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The Collembola fauna of Irish forests – a comparison between forest type and microhabitats within the forests

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Abstract

Forest is the climax vegetation for most of Ireland. Yet, at the beginning of the twentieth century, because of deforestation, only 1.4% of the land area was afforested. Currently government policy encourages afforestation and at present approximately 10% of the land is forested. More than 90% of these forests are plantation forests and most of this new forest consists of exotic trees, such as Sitka spruce (*Picea sitchensis*) introduced from North America. Little is known of the invertebrate fauna of these plantations and it is of interest to know the composition of the fauna and whether it differs from those of native tree species. In the current study we focus on the Collembola fauna occurring in the canopy and soil microhabitats of Irish forests and show that these differ between tree species and microhabitat within the forest. In particular, native oak forests harbour many more Collembola species than the other forest types investigated and non-native forests appear to harbour fewer species than do forests of native species. However, this is a not a simple relationship as first rotation Sitka spruce forests harboured more species than some native forest types. The main differences in species composition are between those species living in bark or in epiphytic cover on the trees with deciduous species having different species to conifers.

Keywords Introduced species | biodiversity | Collembola | canopy | soil

1. Introduction

In Ireland, forests cover approximately 10% of the land area (Forest Service 2007) which represents a major expansion from the cover of only 1% in 1920. This recent afforestation is a direct result of successive government policies designed to promote the planting of forests and since 1980 a number of EU and government incentives have been introduced to encourage private landowners to plant trees. Indeed the 1996 Strategic Plan for the Development of the Forestry Sector in Ireland set an afforestation target of 25,000 hectares per annum (Department of Agriculture, Food and Forestry 1996).

The climatic climax forest species in Ireland would be predominantly oak at lower altitudes and Scots pine at higher altitudes but over 50% of the current forest cover is Sitka spruce, a North American species which is a particularly productive canopy species (Forest Service 2000). In Ireland therefore no native animal species will have co-evolved with these trees and this has lead to a perception that these forests harbour a depauperate fauna and that their invertebrate biodiversity is low. However, little is known of the fauna of these plantations (Bolger 2004) and this is especially true for invertebrate species (Fahy & Gormally 1998) which means that little evidence exists to either support or reject these ideas.

In particular, relatively little is known about the Collembola fauna of Irish woodlands. There have been a number of incidental records (e.g. Halbert 1915, Bagnall 1940, 1941), a single study of Collembola from a beech woodland (Lambert 1972) and a study was carried out on short rotation forestry on peatland (Bolger 1985). However, the only studies which concentrated on the microarthropod fauna in forests examined the fauna of

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both soil and fungal fruiting bodies in these habitats (Heneghan & Bolger 1996a,b, 1998; O'Connell & Bolger 1997a,b). It was therefore decided to examine the Collembola occurring in various microhabitats in a variety of native and non-native forest types in Ireland.

Collembola are abundant and diverse in forest soils. Populations of up to 250 × 10^3 m^{-2} have been recorded from boreal coniferous forests soils and mean annual densities between 40 and 70 × 10^3 m^{-2} have been recorded from temperate deciduous forests (Petersen & Luxton 1982). However, microarthropods are also abundant and diverse is various microhabitats in tree canopies (Walter & Behan-Pelletier 1999, Lindo & Winchester 2006, Arroyo et al. 2010a,b). Diverse Collembola assemblages have been found in epiphytic moss cover (Lambert 1972, Cutz-Pool et al. 2010) and many soil dwelling Collembola are able to migrate from the soil into arboreal habitats (Bowden et al. 1976). They are therefore important components of the forest biodiversity occupying many microhabitats and serving important functional roles in decomposition (Faber & Verhoef 1991, Lavelle et al. 1995). In addition, Collembola have been shown to be affected by the introduction of exotic species. For example, in Portugal, afforestation with eucalyptus as distinct from native species was shown to affect Collembola assemblages (Pinto et al. 1997, Sousa et al. 1997, Barrocas et al. 1998).

In this study we test the hypotheses that Collembola assemblages differ between native and non-native forest types and that the diversity within native woodlands will be higher than within woodlands of non-native species. We also examine whether assemblages vary between microhabitats within the forest and whether there are consistent differences across forest types.

2. Material

2.1. Type specimens investigated

The Collembola fauna of five forest types were examined in this study. Two of these were broadleaved native species, *Quercus petraea* (Matt.) Liebl. and *Fraxinus excelsior* L. (oak and ash); Scots pine (*Pinus sylvestris* L.) which, although generally considered to be a native conifer, most of the current trees are believed to derive from seed originally imported from Scotland (Hickie 2002); and first and second rotation Sitka spruce (*Picea sitchensis* (Bong.) Carrière).

In order to get a geographical spread across Ireland, a single stand of each forest type was selected in four broadly defined regions of the country (North-West, South-West, Midlands and East) (Tab. 1). Sites within a region were sometimes relatively far apart (maximum distance 80 km) because, to a large extent, geographical and environmental factors determine where particular tree species are planted. Sites were selected from the national

Table 1. Name, forest type and location of sites sampled.

Forest Name	Tree Type	County	Latitude	Longitude
Donadea	Ash	Kildare	53°20'N	06°45'W
Killough Hill	Ash	Tipperary	52°36'N	07°50'W
Ross Island	Ash	Kerry	52°03'N	09°32'W
St John's Wood	Ash	Roscommon	53°33'N	08°00'W
Kilmacrea Wood	Oak	Wicklow	52°54'N	06°10'W
Raheen	Oak	Clare	52°53'N	08°31'W
Tomies Wood	Oak	Kerry	52°02'N	09°35'W
Union Wood	Oak	Sligo	54°12'N	08°29'W
Ballygawley	Scots Pine	Sligo	54°12'N	08°27'W
Ballymanus	Scots Pine	Wicklow	52°58'N	06°09'W
Bansha	Scots Pine	Tipperary	52°27'N	08°06'W
Torc	Scots Pine	Kerry	52°00'N	09°31'W
Cloonagh	Sitka Spruce (1st Rotation)	Sligo	54°10'N	08°21'W
Derrybrien	Sitka Spruce (1st Rotation)	Galway	53°08'N	08°35'W
Quitrent Mountain	Sitka Spruce (1st Rotation)	Cork	52°16'N	08°27'W
Moneyteige	Sitka Spruce (1st Rotation)	Wicklow	52°48'N	06°18'W
Ballygawley	Sitka Spruce (2nd Rotation)	Sligo	54°12'N	08°28'W
Ballyguyroe North	Sitka Spruce (2nd Rotation)	Cork	52°15'N	08°29'W
Bohatch	Sitka Spruce (2nd Rotation)	Clare	52°57'N	08°27'W
Stranahely	Sitka Spruce (2nd Rotation)	Wicklow	53°00'N	06°31'W

forest inventory database (Forest Service 2007). Within the database the sites were described as monocultures; however, other vegetation regularly occurred in the stands and this differed significantly between the monocultures (Coote et al. 2012). For the purposes of this study, this was considered to be part of the character of these forests which affects the biodiversity of the fauna. The sites varied in size but all trees sampled were at least 10 m apart within the sites.

2.2. Sampling and extraction of Collembola

Within each site five random trees were selected and nine types of sample collected from each. These were moss from the upper, middle and lower canopy, branches from the upper middle and lower canopy (for examination of the fauna of bark), and moss, the soil organic horizon and of the upper five centimetres of mineral soil from the base of the tree.

Canopy samples were collected from each tree following protocols developed by Finnamore et al. (1998). Climbers collected five sections of a single branch (approximately 40 cm in length) from the top of the living crown, mid-crown and at the bottom of the living canopy in each tree. The epiphytic moss cover was removed and the branches and twigs were bathed in a dilute solution of NaOH for 48 hours. The liquid was then filtered and the animals collected. The five sections of branch from a particular height on a tree were pooled to give a single bark sample. Thus there were three compound samples for each tree.

Samples of the moss occurring in the canopy were collected at each height on each tree using a scraper and pooled for each particular height and tree. The sizes of these samples varied depending on the amounts of moss present on the trees. Finally, one moss sample was collected from the mats on the bark at the base (0–50 cm) of each of the trees sampled. All the fauna inhabiting moss habitats were extracted using a Macfadyen extractor. Samples of the organic and mineral soil horizons were collected using a 5cm diameter corer and the animals extracted from these using the Macfadyen extractor. The Collembola were identified using Hopkin (2007).

2.3. Statistical Analysis

Comparisons of the abundances of all species for which more than fifty individuals were recovered were made using a randomised block design analysis of variance where the regions were blocks and the forest types were treatments within those blocks. The $\log_{10}(n+1)$ transformed total number of individuals of each species found within a site was used as the observation, i.e. the total number of individuals found on each tree and in each microhabitat were summed to give a single observation per site. Similarly, species richness for each forest type was compared using a randomised block design analysis of variance of the total number of species found in each site. These calculations were all carried out using SAS 4.2. Rarefaction and Chao-1 indices were calculated using the calculator at http://www.biology.ualberta.ca/jbrzusto/rarefact.php#ColCod1994. Assemblage structures were compared using Redundancy Analysis in CANOCO for Windows version 4.02 (ter Braak & Šmilauer 1998). In order to avoid overcrowding of biplots the lower axis minimum fit in the inclusion rules of the CanoDraw project settings was set to 2 for species (Lepš & Šmilauer 2003).

3. Results

Forty four taxa were distinguished (Tab. 2). Three of these species *Xenylla grisea, Anurophorus laricis* and *Xenylla maritima* were particularly abundant in the samples and represented almost 80 % of the individuals recovered. Of the species for which more than fifty individuals were recovered, only *Entomobrya albocincta,* which was not found in the Sitka spruce stands, showed significant differences in abundance between the forest types ($F_{4,12} = 3.5$, $p < 0.05$).

Similarly the taxon richness did not vary significantly between the forest types when individual sites were taken as replicates ($F_{4,12} = 0.93$, n.s.). However, the total number of individuals recovered varied very markedly between the forest types with 2026 individuals being recovered from the second rotation Sitka spruce sites, 618 from first rotation Sitka spruce and the others having intermediate values (Tab. 3). Therefore rarefaction and Chao-1 indices were calculated. These suggest that, for some forest types, such as ash and second rotation Sitka spruce, most of the taxa present have been recovered but that for oak and Scots pine only about 75 % of the species present have been found and for first rotation Sitka spruce the proportion may be as little as 50 %. In addition, for oak the associated error is relatively large which suggests that the fauna is under-sampled.

It is obvious from the rarefaction curves and the Chao-1 indices that the fauna in oak forests is clearly richer than those occurring in the forest types and that the pattern of richness is lowest and virtually identical in the two Sitka spruce rotations (Fig. 1). The richness in ash and Scots pine are very similar. The Chao-1 estimator for oak is almost twice that of Sitka spruce (Tab. 3).

Table 2. Collembola taxa recovered with abbreviations used in later diagrams.

Taxon	**Abbreviation**
Anurophorus laricis Nicolet, 1842	**Anu lar**
Deuteraphorura inermis (Tullberg, 1871)	**Deut iner**
Entomobrya albocincta (Templeton, 1835)	**Ent alb**
Entomobrya lanuginosa (Nicolet, 1841)	**Ent lan**
Entomobrya nivalis (Linnaeus, 1758)	**Ent niv**
Folsomia brevicaudia Agrell, 1939	**Fol brev**
Folsomia candida Willem, 1902	**Fol can**
Folsomia inoculata Stach, 1947	**Fol inoc**
Folsomia quadrioculata (Tullberg, 1871)	**Fol quad**
Folsomia spinosa Kseneman, 1936	**Fol spin**
Folsomia sp.	**Fol sp**
Friesea mirabilis (Tullberg, 1871)	**Fri mir**
Friesea truncata Cassagnau, 1958	**Fri trun**
Friesea sp.	**Fri sp**
Isotoma viridis Bourlet, 1839	**Iso vir**
Isotomiella minor (Schäffer, 1896)	**Isoto min**
Kalaphorura burmeisteri (Lubbock, 1873)	**Kal burm**
Lepidocyrtus cyaneus Tullberg, 1871	**Lep cyan**
Lepidocyrtus lanuginosus (Gmelin, 1788)	**Lep lan**
Lepidocyrtus lignorum (Fabricius, 1775)	**Lep lig**
Lepidocyrtus sp.	**Lep sp**
Micranurida sensillata (Gisin, 1953)	**Mic sen**
Neanura muscorum (Templeton, 1835)	**Nean mus**
Paristoma notabilis Schäffer, 1896	**Par not**
Sminthurinus niger (Lubbock, 1867)	**Smin nig**
Sphaeridia pumilis (Krausbauer, 1898)	**Sph pum**
Tetracanthella brachyura Bagnall, 1949	**Tet bra**
Tetracanthella wahlgreni Axelson, 1907	**Tet wah**
Tetracanthella sp.	**Tet spp**
Tomocerus minor (Lubbock, 1862)	**Tom minor**
Uzelia setifera Absolon, 1901	**Uze set**
Vertagopus arboreus (Linnaeus, 1758)	**Ver arb**
Vertagopus cinereus (Nicolet, 1841)	**Ver cin**
Vertagopus sp.	**Ver sp**
Willowsia buski (Lubbock, 1869)	**Wil bus**
Willowsia planti (Nicolet, 1841)	**Wil pla**
Willowsia sp.	**Wil sp**
Xenylla boerneri Axelson, 1905	**Xen boe**
Xenylla grisea Axelson, 1900	**Xen gri**
Xenylla maritima Tullberg, 1869	**Xen mar**
Xenylla welchi Folsom, 1916	**Xen wel**
Xenylla sp.	**Xen sp**

There were significant differences between the assemblage structures in the different forests types (Fig. 2). The first axis separates the broadleaves from the conifer species and there appear to be far more species which show preferences for the broadleaves. For example, *X. grisea* favours both oak and ash while *Tetracanthella brachyura*, *Tetracanthella wahlgreni* and *Folsomia brevicauda* were particularly associated with oak. There are only two species which appear to favour the conifers with *X. maritima* being particularly prominent in the first rotation Sitka spruce forests and *Anurophorus laricis* favouring the second rotation Sitka spruce and the Scots pine.

There were also significant differences between the fauna of the microhabitats sampled (Fig. 3). There were clear distinctions between the assemblages on the bark, those on the moss in the canopy and the soil and moss on soil surface habitats. Only two species, *X. maritima* and *Micronurida sensillata* were found primarily on the bark while much larger diversity were seen in the other habitats. Those found in the moss in the canopy were *X. grisea*, *E. albocincta* , *T. brachyura*, *T. wahlgreni.* and *Willowsia planti* while the largest group of species were found primarily in the soil.

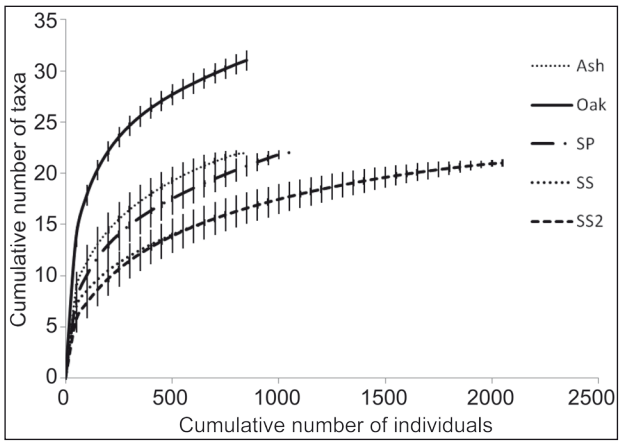


Figure 1. Rarefaction curves for each forest type (± s.d.).
SP – Scots pine; **SS** – Sitka spruce (first rotation); **SS2** – Sitka spruce (second rotation).

Table 3. Numbers of individuals and taxa recovered from each forest type with their associated Chao-1 estimators.

Forest Type	Number of individuals sampled	Total number of taxa recovered	Chao-1 estimator (±s.d)
Ash	818	22	24.5±2.5
Oak	846	31	43.3±9.6
Scots pine	1028	22	30.2±6.5
Sitka spruce rotation 1	618	15	27.5±11.6
Sitka spruce rotation 2	2026	21	22.6±1.8

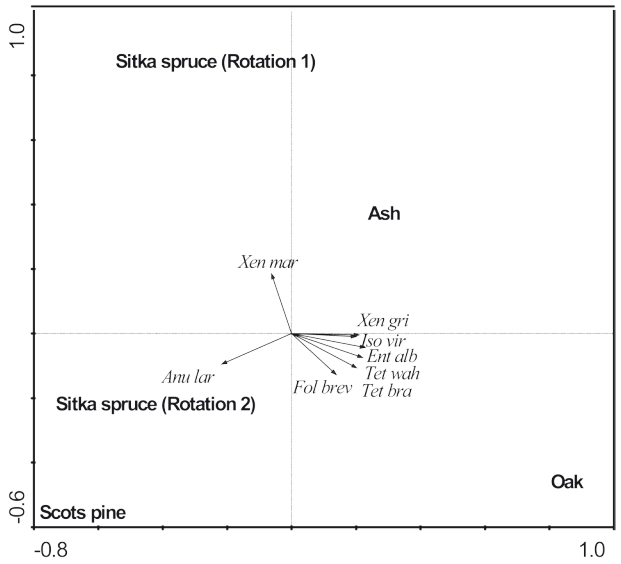


Figure 2. Redundancy analysis of the effects of forest type on Collembola assemblages (log10+1 transformed) with region and microhabitat as blocking factors. Taxon abbreviations provided in Table 2. The first two axes account for 84.6% of the species environment relationships and the first axis and trace are significant (F=4.914, and p=.012; F=2.017, p=.006 respectively).

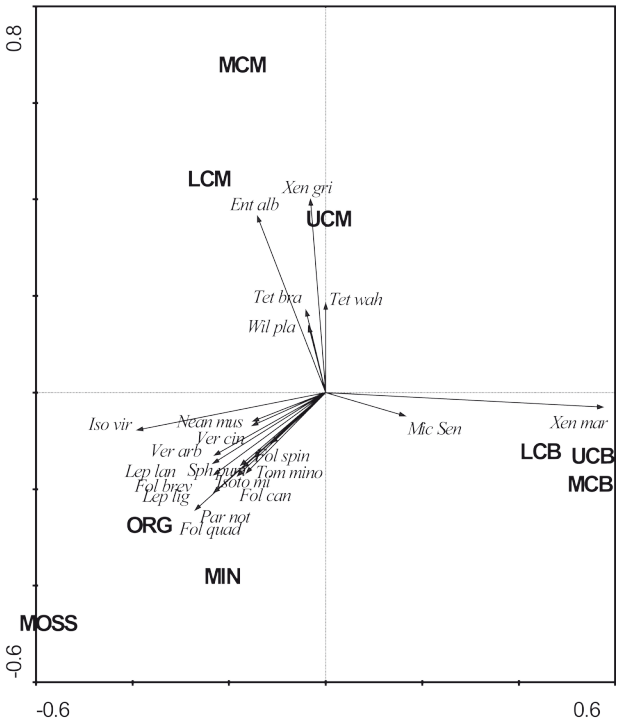


Figure 3. Redundancy analysis of the effects of microhabitat on Collembola assemblages (log10+1 transformed) with region and forest type as blocking factors. The first two axes account for 81.8% of the species environment relationships and the first axis and trace are significant (F=17.285, and p=.002; F=4.543, p=.002 respectively). Taxon abbreviations provided in Table 2.

LCB – Bark in lower canopy, **MCB** – Bark in mid canopy, **UCB** – Bark in upper canopy, **LCM** – moss from lower canopy, **MCM** – moss from mid canopy, **UCM** – moss from upper canopy, **MOSS** – moss on soil surface, **ORG** – organic horizon in soil, **MIN** – top 5 cm of mineral horizon in soil.

4. Discussion

The importance of maintaining biodiversity within ecosystems and its importance in ensuring the continued functioning of these systems is well recognised (e.g. Loreau 2010). Therefore it is essential to understand any management practice which might limit biodiversity. The data reported here confirm our hypotheses that Collembola assemblages differ significantly between native and non-native forest types. Although the average taxon richness per site did not differ significantly between forest types, rarefaction and Chao-1 indices suggest that the fauna of the total richness of Collembola in native forests is significantly greater than in Sitka spruce plantations. The fauna of oak forests was particularly diverse with those of ash and Scots pine forests similar to each other and intermediate. The most abundant species are all known to occur either specifically associated with the bark of trees, among leaf litter or in dry habitats and are thus the type of species that would be expected in these habitats (Hopkin 2007).

These results are similar to those observed in several earlier studies. Deharveng (1994) showed reduced diversity and a loss of endemic species associated with the replacement of semi-natural beech forest with non-native coniferous forests. Others have showed that the replacement of native conifer, *Pinus pinaster,* forests with introduced eucalyptus lead to significant reductions in species richness (da Gama et al. 1995, Barrocas et al. 1998). However, this has not been the case universally and Kovác et al. (2005) did not find any consistent reductions in comparisons of native cornel-oak woods with introduced *Pinus nigra*.

The current study adds to these studies not alone in examining both above and belowground components of the Collembola fauna but also in showing different degrees of difference between the fauna of the non-native species and various native species. The total number of taxa collected from oak forest was far greater than that collected from any of the other species (31 as distinct from an average of 18 in the Sitka spruce) and this would have been expected because Southwood (1961) and Southwood et al. (2005) showed that native species generally have more insect species associated with them than non-native or recently introduced species. This contention would also appear to be supported by our data and the data from most of the other studies mentioned earlier. However, ash and Scots pine are also native species or at least have been in Ireland for a longer time than Sitka spruce. Yet, the diversity found and predicted in first rotation Sitka spruce forests are higher than ash and similar to Scots pine. Therefore the effect cannot simply be a reflection of the history of the species. This

may not be surprising for taxa such as Collembola, which do not generally feed directly on the plant tissue, but may either use it simply as a habitat or feed on the microbial or other animal species which occur in association with them. In addition, although some studies have shown that particularly Collembola species are associated with the rhizospheres of particular plant species (Blackith 1974), many studies of the soil fauna have shown that the effects are quantitative rather than qualitative, i.e. that changes occur in abundances but not in species identity (e.g. Bornebusch 1930, Curry & Ganley 1977).

However, our analyses do indicate that assemblage structures vary among tree species. In particular, broadleaved species appear different to conifers but most of the species that seem to show preferences either occur on the tree bark or in moss mats on the trees. For example, *X. maritima* and *A. laricis* which occur primarily on bark or in moss are associated with the conifers while *X. grisea*, *T. brachyura* and *T. wahlgreni* particularly favour broadleaves. This may go some way to explaining the apparent discrepancies with the previous studies which concentrated on soil fauna. The bark of these trees varies very markedly with oak having a complex rough bark and ash having a smoother surface. In addition, the epiphytic flora occurring on trees varies and is known to be affected by properties of the bark such as pH. This suggests that closer consideration should be given to the microhabitat requirements of the Collembola species which occur in woodland and, in particular, that the relationship between the habitat complexity offered by bark needs to be investigated in terms of the Collembola species which occurs on different tree species.

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6. References

Arroyo, J., M. L. Moraza & T. Bolger (2010a): The mesostigmatid mite (Acari, Mesostigmata) community in canopies of Sitka spruce forests in Ireland and a comparison with ground moss habitats. – Graellsia **66**: 29–37.

Arroyo, J., P. Neville & T. Bolger (2010b): Mites occurring in the canopy of Sitka Spruce growing in Ireland. – In: Sabelis M.W. & J. Bruin (eds) Trends in Acarology. – Proceedings of the 12th International Congress. Springer, Dordrecht: 105–109.

Bagnall, R. S. (1940): Notes on British Collembola. – Entomologists' Monthly Magazine **76**: 163–174.

Bagnall, R. S. (1941): Notes on British Collembola. – Entomologists' Monthly Magazine **77**: 217–226.

Barrocas H. M., M. M. da Gama, J. P. Sousa & C. S. Ferreira (1998): Impact of reafforestation with *Eucalyptus globulus* Labill. on the edaphic collembolan fauna of Serra de Monchique (Algarve, Portugal). – Miscellania Zoologica **21**: 9–23

Blackith, R. E. (1974): The ecology of Collembola in Irish blanket bogs. – Proceedings of the Royal Irish Academy **74**B: 203–226.

Bolger, T. (1985): The rate of disappearance of *Salix* litter on cutaway bog and the microarthropods associated with it. – Pedobiologia **28**: 145–153.

Bolger, T. (2004): Examining the effects of land use, particularly afforestation, on biodiversity. – In: MacLennan, L. (ed.): Opportunities for Biodiversity enhancement in plantation forest. Proceedings of COFORD seminar, Cork, Ireland, 24 October 2002. – COFORD, Dublin: 23–28.

Bornebusch, C. H. (1930): The fauna of forest soil. – Der forstilge Forsogsvaesen in Danmark **11**: 1–158.

Bowden, J., I. H. Hains & D. Mercer (1976): Climbing Collembola. – Pedobiologia **16**: 298–312.

Coote, L., L. J. French, K. M. Moore, F. J. G. Mitchell & D. L. Kelly (2012): Can plantation forests support plant species and communities of semi-natural woodland? – Forest Ecology and Management **283**: 86–95.

Curry, J. P. & J. Ganley (1977): The arthropods associated with the roots of some common grass and weed species of pasture. – In: Lohm, U. & T. Persson (eds): Soil Organisms as Components of Ecosystems. Proceedings of the VI. International Colloquium on Soil Zoology. – Ecological Bulletin (Stockholm) **25**: 330–339.

Cutz-Pool, L. Q., G. Cataño-Menenses, J. G. Palacios-Vargas & Z. Cano-Santana (2010): Distribución vertical de colémbolos muscícolas en un bosque de *Abies religiosa* del Estado be México, México. – Revista Mexicana de Biodiversidad **81**: 457–463.

da Gama, M. M., J. P. Sousa & T. M. Vasconcelos (1995): Comparison of the collembolan populations structure from Portuguese forests of *Pinus pinaster* Aiton and *Eucalyptus globulus* Labill. – Bulletin Entomologique de Pologne **64**: 77–89.

Deharveng, L. (1994): Soil Collembola diversity, endemism, and reforestation: A case in the Pyrenees (France). – Conservation Biology **10:** 74–84

Department of Agriculture, Food and Forestry (1996): Growing for the Future - the Strategic Plan for the Development of the Forestry Sector in Ireland. – The Stationary Office, Dublin: 98 pp.

Faber, J. H. & H. A. Verhoef (1991): Functional differences between closely-related soil arthropods with respect to decomposition processes in the presence or absence of pine tree roots. – Soil Biology and Biochemistry **23**: 15–23.

Fahy, O. & M. Gormally (1998): A comparison of plant and carabid communities in an Irish oak woodland with a nearby conifer plantation and a clear felled site. – Forest Ecology and Management **110**: 263–273

Finnamore, A. T., N. N. Winchester & V. M. Behan-Pelletier (1998): Protocols for Measuring Biodiversity: Arthropod Monitoring in Terrestrial Ecosystems. – Biodiversity Science Board of Canada, Ecological Monitoring and Assessment Network, Burlington, Ontario: 53 pp.

Forest Service (2000): Forest Biodiversity Guidelines. – Department of the Marine and Natural Resources, Dublin: 8 pp.

Forest Service (2007): National Forest Inventory, Republic of Ireland. Results. – Department of Agriculture, Fisheries and Food. Wexford: 256 pp.

Halbert, J. N. (1915): Clare Island Survey. 39. Acarinida. ii. Terrestrial and marine Acarine. – Proceedings of the Royal Irish Academy **31**B: 45–136.

Heneghan, L. & T. Bolger (1996a): Effects of acid rain components on soil microarthropods: a field manipulation. – Pedobiologia **40**: 413–438.

Heneghan, L. & T. Bolger (1996b): Effects of the components of 'acid rain' on the contribution of soil microarthropods to ecosystem function. – Journal of Applied Ecology **33**: 1329–1344.

Heneghan, L. & T. Bolger (1998): Soil microarthropod contribution to forest ecosystem processes: the importance of observational scale. – Plant and Soil **205**: 113–124.

Hickie, D. (2002): Native Trees and Forests of Ireland. – Gill & Macmillan, Dublin, xvii: 119 pp.

Hopkin, S. P. (2007): A key to the Collembola (Springtails) of Britain and Ireland. – Field Studies Council, Shrewsbury: 246 pp.

Kovác, L., N. Kostúrová & D. Miklisová (2005): Comparison of collembolan assemblages (Haxapoda, Collembola) of thermophilous oak woods and *Pinus nigra* plantations in the Slovak Karst (Slovakia). – Pedobiologia **49**: 29–40.

Lambert, M. K. R. (1972): A vertical succession of Collembola and their relationship to other arthropods in Irish woodland. – Entomologists' Monthly Magazine **108**: 240–247.

Lavelle, P., C. Lattaud, D. Trigo & I. Barois (1995): Mutualism and biodiversity in soils. – Plant and Soil **170**: 23–33.

Lepš, J. & P. Šmilauer (2003): Multivariate analysis of ecological data using CANOCO. – Cambridge University Press, Cambridge. xi: 269 pp.

Lindo, Z. & N. N. Winchester (2006): A comparison of micro arthropod assemblages with emphasis on oribatid mites in canopy suspended soils and forest floors associated with ancient western red cedar trees. – Pedobiologia **50**: 31–41.

Loreau, M. (2010): Linking biodiversity and ecosystems: towards a unifying ecological theory. – Philosophical Transactions of the Royal Society Series B **365**: 49–60

O'Connell, T. & T. Bolger (1997a): Fungus fruiting bodies and the structure of fungus-microarthropod assemblages. – Biology and Environment **97**B: 249–262.

O'Connell, T. & T. Bolger (1997b): Stability, ephemerality and dispersal ability: Soil microarthropod assemblages on fungal sporophores. – Biological Journal of the Linnean Society **62**: 111–131.

Petersen, H. & M. Luxton (1982): A comparative analysis of soil fauna populations and their role in decomposition processes. – Oikos **39**: 288–388.

Pinto, C., J. P. Sousa, M. A. S. Graca & M. M. daGama (1997): Forest soil Collembola. Do tree introductions make a difference? – Pedobiologia **41**: 131–138

Sousa, J. P., J. V. Vingada, H. Barrocas & M. M. daGama (1997): Effects of introduced exotic tree species on Collembola communities: The importance of management techniques. – Pedobiologia **41**: 145–153.

Southwood, T. R. E. (1961): Number of species of insect associated with various trees. – Journal of Animal Ecology **30**: 1–8.

Southwood, T. R. E., G. R. W. Wint, C. E. J. Kennedy & S. R. Greenwood (2005): The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). – European Journal of Entomology **102**: 65–72.

ter Braak, C. J. F. & P. Šmilauer (1998): CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). – Microcomputer Power (Ithaca, NY USA): 352 pp.

Walter D. E. & V. M. Behan-Pelletier (1999): Mites in forest canopies: filling the size distribution shorfall? – Annual Review of Entomology **44**: 1–19.