forest should help to prevent endangered carabid beetles extinction since threatened ones are mainly forest specialist and hygrophilous (Bonn and Schröder, 2001). Secondly, the protection of current forest edges and the development of more inner forest borders should increase ground beetle diversity in those areas and mitigating entry of open areas specialists or habitat generalists in forests. Lastly, forest management should preserve connection between habitats patches, especially for habitat specialist or apterous carabid beetles that have low dispersal abilities (de Vries *et al*, 1996; Ings and Hartley, 1999).

5. Conclusions

In conclusion, this study has shown that three communities of ground beetles occupy Lauzelle Forest despite the small sample. This result adds a third community to those identified by Nedergedaelt in 1981. Those communities are mainly determined by habitat openness (heathlands compared to wooded areas) and humidity gradient (valley bottoms compared to sandy plateaus and upper slopes) and thus strengthening scientific consensus on the main role these two factors impact ground beetle assemblages. Nevertheless, ground beetle abundance, species richness and MIB seems to be influenced by different factors. This inventory identified 18 new species and bring the total diversity of ground beetles in the wood to 37. This study has thus made new data available for the monitoring of ecological succession and ground beetle assemblages after clear-cuts inside the Lauzelle forest.

6. References

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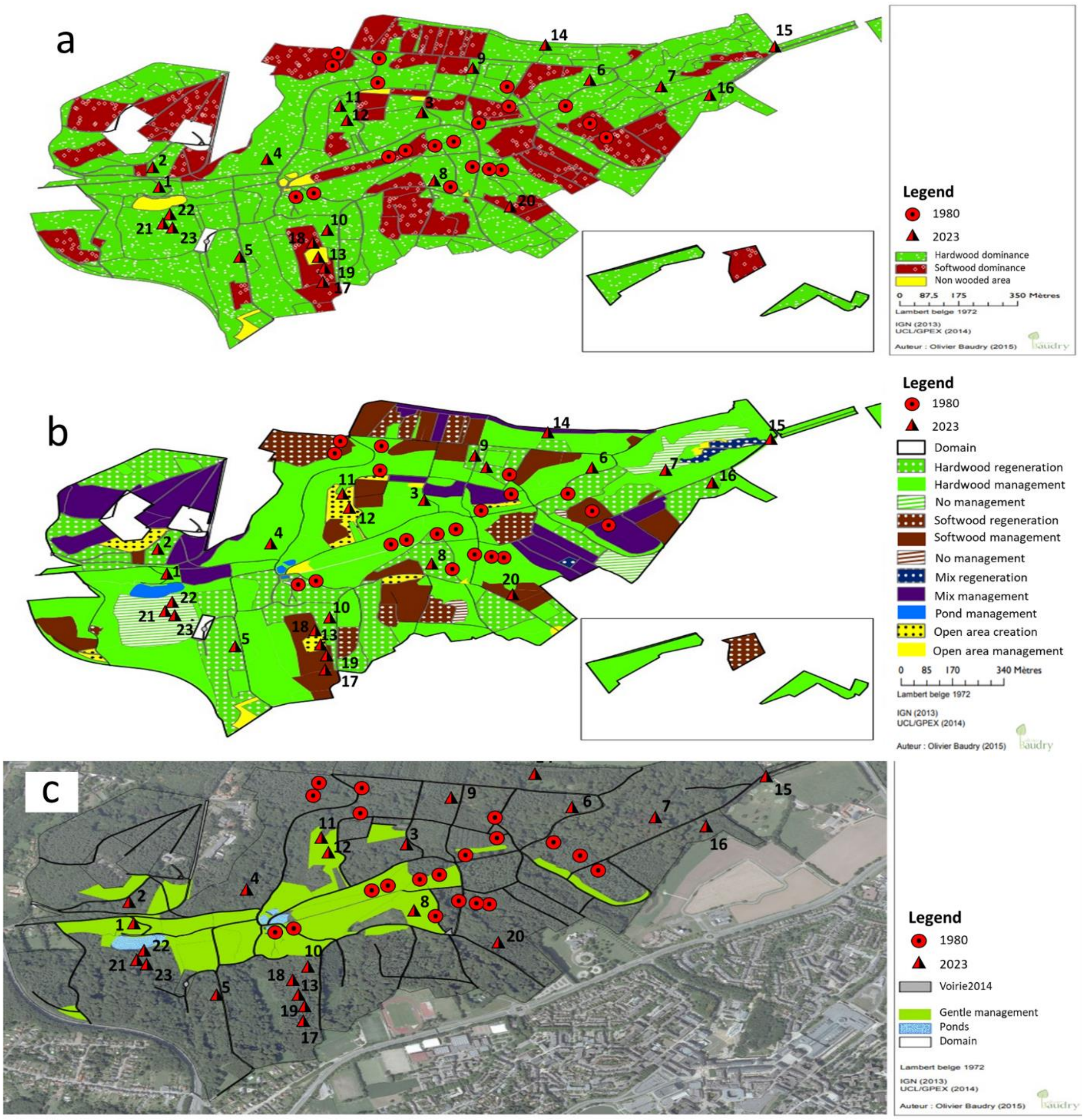
7. Appendices

A. Maps

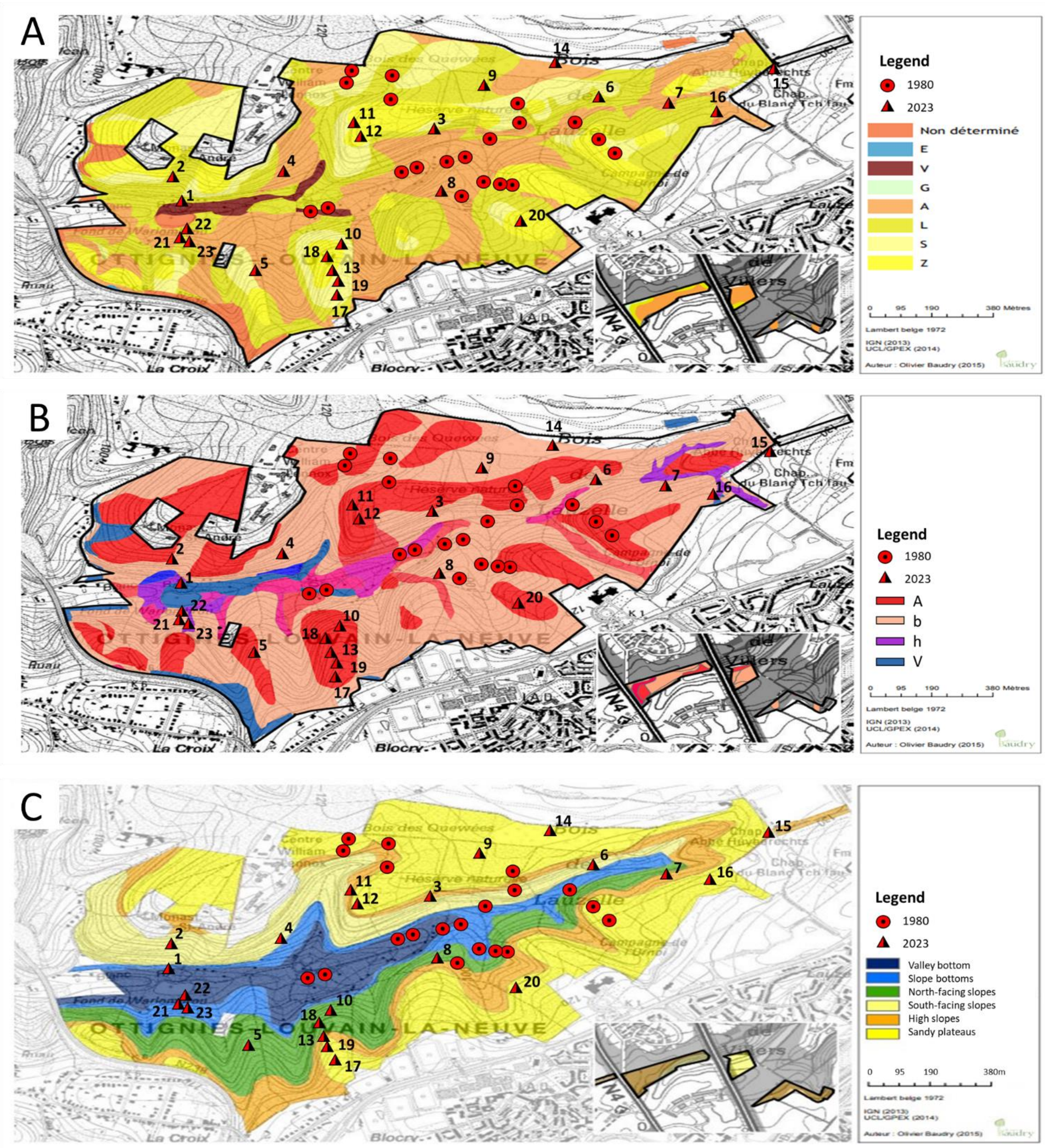
Management of the Lauzelle Forest

Maps of the Lauzelle Forest used to select the 23 sampling stations. The stations of ground beetles sampling of 1980 (Nedergedaelt, 1981) and 2023 (numbered from 1 to 23) were added to the maps of Olivier Baudry (2015) describing the wood domain given by the forest ranger Thibaut Thyrion.



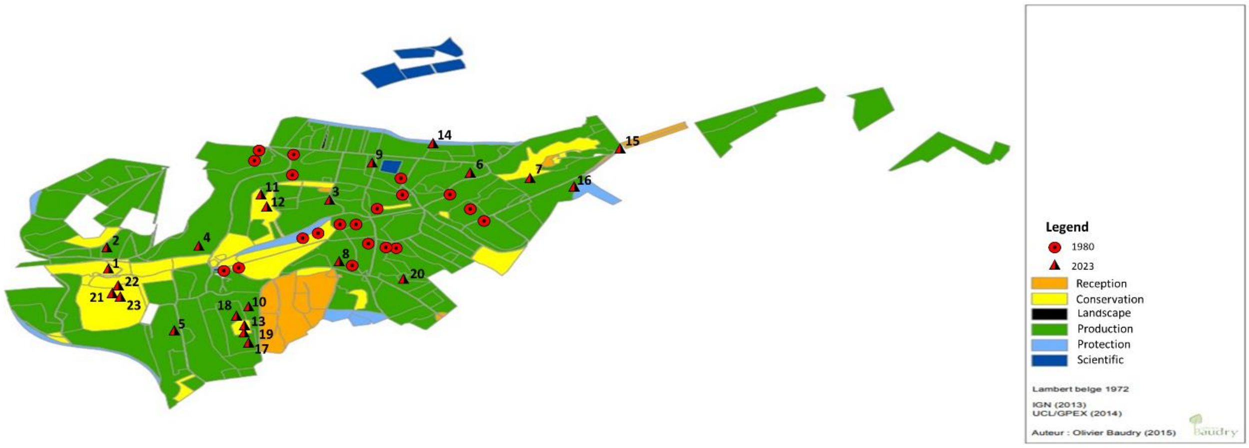
A.1: Tree stands types and non-wooded areas (**a**) and the management methods used in wooded areas (deciduous or coniferous) and open areas of the Lauzelle Forest (**b** and **c**).

Geomorphology of the Lauzelle Forest



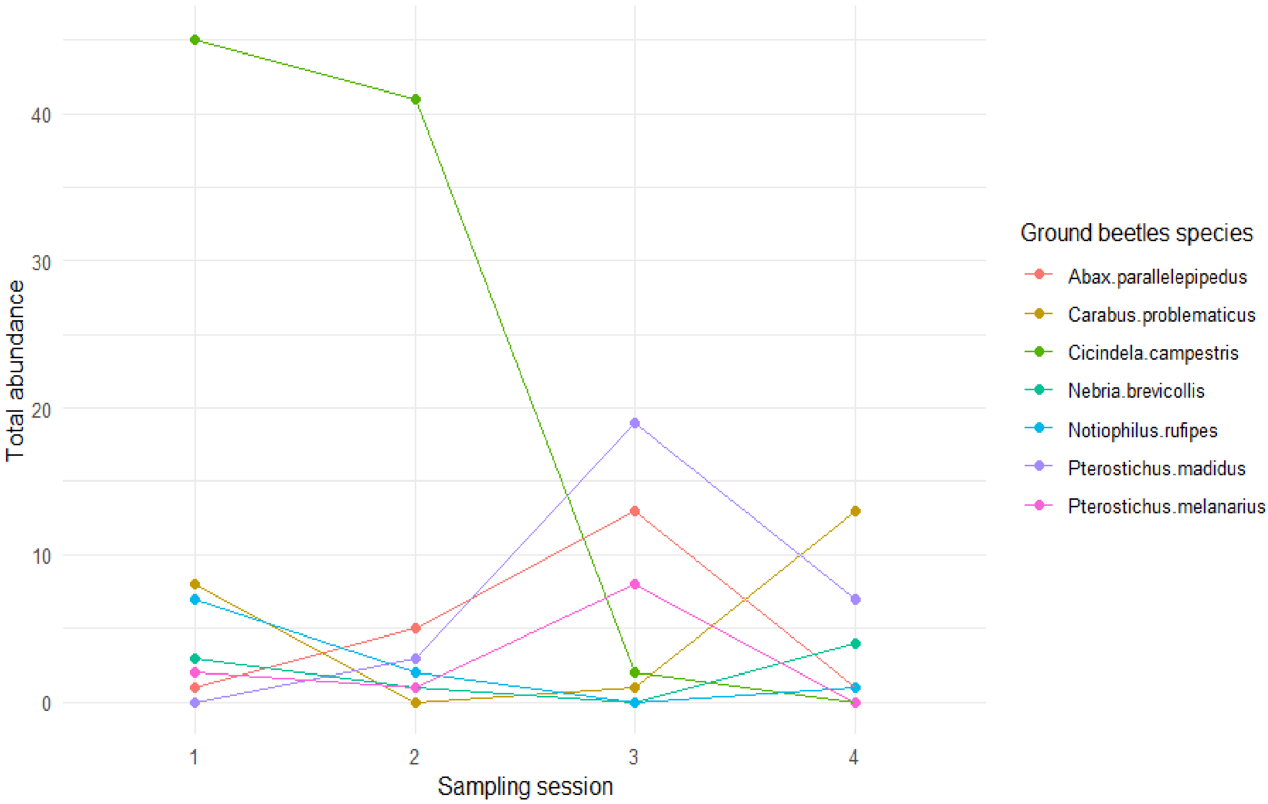
A.2: Soil texture (A), drainage categories (B) and topology (C) in the Lauzelle Forest.

Tree plots use and objectives in the Lauzelle Forest



A.4: Tree plots use and objectives at large scale in the Lauzelle Forest.

B. Additional descriptive figures

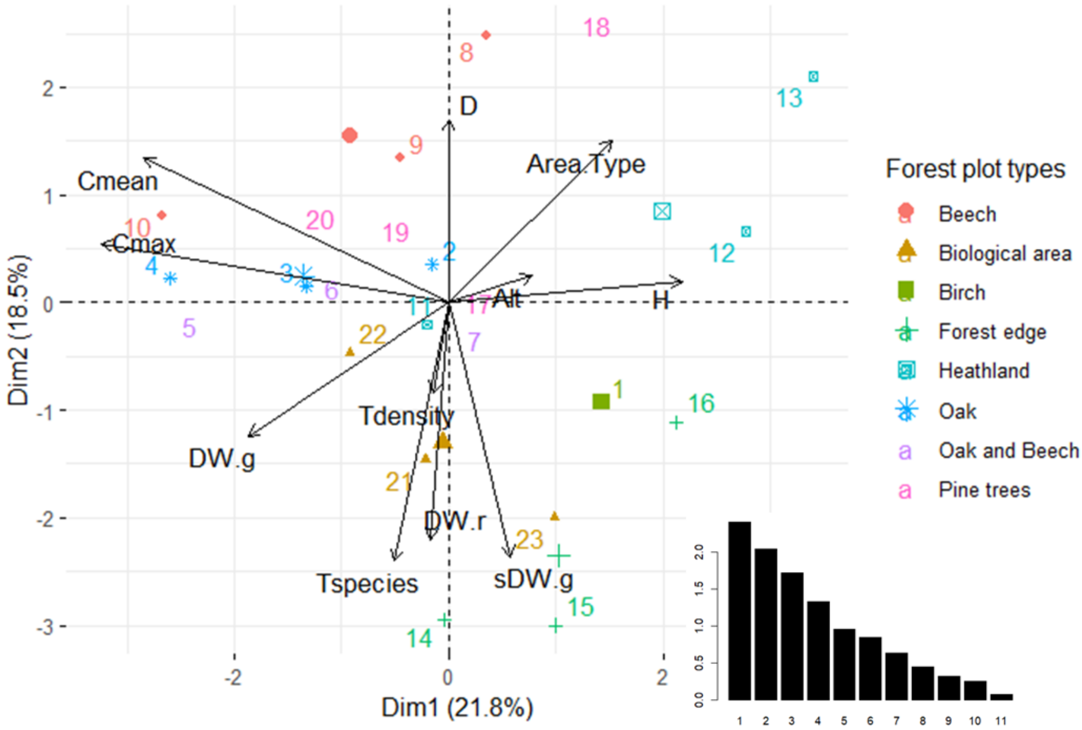


B.1: Total abundance of the seven most trapped species during the sampling sessions

C. Additional multivariate analyses

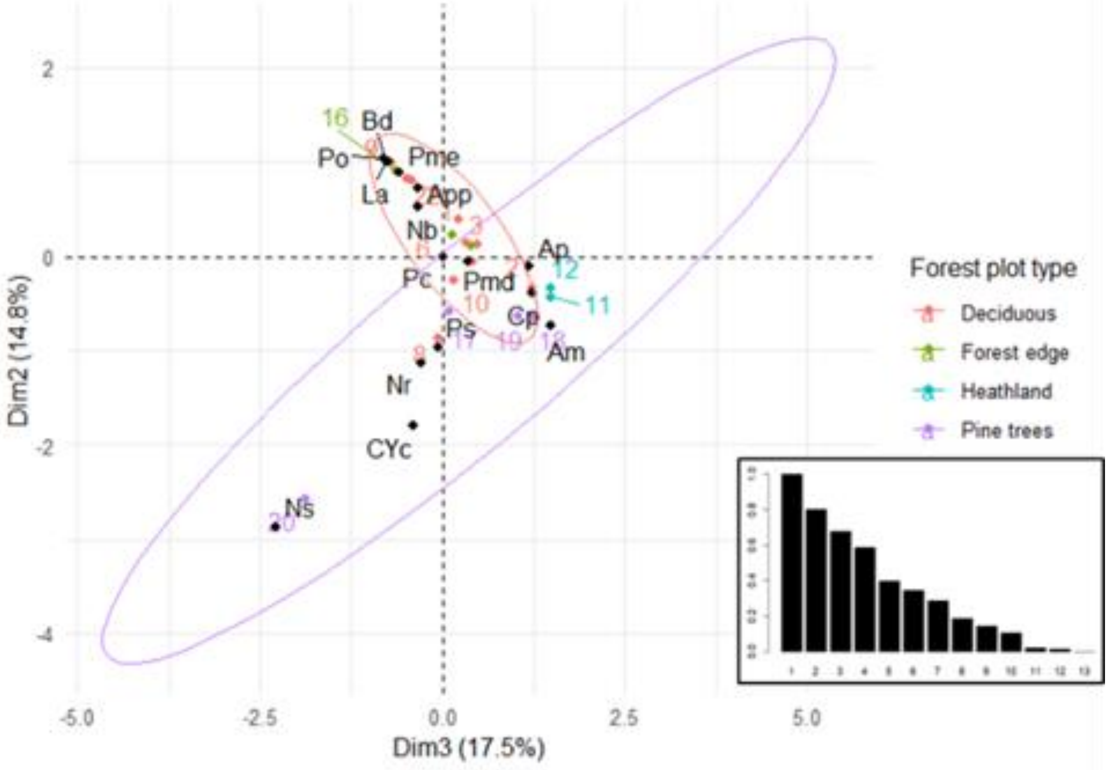
Principal component analysis (PCA)

The principal component analysis (PCA) performed with all studied characteristics. The observed variability is explained at 40.3% by the two first dimensions. The horizontal axis (Dim1 = 21.8%) seems to be defined by a gradient from closed forest to open areas (from left to right) that can be described by larger trees and more covered herbaceous layer. The vertical axis (Dim2 = 18.5%) seems characterized by drainage intensity or dead wood quantity.

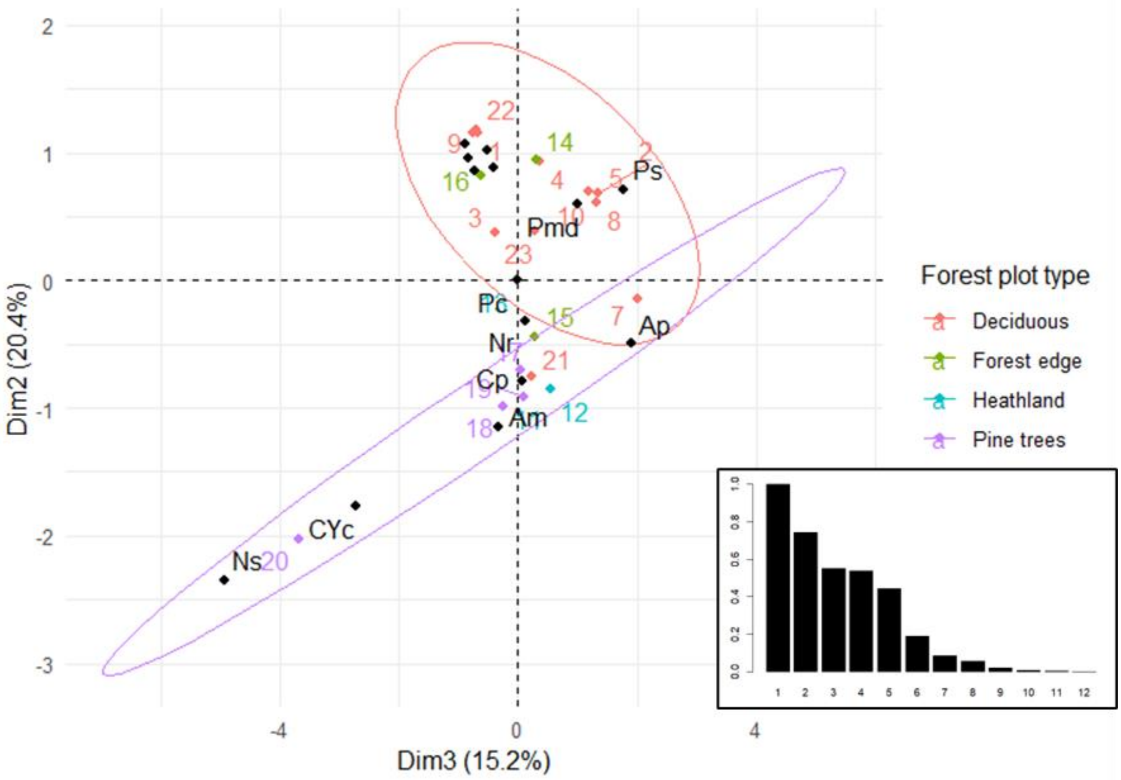


C.1: Principal Component Analysis (PCA) of the 23 sampling stations grouped by forest plot types. Each forest plot type was attributed a colour and a big symbol to indicate their mean position in the 1-2 dimensions. Area.Type – Openness attractivity according to IPB ; H – density of the herbaceous layer ; sDW.g – small dead wood quantity on the ground ; DW.r – rooted dead wood quantity ; DW.g – large dead wood quantity on the ground ; Tspecies – number of tree species ; Tdesnity – tree density ; Cmax – maximum tree circumference ; Cmean – mean tree circumference ; D – drainage ; Alt – altitude in meters. Arrow length indicates the representation quality of the different environmental characteristics.

Factorial Correspondence Analyses (AFC)

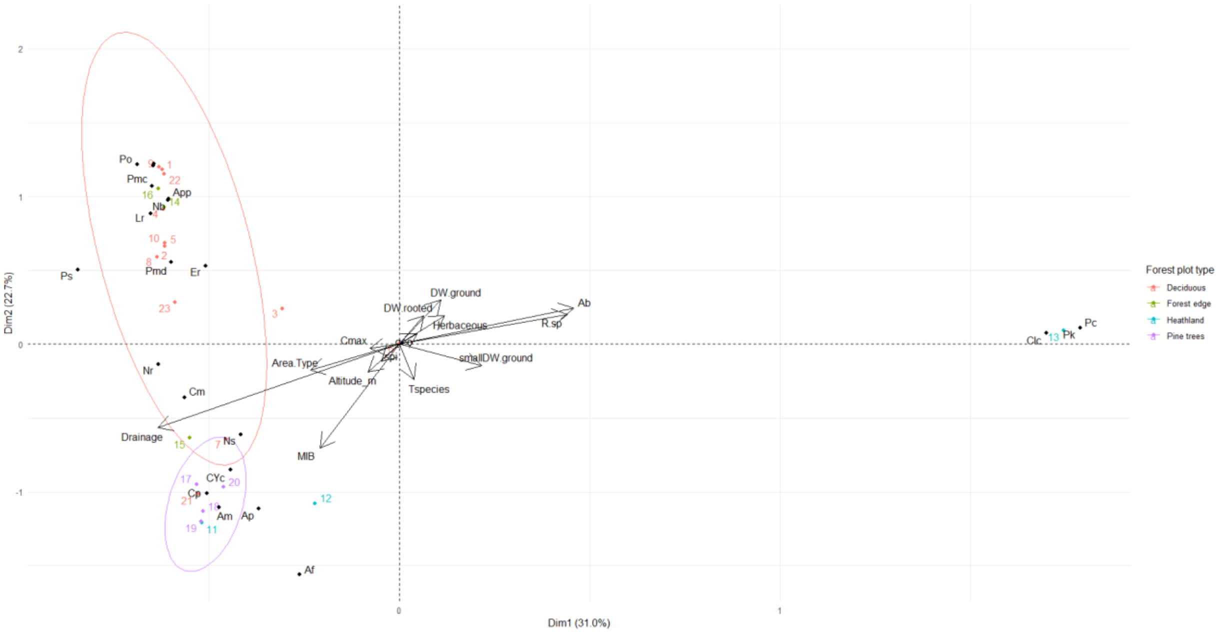


C.2: AFC of stations distribution according to abundance of the different ground beetle species (without marginal species).

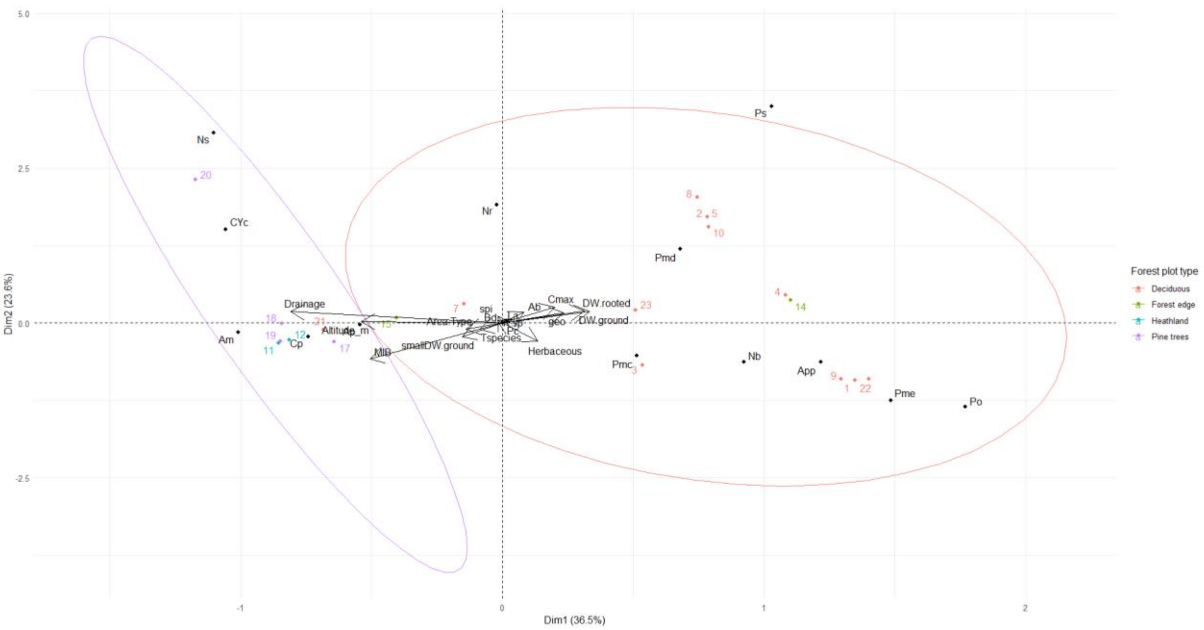


C.3: AFC of stations distribution according to biomass of the different ground beetle species (without marginal species)

Canonical-Correlation Analyses (CCA)



C.4: ACC of stations and ground beetles with all the species and all the stations but adding the abundance of dung beetles (geo) and the abundance of spiders (spi). The two variables are very poorly represented in the 1-2 plane but they seem to be anti-correlated. spi is strongly correlated with the MIB variable and drainage, whereas geo seems to be correlated with the density of the herbaceous layer and the presence of dead wood. This is not particularly surprising, as areas with a denser herbaceous stratum can attract large mammals, and dead wood is found in greater amounts in the most conserved sites.



C.5: After removing stations 6, 13 and 16 and marginal species. Spiders and geotrupes abundance are still poorly represented in 1-2 plane and spider abundance seems independent from environnemental variables.

D. Ground beetle life history traits

D.1: Number of individuals (N) from each ground beetles species caught and their life history traits according to scientific literature (Jeannel, 1941; Wilson, 1978; Hering and Plachter, 1997; Luff, 1998; Assmann, 1999; Judas *et al*, 2002; Brandmayr *et al*, 2009; Fuller *et al*, 2011; Brigić *et al*, 2014; Kosewska and Nietupski, 2015; Belova and Makarova, 2017; Kirichenko-Babko *et al*, 2020; Ludwiczak *et al*, 2020; Vladic and Jelaska, 2020). Habitat preference (F – forest specialist, G – generalist, O – open habitat specialist) ; Humidity preference (H – hygrophilous, M – mesophilous, X – xerophilous) ; body size categories (L – large >12 mm, M – medium 8-12 mm, S – small <8 mm) ; feeding behaviour (G – generalist predators , P – phytophageous, S - specialist predators) ; flight ability (d – dimorphic species, f – macropterous, able to fly , n – brachypterous or apterous, not able to fly). Abbreviation: % - share in the sampled assemblage.

Abr.	**Species**	**N (%)**	**Habitat preference**	**Humidity preference**	**Body size categories**	**Feeding behaviour**	**Flight ability**
App	*Abax parallelepipedus*	20 (8.84)	G	H	L	G	n
Ap	*Abax parallelus*	2 (0.88)	F	H	L	G	n
Am	*Amara montivaga*	2 (0.88)	O	X	S	G	f
Bd	*Bembidium deletum*	2 (0.88)	F	H	S	G	f
Cp	*Carabus problematicus*	22 (9.73)	G	X	L	G	n
CIc	*Cicindela campestris*	88 (38.9)	O	X	L	G	f
CYc	*Cychrus caraboides*	2 (0.88)	F	H	L	S	n
La	*Limodromus assimilis*	2 (0.88)	G	H	L	G	f
Nb	*Nebria brevicollis*	8 (3.53)	G	M	M	G	n
Nr	*Notiophilus rufipes*	10 (4.42)	F	X	S	S	f
Ns	*Notiophilus substriatus*	5 (2.21)	O	X	S	S	f
Pc	*Poecilus cupreus*	2 (0.88)	O	X	M		f
Pmc	*Pterostichus macer*	7 (3.09)	O	H	L		f
Pmd	*Pterostichus madidus*	29 (12.8)	G	X	L	G	n
Pme	*Pterostichus melanarius*	11 (4.87)	O	H	L	G	d
Po	*Pterostichus ovoideus*	3 (1.33)	O	H	S		n
Ps	*Pterostichus strenuus*	2 (0.88)	G	M	S	G	d
Marginal species							
Af	*Amara familiaris*	1 (0.44)	O	X	S	P	f
Cm	*Calathus melanocephalus*	1 (0.44)	O	X	S	G	n
Er	*Elaphrus riparius*	1 (0.44)	G	M	S		f
Lr	*Leistus rufomarginatus*	1 (0.44)	F	H	M		f
Oo	*Oxypselaphus obscurus*	1 (0.44)	G	H	S		f
Pa	*Paranchus albipes*	1 (0.44)	G	H	M		n
Pk	*Poecilus kugelanni*	1 (0.44)	O	X	L	G	f
Pnr	*Pterostichus niger*	1 (0.44)	F	H	L	G	n
Pna	*Pterostichus nigrita*	1 (0.44)	G	H	M	G	f