

# **Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of *Peltigera* (Lecanorales, Ascomycota) in Estonia**

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## **Abstract**

The widespread cyanolichen genus *Peltigera* comprises many insufficiently known poorly delimited and/or undescribed species. Phylogenetic analysis of 252 *Peltigera* specimens from a wide range of habitat types in Estonia revealed 31 putative taxa (OTUs). Multivariate analysis revealed habitat-specific segregation between the *Peltigera* species along a gradient from humid eutrophic forests to dry oligotrophic forests and grasslands and along a soil pH gradient from alkaline soils of alvar grasslands to acidic soils of conifer forests. The diversity of *Peltigera* was the highest on roadsides and dunes and the lowest in alvar habitats which, however, supported the unique assemblage of undescribed *Peltigera* taxa. Deciduous broad-leaved forests, too, included several undescribed or rare and red-listed species. The results demonstrate that in Estonia many *Peltigera* species have narrow habitat requirements and are at present threatened by habitat loss and degradation.

## **Key words:**

Diversity, cryptic species, habitat ecology, substrate specificity, dunes, roadsides, alvars, forests, parks

## **Introduction**

Lichen symbioses are ecologically important in many terrestrial ecosystems. The cyanolichens, including *Peltigera* (Peltigeraceae, Lecanorales) species, play a particularly significant role as they can both photosynthesize and fix atmospheric nitrogen. Thus they are able to grow in nitrogen-limited environments and can also provide other organisms with fixed nitrogen (Hodkinson et al. 2014). Most *Peltigera* species are bipartite symbioses between the lichen-forming fungus (mycobiont) and one cyanobacterial photobiont (cyanobiont) which invariably belongs to the genus *Nostoc*. Some species represent more complex tripartite symbioses between the mycobiont and two photobionts, i.e. a photosynthetic green alga (*Coccomyxa*) and a nitrogen-fixing cyanobiont (*Nostoc*), respectively (Vitikainen 2007; Rikkinen 2015, 2017).

Delimitation of morphological species in *Peltigera* is notoriously difficult (Holtan-Hartwig 1993; Vitikainen 1994, 2007; Goward et al. 1995). Although DNA studies have resolved some problems, in recent years, other problems still remain unresolved. Miadlikowska and Lutzoni (2000) showed that the genus includes eight well supported monophyletic lineages (sections) that include a number of well-established morphological species and many more poorly delimited and undescribed taxa. A recent worldwide survey of the section *Polydactylon* identified many previously unrecognized putative species effectively doubling the number of known taxa in the section (Magain et al. 2017). These and concurrent findings indicate that biodiversity surveys that rely solely on phenotype characteristics can easily underestimate the true diversity of *Peltigera* species within a given region or environment (O'Brien et al. 2009; Zúñiga et al. 2015).

Most *Peltigera* species are terricolous lichens growing on mineral soil, on peat, or among ground-dwelling bryophytes. Many of them are pioneer lichens that thrive in early successional communities while others prefer mature forests where they typically grow on moss-covered soil and boulders, and on tree bases (Goward et al. 1995; Galloway 2000; Martínez et al. 2003; Vitikainen 2007; Smith et al. 2009). Some taxa in the latter group are quite specific about their requirements and susceptible to human induced changes in habitat quality. Therefore, a number of *Peltigera* species are categorized under threatened species in regional Red Lists (e.g. Liška et al. 2008; Randlane et al. 2008; Jääskeläinen et al. 2010; Marmor et al. 2017).

Recognition of cryptic fungal diversity is crucial for effective conservation of biological resources (Leavitt et al. 2013; Yahr et al. 2016). In Northern Europe habitat loss threatens not only pristine natural habitats (e.g. old-growth forests, dune environments) but also many semi-natural habitat types, including calcareous grasslands (Kuussaari et al. 2009; Cousins et al. 2015). For example, the gradual cessation of traditional land use practices in semi-natural alvar grasslands of NE Europe directly threatens many vascular plants, associated arthropods, and fungi (e.g. Eriksson et al. 2002; Öster 2008; Sang et al. 2010), as well as terricolous lichens (Leppik et al. 2013, 2015).

A number of epiphytic cyanolichens are known to be sensitive to environmental change (Ellis 2013; Rikkinen 2015). Their vulnerability to habitat loss and forest degeneration is well studied and documented (Goward and Arsenault 2000; Richardson and Cameron 2004). The diversity of epiphytic cyanolichens tends to correlate with tree species composition (Campbell et al. 2010; Aragón et al. 2013), as well as with stand age and continuity (Benson and Coxson 2002; Campbell and Freeden 2004). Because of their relatively poor dispersal ability, many cyanolichens are slow to colonize new habitats (Werth et al. 2006; Fedrowitz et al. 2012). While the influence of habitat quality on terricolous cyanolichens has not yet received much attention, some negative impacts of decreasing habitat quality on the diversity of terricolous cyanolichens have been reported (Ramírez-Fernández et al. 2013). The effect of habitat scale factors on cyanolichen communities is typically intermingled with impact of large-scale processes such as air pollution and climate change (Ellis and Coppins 2007; Geiser and Neitlich 2007; Ellis 2012). In their recent analysis of the Mediterranean region, Rubio-Salcedo et al. (2016) found that cyanobacterial macrolichens are especially vulnerable to climate change.

In this study we focus on the diversity of *Peltigera* in natural and semi-natural habitats in Estonia. The habitats include different grassland and forest types and collectively represent a natural gradient of decreasing atmospheric humidity, increasing soil pH, and increasing disturbance from acidic forest soils to basic alvar soils. We hypothesize that different *Peltigera* taxa are not randomly distributed along this complex environmental gradient, but that their species-specific distribution correlates with specific growth conditions and habitat types.

## Material and Methods

### Study region

Estonia is located in NE Europe on the eastern coast of the Baltic Sea, in the hemi-boreal sub-zone of the boreal forest zone. The region has a mild maritime climate with a mean annual temperature of 6.2 °C and precipitation of 600 mm (<http://www.emhi.ee>). The bedrock in Northern, Western and Central Estonia consists mainly of Ordovician and Silurian carbonate limestones, marls and dolomites, while Southern Estonia has Devonian sandstones and locally carbonate rocks, often covered by thick till layers (Raukas 1995). Sand dunes occur sporadically both near the coast and further inland (fossil dunes). Alvars are typical of the Baltic islands and occur also near the mainland's coastline. They are calcareous grasslands restricted to shallow skeletal soil (thickness less than 20 cm) on Ordovician or Silurian calcareous sediments or on monolithic calcareous rock. Alvars have a rather limited overall distribution; in Northern Europe they only occur on the coasts and islands of the Baltic Sea (Rosén 1982; Pärtel et al. 2007; Johansson and Petersson 2016).

### Study sites and sampling

In 2012–2016, a total of 271 specimens of *Peltigera* were collected from 75 study sites. The study sites were distributed all over Estonia and included three different wooded habitat types (oligotrophic forests, eutrophic forests, and park stands) and three different grassland types (alvars, dunes, and roadsides). The oligotrophic forests represented *Cladina* and *Vaccinium vitis-idaea* boreal forest site types dominated by Scots pine (*Pinus sylvestris*) on nutrient-poor soils. The eutrophic forests represented eutrophic and mesotrophic forest types, including herb-rich mixed forest on fertile soil, dominated either by temperate broad-leaved tree species (*Aegopodium* and *Hepatica* boreo-nemoral forest site types) or Norway spruce (*Vaccinium myrtillus* and *Oxalis* boreal forest site types). The park stands occurred in rural churchyards, cemeteries, or manor parks, dominated by broad-leaved trees and their stand structure was generally comparable to that of broad-leaved deciduous forests (Liira et al. 2012). The alvar grasslands mostly represented plate and ryhk alvars (Leppik et al. 2013, 2015; Jüriado et al. 2015). The dune grasslands were located along the seashore in Western Estonia and along the shores of Lake Peipsi in the northeast. The pioneer grasslands and the herb-rich grasslands prevailed on grey dunes (called 'grey' partly because of their dense lichen cover); communities of *Calluna vulgaris* and *Empetrum nigrum* were found on dune heaths (Jüriado et al. 2016). The roadside grasslands were mesic and xeric grasslands in the immediate vicinity of paved or unpaved roads.

At each study site, up to three specimens of each morphologically distinguishable *Peltigera* taxon were collected for DNA analysis. Three substrate types were distinguished: ground, tree trunks, and rock. To further broaden the geographical cover of sampling, 32 *Peltigera* specimens from the herbarium of the Natural History Museum at the University of Tartu (TU) were included in the dataset (Table S1). To determine soil pH (KCl), organic matter and nutrient content (Ca, Mg, K, P, N), soil samples, representing all studied habitat types except for the mesotrophic forests, were taken from 35 collection sites. These samples were analysed at the Laboratory of Plant Biochemistry of the Estonian University of Life Sciences. Prior to analysis, the samples were dried at 50°C, ground and sieved, using a 2 mm sieve. The pH was determined in a suspension of 10 g of soil and 25 ml of 1 N KCl. Total soil N was determined after Kjeldahl (Tecator ASN 3313 AOAC 2001.11, Page et al. 1982). Determination of available P in soil was done using Flow Injection Analysis (Page et al. 1982). Available K was determined from the same solution (ammonium lactate solution) by the Flame Photometric Method (956.01, KLK 1965). Exchangeable Mg was determined by Flow Injection Analysis (Page et al. 1982). Exchangeable Ca was determined from the same solution (1M ammonium acetate solution, pH = 7.0) by the Flame Photometric Method. Soil organic matter (loss on ignition) was determined after Schulte (1995).

#### Molecular data

Healthy *Peltigera* thalli without any visible symptoms of fungal infection were selected for molecular analysis. For DNA extraction, small thallus fragments from the terminal parts of lobes were taken under a dissecting microscope. The DNA was extracted using the GeneJET Genomic DNA Purification Kit (Thermo Scientific) following the manufacturer's protocol for Gram-Negative Bacteria. Amplification of the Internal Transcribed Spacer (ITS) region was done with the primer pair ITS 5F and ITS 4R (White et al. 1990) in a 50-ml volume containing 4 µl genomic DNA, 37 µl of sterile distilled water, 5 µl of 10 × buffer, 1 µl dNTP (10 mM), 0.5 µl ITS4, 0.5 µl ITS5, 1.25 µl BSA (20 mg/ml) (Thermo Scientific), 0.75 µl Dynazyme II (2 U/µl) (Thermo Scientific). The heating cycle was the following: initial denaturation of 2 min at 94 °C was followed by 35 cycles of 30 sec at 94 °C, 30 sec at 57 °C, and 30 sec at 72 °C, with a final extension of 10 min at 72 °C. The amplification products were purified with the GeneJET PCR Purification Kit (Thermo Scientific). Sequencing was performed by Macrogen Inc. in Europe. The chromatograms of all sequences were checked, manually edited, and assembled using the program BioEdit 7.0.9 (Hall 1999) and CodonCode Aligner 6.0.2 (CodonCode Corporation, Dedham, MA, USA). All newly obtained sequences are deposited in the NCBI GenBank database (**LT852805–LT853056**) (Table S1). The voucher specimens are deposited in the lichenological herbarium of the Natural History Museum at the University of Tartu (TU).

#### Mycobiont ITS alignments and phylogenetic analyses

On the basis of Blast searches in the NCBI GenBank (<http://blast.ncbi.nlm.nih.gov/Blast.cgi>), each ITS sequence obtained from the *Peltigera* specimens analysed was classified under one of the five groups corresponding to the *Peltigera* sections *Chloropeltigera*, *Horizontales*, *Peltidea*, *Peltigera*, and *Polydactylon*, respectively (Miadlikowska and Lutzoni 2000). Alignments were performed separately for

each group. Additionally, the sequences downloaded from the NCBI GenBank were included in the alignments to encompass the full known diversity of the studied groups.

The preliminary alignments of the fungal ITS sequences were performed using MAFFT (Katoh and Standley 2013). The reliability of the alignments was checked using the GUIDANCE server (Penn et al. 2010) and the alignments were corrected manually in PhyDE® 1.0 (Müller et al. 2005). Because of the very high sequence variation within the *Peltigera* section *Peltigera*, preliminary analyses were performed using the more conserved parts of the ITS region only. Based on these and previous results (Miadlikowska and Lutzoni 2000; Miadlikowska et al. 2003), the section *Peltigera* was further divided into two well supported phylogenetic groups: the *Peltigera canina* group, including the nominal species, and *P. praetextata*, *P. membranacea*, *P. degenerii*, the putative species *P. "neocanina"* (Miadlikowska et al. 2003), and closely related taxa; and the *Peltigera rufescens* group, including the nominal species, *P. didactyla*, *P. ponojensis*, and closely related taxa. For further analyses, these two groups were aligned separately. Before final analyses, the unalignable part of the ITS1 region was removed and the length of the long single nucleotide repeat region was standardized within each taxon to remove possible variation caused by sequencing defaults. Alignment information (number of variable sites; Table S2) was calculated using DnaSP v5 (Librado and Rozas 2009).

The outgroups for the final analyses were selected on the basis of previous studies (Miadlikowska and Lutzoni 2000; Miadlikowska et al. 2003; Kaasalainen et al. 2013; Magain et al. 2017). The Bayesian analyses were performed with MrBayes 3.2.6 (Huelsenbeck and Ronquist 2001) on CIPRES Science Gateway (Miller et al. 2010). The dataset was divided into subsets corresponding to the regions ITS1, 5.8S, and ITS2. The best fitting nucleotide substitution model for each region was selected by means of the jModelTest using the Akaike and Bayesian information criteria (Posada 2008), and the General Time Reversible nucleotide substitution model with Gamma distributed rate variation among the sites and the proportion of Invariable sites (GTR+Γ+I) was applied for all regions. The posterior probability distributions of the trees were calculated using the Metropolis-coupled Markov chain Monte Carlo (MCMCMC) method and the search strategies suggested by Huelsenbeck et al. (2001, 2002). Four runs with four chains ( $1.5 \times 10^7$  generations each) were set off simultaneously, with default settings. The chains were sampled for every 1,000 generations and the calculations of the consensus tree and of the posterior probability of the clades were performed based upon trees with a cut-off of 25 %. The convergence of the chains was confirmed with Tracer 1.5 (Rambaut and Drummond 2009). The trees were visualized, using TreeGraph 2.8.0 (Stöver and Müller 2010), and edited manually (Figures 1–3 and Supplementary material figures S1–S3). The nomenclature of *Peltigera* follows Vitikainen (2007).

#### Analyses of the ecological data

Direct ordination methods were used to assess the significance of the associations between lichen taxa and environmental variables. Canonical correspondence analysis (CCA) implemented in the program package CANOCO 5.0 (Šmilauer and Lepš 2014) was applied to evaluate the descriptive power of the environmental variables for species composition. The interactive forward selection procedure with

randomization tests (Monte-Carlo permutation test) was employed to select the most important environmental variables influencing species composition.

To test the explanatory value of the habitat and substrate types, a dataset with 31 taxa from 107 study sites was compiled. Each specimen was assigned habitat type (alvar grassland, dune, roadside, eutrophic forest, oligotrophic forest, and park stands) and substratum type (tree, rock, ground) variables. In analyses, the substratum and habitat variables were combined ('ground\_alvar', 'ground\_dune', 'ground\_eutrophic\_forest', 'tree\_eutrophic\_forest', 'rock\_roadside', 'rock\_eutrophic\_forest' etc.). Rare taxa (with only 1–2 occurrences) and redundant specimens (several specimens of the same mycobiont ITS genotype from the same site) were excluded from ordination analyses. After exclusion, the final data matrix included 238 *Peltigera* specimens. Differences in species composition between the different habitats and substratum types were tested using the Multi-Response Permutation Procedures (MRPP) with the Euclidean distance, implemented in the program PC-ORD 6.15 (McCune and Mefford 2011). The Shannon Index (H) (Spellerberg and Fedor 2003) of diversity of *Peltigera* taxa in each habitat type was calculated using the same program. The Shannon index takes into account both the number of specimens and the number of taxa and varies from 0 for communities with a single taxon to high values for communities with numerous taxa, each with a few individuals.

To test the explanatory value of soil properties, a smaller dataset was compiled including 12 terricolous *Peltigera* taxa from 35 study sites, with 67 *Peltigera* specimens. The sites represented five different habitat types (4 oligotrophic forests, 4 parks, 11 dunes, 7 roadsides, and 9 alvar grasslands). The soil properties used as the explanatory variables were pH, organic matter content, and soil Ca, Mg, K, N, and P content. With the exception of soil pH, all variables were log transformed prior to analysis in order to reduce the effect of outlying values. The Kruskal-Wallis tests implemented in the program Statistica (StatSoft Inc.) were used to determine the statistical significance of the observed differences in soil chemistry between the different habitats.

## Results

### Phylogenetic delimitation of the lichen taxa

The phylogenetic analyses of the 252 fungal ITS sequences obtained from the *Peltigera* specimens grouped them into 31 OTUs (operational taxonomic units) (Table 1). The specimens represented five different sections of the genus *Peltigera* corresponding to the sections *Chloropeltigera*, *Horizontales*, *Peltidea*, *Peltigera*, and *Polydactylon*, respectively (Miadlikowska and Lutzoni 2000). Most specimens (200) belonged to the *Peltigera* section *Peltigera* (Figs 1–3), comprising nine widely recognized or 'classical' *Peltigera* species (*P. degenii*, *P. membranacea*, *P. praetextata*, *P. canina*, *P. extenuata*, *P. didactyla*, *P. ponjensis*, *P. lepidophora*, and *P. rufescens*), one recently described species (*Peltigera islandica*; Manoharan-Basil et al. 2016), three putative species (*P. "fuscoponjensis"*, *P. "neocanina"*, and *P. "neorufescens"*), first identified by Miadlikowska et al. (2003), and several new putative species. The single specimen of *P. islandica* among the collected material shared an identical ITS sequence with previously analysed *P. islandica* specimens from other regions (Fig. 1). The putative new species included *P. aff. "neocanina"* (Fig. 1), and two or three species closely related to *P. "neorufescens"* and

*P. "fuscoponjensis"* (in the *P. "neorufescens"* aggregate; Fig. 3). The Estonian specimens of *P. canina* s. lat. (Fig. 1) are divided into three groups, including monophyletic *P. canina* I and *P. canina* III (corresponding to *P. canina* s. lat. and *P. canina* s. str. in Manoharan-Basil et al. 2016), and paraphyletic *P. canina* II. Furthermore, *P. didactyla* includes three and *P. ponjensis* includes two phylogenetically distinct and well supported clades.

Altogether 21 of the Estonian specimens grouped into the *Peltigera* section *Polydactylon* and represented three different taxa: *P. polydactylon* (subsp. *polydactylon*; Magain et al. 2016), *P. neopolydactyla*, and *P. hymenina* (Fig. S1). The section *Peltidea* was represented by 14 Estonian specimens, including *P. aphthosa* and *P. malacea* (Fig. S2A); the section *Horizontales*, by 11 specimens and two species, *P. collina* and *P. neckeri* (Fig. S3); and the section *Chloropeltigera*, by six specimens of *P. leucophlebia* fell into two clades, *P. leucophlebia* I (O'Brien et al. 2009) and *P. leucophlebia* IV (Fig. S2B).

#### Habitat and substrate preferences

Most *Peltigera* specimens (73 %) were collected from the ground. Some specimens were collected from tree bases or logs (17 %) and mossy rocks (10 %) (Table 2). All *Peltigera* specimens from alvars and dunes grew on soil; in all other habitats, specimens were also collected from mossy rocks (Table 2). In eutrophic forests specimens were largely collected from mossy tree bases and logs, most frequently those of *Populus tremula*, *Quercus robur*, *Fraxinus excelsior*, or *Salix caprea*. The number of *Peltigera* taxa was the highest in eutrophic forests and the lowest in oligotrophic forests and alvars (Table 2). The Shannon diversity index was the highest for roadside grasslands, parks and dunes, and the lowest for alvars (Table 2).

The CCA ordination of the *Peltigera* taxa and the combined variables of the substrate and habitat reveals differences in the habitat preferences of the different *Peltigera* taxa (Figs 4–5). The eigenvalues of the first three ordination axes are 0.63, 0.51, and 0.28, respectively, and the explanatory variables explained 18% of total variance in the large species dataset. Forward selection of the explanatory variables showed that the variables 'ground\_alvar' and 'tree\_eutr.forest' made the largest contribution to the ordination result and explained the main division of the taxa in ordination analyses. *Peltigera leucophlebia*, *P. "neorufescens"* and *P. "neorufescens"* agg. III exhibited pronounced preference for the ground in alvar habitats (Fig. 4). *Peltigera polydactylon* and *P. praetextata* preferred tree bases and logs in eutrophic forests (Fig. 4). Also *Peltigera* aff. "neocanina", *P. membranacea*, and *P. degenii* preferred forest habitats whereas *Peltigera* aff. "neocanina" grew mainly on tree bases and *P. membranacea* and *P. degenii* preferred the ground and mossy stones and boulders (Fig. 4). *Peltigera canina* II, *P. canina* III, *P. didactyla* II and *P. hymenina* grew both on tree bases in sheltered woody habitats and in open dune grasslands (Fig. 4). The remaining taxa grew on the ground in xeric woodlands (park stands, oligotrophic forests), dunes or roadsides. Differences in the habitat preferences of these taxa are visualized along the third ordination axis (Fig. 5). *Peltigera aphthosa*, *P. malacea* and *P. extenuata* grew frequently on the soil in oligotrophic forests, whereas *P. rufescens*, *P. neckeri* and the putative species *P. "fuscoponjensis"* were found on the ground in various habitats, most frequently on sand dunes (Fig. 5).

*Peltigera ponojensis* I & II, *P. canina* I and *P. didactyla* I were the most common in roadside grasslands and the putative species *P. "neorufescens"* agg. II preferred the soil in park stands (Fig. 5).

The MRPP tests confirmed that differences in the composition of the *Peltigera* species between the different habitats ( $A = 0.048$ ,  $P < 0.0001$ ) and substratum types ( $A = 0.027$ ,  $P < 0.0001$ ) were highly significant. In pairwise comparisons, significant differences in species composition were detected between alvars and all other habitat types ( $P < 0.01$  and  $P < 0.0001$ ), and between eutrophic forests and all other habitats ( $P < 0.01$  and  $P < 0.0001$ ), except for park stands ( $p = 0.26$ ). Differences in species composition were significant also between 'trees' and the other two substratum types ( $P < 0.01$ ) but not between 'ground' and 'rock' ( $p = 0.123$ ).

In the second CCA ordination analysis, the soil property variables explained 42.4% of total variance in the smaller species dataset. The eigenvalues of the first two ordination axes are 0.65 and 0.41, respectively (Fig. 6). Assessment of the effects of each environmental variable demonstrated that all soil parameters, except for P content, contributed significantly to the CCA model ( $p < 0.05$ ). However, among the habitat variables, only 'alvar' was significant ( $p < 0.05$ ) in explaining the habitat preferences of the terricolous *Peltigera* taxa. *Peltigera "neorufescens"* agg. III and *P. "neorufescens"* were predominantly found on alvar soils with high N content. The lichen taxa favouring eutrophic soils, i.e. *P. ponojensis* I, *P. canina* I, and *P. fuscoponojensis*, grew frequently in roadside grasslands. Also *P. ponojensis* II and *P. canina* II preferred eutrophic soils while *P. extenuata*, *P. canina* III, and *P. didactyla* I grew frequently on acidic nutrient-poor soils (Fig. 6). The Kruskal-Wallis tests confirmed the statistical significance of the observed differences in soil chemistry between the different habitats. The most acidic soils were found in oligotrophic forests where soil pH was significantly lower than in alvar grasslands ( $H (4, N = 35) = 11.293$ ,  $p = 0.0023$ ) (Fig. S4A). The soils of alvar grasslands had significantly higher N, K, Mg, Ca content, and contained more organic matter than the soils of dunes and oligotrophic forests (Fig. S4B–F). The soils of park stands and roadside grasslands had high P content and differed significantly from the soils of dunes in this respect ( $H = 18.365$ ,  $p = 0.001$ ) (Fig. S4G).

## Discussion

Global biodiversity remains poorly known and most species remain undescribed (Costello et al. 2012, 2013; Pimm and Raven 2017). Among the lichen-forming fungi, many undescribed taxa are known to inhabit poorly studied regions and habitats, especially in tropical forests, and within overlooked taxonomic groups (Lumbsch et al. 2011; Hawksworth 2012; Yahr et al. 2016). Some of the monophyletic groups of *Peltigera* identified in this study show distinct ecological preferences and pending further morphological and chemical analyses, most of them probably represent new, previously unrecognized species. The high resolution of clades in the phylogenetic trees (Figs 1–3, S1–S3) and the accordance of our results with those of other studies, using multiple markers (e.g. Goffinet et al. 2003; Miadlikowska et al. 2003; Magain et al. 2016), support the opinion that in most cases the ITS region alone provides sufficient genetic information for distinguishing species within the genus *Peltigera* (Goffinet and Miadlikowska 1999; Lendemer and O'Brien 2011; Miadlikowska et al. 2014; Han et al. 2015). Our results exemplify also significant hidden diversity within relatively well known lichen groups and in

comparatively well studied areas. Similar observations have recently been made in several other molecular studies (e.g. Lumbsch and Leavitt 2011; Divakar et al. 2016; Magain et al. 2017).

#### Species delimitation and habitat preferences

The studied dataset of the Estonian *Peltigera* specimens was comprehensive, representing five different sections of *Peltigera* (Miadlikowska and Lutzoni 2000), of which the largest and the most diverse was the section *Peltigera*. Miadlikowska et al. (2003) identified two major monophyletic lineages within the section: the *cinnamomea – canina – degenerii* group (CICADE) and the *ponojensis – rufescens – didactyla* group (PORUDI). Both groups were also found and supported by our phylogenetic analyses. The species of the CICADE-group are common in woodlands (mesophytic and subhygrophytic) and occur only rarely at xeric sites; the taxa of the PORUDI-group are xerophytic or at least to a far lesser degree mesophytic (Goward et al. 1995; Miadlikowska et al. 2003).

In the studied region the CICADE-group included four well established species (*Peltigera degenerii*, *P. membranacea*, *P. praetextata*, *P. canina*), one relatively newly described species (*P. islandica*) which has previously only been reported from Iceland and Canada (Manoharan-Basil et al. 2016), the putative species *P. “neocanina”* (Miadlikowska et al. 2003; O’Brien et al. 2009), and a closely related possibly new taxon (*P. aff. “neocanina”*; Fig. 1) which, apart from Estonia, has so far only been reported from Finland (Kaasalainen et al. 2013). *Peltigera aff. “neocanina”* seems to be mesophytic (Fig. 4) as its specimens were mostly collected from tree bases and mossy rocks in overgrown wooded meadows or eutrophic forests. *Peltigera “neocanina”* was only found on two occasions on mossy forest soils.

Phylogenetic analysis divided *Peltigera canina* into several groups, of which two were strongly supported (*P. canina* I and III in Fig. 1). According to Manoharan-Basil et al. (2016), clade III represents *P. canina* s. str. while at least clade I represents an additional distinct taxon. We found a clear difference in habitat ecology between these two clades. All specimens of *P. canina* clade I were collected from the ground mostly in relatively xeric habitats such as roadside grasslands and park stands (Figs 4–5). Conversely, the specimens of *P. canina* clade III were collected either from the ground at highly xeric sites, or from tree bases and rocks in eutrophic forests (Fig. 4). Similar habitat preferences were exhibited by the specimens of *P. canina* clade II. Further studies are required to determine whether the taxa in these lineages differ also in some aspects of thallus morphology and worldwide distribution patterns.

Anstett et al. (2013) found evidence that certain genotypes of *P. praetextata* were associated with particular substrates such as limestone or wood. In our study, all specimens represented the same genotype and were mostly collected from mossy tree bases in eutrophic forests (Fig. 1).

The PORUDI-group included *Peltigera extenuata*, *P. didactyla*, *P. ponogensis*, *P. lepidophora*, *P. rufescens* and several well supported additional putative taxa (Fig. 2). *Peltigera extenuata* typically grew on a sandy soil on dunes and in oligotrophic pine forests, in conditions that were more xeric than those reported by Goffinet and Hastings (1995). The specimens of *P. didactyla* fell into three phylogenetically distinctive clades with strong support. *Peltigera didactyla* clade I (Fig. 2) corresponds to *Peltigera* sp. 2 in a study of Goffinet et al. (2003, Figs 3–4). In our study *Peltigera didactyla* clade III corresponds to

*Peltigera* sp. 3 and clade II represents *P. didactyla* s. str. There are some differences in the habitat ecology of these three clades. The specimens of *P. didactyla* clades I and III were collected from xeric habitats, mostly dunes, while some specimens of clade II grew at humid sites like mossy tree bases in eutrophic forests.

The specimens of *Peltigera ponojensis* grouped into two well supported sister clades, without any clear differences in the habitat preferences between these groups. Most specimens were collected from roadsides and dunes, generally on a eutrophic calcareous soil; in some cases the two genotypes were found in the same locality. *Peltigera lepidophora* is well known to prefer calcareous and/or nutrient-rich substrates (Vitikainen 2007) and it also occurs in alvars (Leppik et al. 2013).

The Estonian *Peltigera rufescens* group included *P. rufescens* s. str., the two tentative species *P. "fuscoponjensis"* and *P. "neorufescens"* (Miadlikowska and Luzoni 2000; Miadlikowska et al. 2003), and three previously unreported, well supported clades forming the *P. "neorufescens"* aggregate in Fig. 3. The specimens of *P. rufescens* s. str. were collected from xeric habitats, frequently on acidic soils. The putative species *P. "fuscoponjensis"* was typically found in xeric grasslands with high soil pH (Fig. 6). *Peltigera "neorufescens"* was found at no less than 12 sites, again from xeric calcareous grasslands with high soil pH.

The new clades of *P. "neorufescens"* agg. have so far only been reported from Estonia. The specimens of clade I and II were collected from several habitat types, whereas the specimens of clade III were restricted to alvar grasslands (Figs 4, 6). Clear differences in ecological preferences between the clades suggests that there are at least two undescribed taxa in the group.

*Peltigera polydactylon* from the section *Polydactylon* was found exclusively in deciduous eutrophic and mixed mesotrophic forests, where it usually grew on tree bases and mossy logs. *Peltigera neopolydactyla* and *P. hymenina* were found only infrequently; both are known to favour humid forest environments (Vitikainen 1994, 2007). Traditionally, *P. neopolydactyla* was thought to have an almost worldwide distribution (Holtan-Hartwig 1993; Vitikainen 1994, 2007; Goward et al. 1995); however, this species concept has since been shown to be polyphyletic (Magain et al. 2017).

*Peltigera leucophlebia*, the sole species of the section *Chloropeltidea* in Estonia, was found on several occasions in dry alvar grasslands. Previous studies have shown that *P. leucophlebia* too consists of several cryptic species with some morphological differences (O'Brien et al. 2009); our phylogenetic analysis also confirmed the existence of several distinct clades (Fig. S2B). Interestingly, one of them (clade IV) includes Estonian specimens only and forms a sister clade to all previously known *P. leucophlebia* clades. According to O'Brien et al. (2009), members of clades I and II have *P. aphthosa*-type venation, which was also observed in one of the Estonian specimens from clade I. However, another Estonian specimen of clade I has a reticulate vein pattern characteristic of typical *P. leucophlebia* in Europe (Vitikainen 1994), and this feature is also shared by all the specimens of clade IV (Fig. S2B). Further research is required to determine whether clades I and II represent new taxa previously unknown in Europe (O'Brien et al. 2009), as well as to elucidate their specific relationships with *P. leucophlebia* s. str.

## Diversity of the *Peltigera* taxa in different habitats

On the basis of substrate and habitat preferences, the analysed *Peltigera* taxa clustered into distinct ecological groups that correspond well to previous observations from other regions (e.g. Holtan-Hartwig 1993; Vitikainen 1994; Goward et al. 1995; Miadlikowska et al. 2003). The group of mesophytic species (e.g. *P. praetextata*, *P. degenii*, *P. membranacea*, *P. polydactyla*) were typically found in humid and sheltered sites including eutrophic forests, and the second group of more xerophytic species (e.g. *P. didactyla*, *P. ponojensis*, *P. neckerii*, *P. rufescens*) were typically found at exposed and often disturbed sites including dunes, alvars, and roadsides, but also oligotrophic pine forests with relatively open canopies. Most of the xerophytic taxa also exhibited clear preferences for specific soil properties. For example, *P. ponojensis*, *P. leucophlebia*, and *P. "neorufescens"* preferred calcareous nutrient-rich soils while *P. aphthosa*, *P. extenuata*, and *P. malacea* preferred nutrient-poor acidic soils. These and other habitat preferences were clearly visualized in the ordination diagrams (Figs 4–6).

The assemblage of *Peltigera* taxa in Estonian eutrophic forests differed significantly from that in all other habitats except for park stands. The similarity in species composition between these two habitat types is not surprising considering that the tree species composition and the canopy structure of moderately managed park stands in Estonia tend to resemble those of broad-leaved deciduous forests and are also known to provide a refugium for a number of forest-specific plant species (Liira et al. 2012). A number of the *Peltigera* species found in eutrophic and mesotrophic forests (e.g. *P. collina*, *P. degenii*, *P. hymenina*) are red-listed in Estonia (Randlane et al. 2008, Marmor et al. 2017) or at least regarded as hemerophobic (e.g. *P. membranacea*, *P. neopolydactyla*) (Trass et al. 1999). Also some rare *Peltigera* species that were not encountered (e.g. *P. horizontalis*) are known to prefer shaded habitats and occur almost exclusively on large deciduous trees in old-growth forests (Vitikainen 2007). In addition, some of the new taxa identified in this study (e.g. *P. "neocanina"*, *P. aff. "neocanina"*) were confined to sheltered forest environments. The regional rarity of these taxa in Estonia is undoubtedly linked to the general scarcity of old-growth deciduous stands in the present forest landscape (Lõhmus et al. 2004; Marmor et al. 2017).

In xeric habitats the diversity of *Peltigera* was the lowest in alvar grasslands and on acidic soils in oligotrophic forests while higher diversity was found from in roadside grasslands and dunes. Cyanolichen diversity is often the highest on sub-neutral substrates as many cyanolichens are quite sensitive to acidification (Rikkinen 2015). The relatively low soil pH of oligotrophic pine forests is clearly not optimal for several *Peltigera* taxa, even though some species (e.g. *P. extenuata*, *P. didactyla* s.lat., *P. rufescens*, *P. malacea*, *P. aphthosa*) do particularly well in this habitat. Dunes supported the high diversity of *Peltigera* species, presumably partly because of the highly variable Ca content of sand (Fig. S4E) but also because of favourable light conditions and weak competition from vascular plants (Jun and Rozé 2005; Ketner-Oostra et al. 2012; Jüriado et al. 2016). Also the relatively high *Peltigera* diversity in roadside habitats may be largely explained by the presence of limestone as limestone gravel is widely used for road construction in Estonia. Both roadsides and dunes are affected by relatively high levels of disturbance and human activity. Periodic removal of trees from dunes (Riksen et al. 2006; Jüriado et al. 2016) and mowing of roadside meadows (Parr and Way 1988) is needed for the long-term preservation of these habitats and the species diversity of their terricolous lichen communities.

One previously undocumented feature found in this study is the existence of a relatively species-poor but very characteristic *Peltigera* community of alvar grasslands. Alvar grasslands are in many respects extreme habitats which are subjected to high environmental stress and considerable natural disturbance. The thin soil over monolithic rock is highly susceptible to extreme drought in summer, frost-induced soil movements in winter, and frequent small-scale flooding in spring (Rosén 1982; Ott et al. 1997). Because of calcareous base rock, alvar soils are rich in inorganic nutrients (Ca, Mg, P, K) (Fig. S4B–E). Additionally, the common occurrence of terricolous cyanobacteria may promote nitrogen availability (Büdel et al. 2014). The only frequent *Peltigera* species at alvar sites were the two putative taxa *P. "neorufescens"* and *P. "neorufescens"* agg. III. These lichens tolerate well grazing and other land use practices, which has modified Estonian alvars over recent millennia (Pärtel et al. 2005, 2007). They represent an interesting new addition to the long list of lichens characterizing alvar habitats (Fröberg 1988; Ott et al. 1996, 1997; Leppik et al. 2013, 2015). Unfortunately, in recent decades, habitat loss and degradation, mainly caused by ongoing changes in land use practices (Rosén and Bakker 2005), have started pose serious threat to alvars and their unique biota (Helm et al. 2006; Kasari et al. 2016). Effective conservation of alvar communities must involve promotion of lichen growth by suppressing shrubs and herbs via grazing or other means, and by allowing recurrent small-scale soil disturbances (Leppik et al. 2013, 2015).

In conclusion, our study revealed high, previously unrecognized diversity within the genus *Peltigera* in Estonia. Several undescribed species are confined to specific habitat types, including threatened alvar grasslands and deciduous broad-leaved forests. These results emphasize the potential importance of cryptic fungal diversity. It is evident that lichen surveys relying solely on phenotype characteristics can easily underestimate the true diversity of *Peltigera* taxa within given regions and habitat types. Continuing habitat loss threatens the diversity of *Peltigera* not only in pristine natural habitats (e.g. forests, dunes) but also in semi-natural habitat types, including alvar grasslands.

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Table 1. List of the *Peltigera* taxa found in Estonia in this study. The number of fungal ITS sequences, different genotypes, and collection localities (sites) is given for each taxon. The last column (Ord) shows which of the taxa were included in the ordination analyses (+).

Taxa	Sequences	Genotypes	Sites	Ord
<i>Peltigera aphthosa</i> (L.) Willd.	4	3	4	+
<i>Peltigera canina</i> (L.) Willd. s. lat.				
<i>P. canina</i> I	9	2	6	+
<i>P. canina</i> II	16	3	13	+
<i>P. canina</i> III	26	5	20	+
<i>Peltigera collina</i> (Ach.) Schrad.	1	1	1	
<i>Peltigera degenerii</i> Gyeln.	3	1	3	+
<i>Peltigera didactyla</i> (With.) J.R.Laundon s. lat.				
<i>P. didactyla</i> I	4	2	3	+
<i>P. didactyla</i> II	6	4	6	+
<i>P. didactyla</i> III	3	2	2	
<i>Peltigera extenuata</i> (Nyl. ex Vain.) Lojka	7	1	3	+
<i>Peltigera "fuscoponponensis"</i> <sup>1</sup>	7	3	5	+
<i>Peltigera hymenina</i> (Ach.) Delise	3	1	3	+
<i>Peltigera islandica</i> Goward & Manoharan-Basil	1	1	1	
<i>Peltigera lepidophora</i> (Vain.) Bitter.	2	2	2	
<i>Peltigera leucophlebia</i> (Nyl.) Gyeln. s. lat.				
<i>P. leucophlebia</i> I	2	1	2	
<i>P. leucophlebia</i> IV	4	2	4	+
<i>Peltigera malacea</i> (Ach.) Funck	10	2	8	+
<i>Peltigera membranacea</i> (Ach.) Nyl.	4	3	3	+
<i>Peltigera neckeri</i> Hepp ex Müll.Arg.	10	5	8	+
<i>Peltigera aff. "neocanina"</i>	9	5	6	+
<i>Peltigera "neocanina"</i> <sup>1</sup>	2	2	1	
<i>Peltigera neopolydactyla</i> (Gyeln.) Gyeln.	1	1	1	
<i>Peltigera "neorufescens" agg.</i>				
<i>P. "neorufescens" agg. I</i>	2	2	2	
<i>P. "neorufescens" agg. II</i>	5	5	4	+
<i>P. "neorufescens" agg. III</i>	8	6	3	+
<i>Peltigera "neorufescens"</i> <sup>1</sup>	29	24	12	+
<i>Peltigera polydactylon</i> (Neck.) Hoffm.	17	3	10	+
<i>Peltigera ponogensis</i> Gyeln. s. lat.				
<i>P. ponogensis</i> I	9	6	7	+
<i>P. ponogensis</i> II	8	6	7	+
<i>Peltigera praetextata</i> (Flörke ex Sommerf.) Zopf	13	1	11	+
<i>Peltigera rufescens</i> (Weiss) Humb.	27	20	14	+

<sup>1</sup> Taxa defined by Miadlikowska et al. (2003)

Table 2. Number of sequenced *Peltigera* specimens from different substrates (ground, rock, tree) and habitat types; number of taxa (S); and value of Shannon diversity index (H) for each habitat type.

Habitat	Ground	Rock	Tree	S	H
Oligotrophic forests	27	1	–	10	2.09
Eutrophic forests	21	9	44	18	2.37
Park stands	15	10	–	14	2.47
Alvars	43	–	–	10	1.49
Dunes	47	–	–	15	2.46
Roadsides	30	5	–	14	2.48
Total	183	25	44		
Average				13.5	2.22

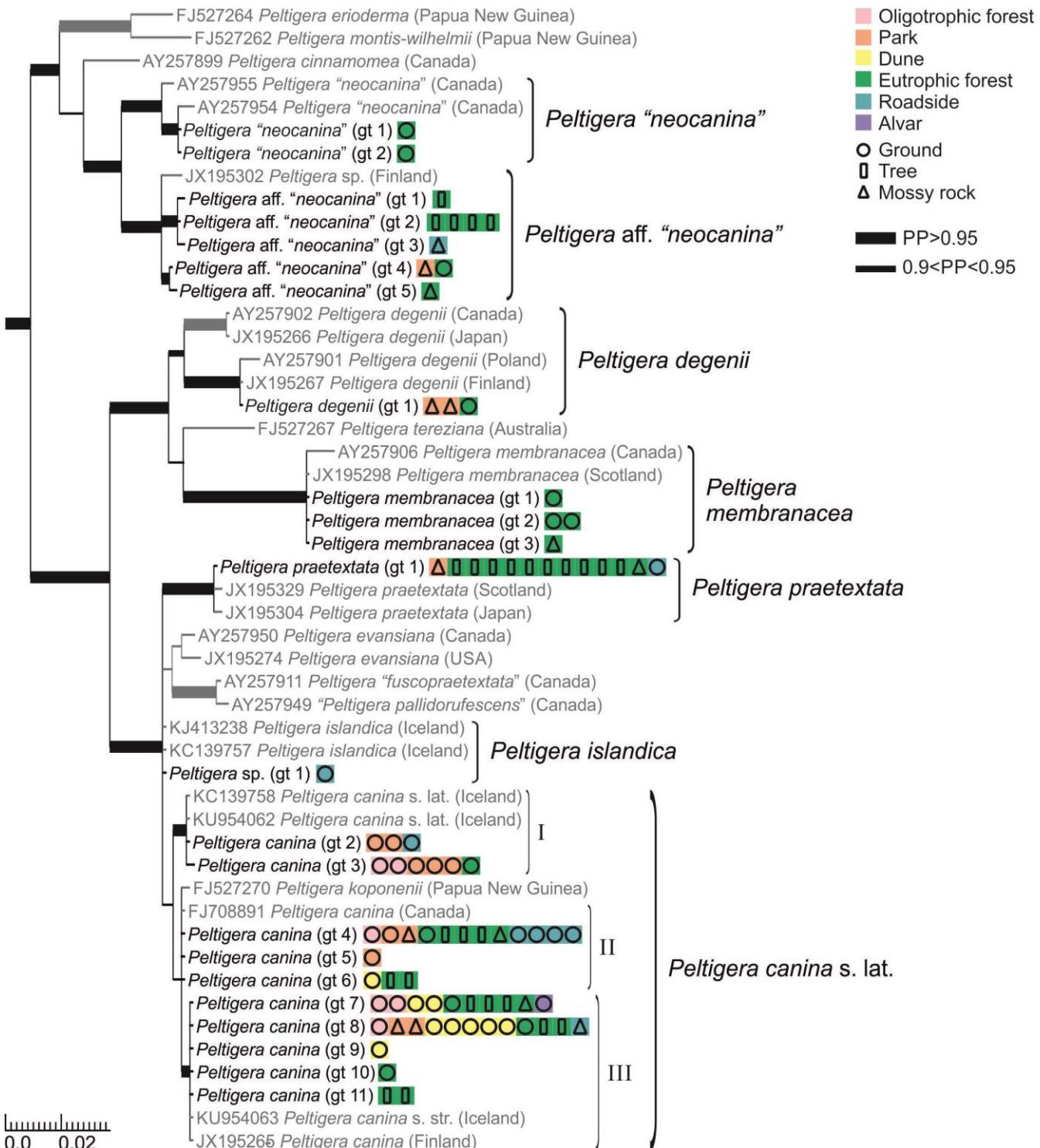


Figure 1. Phylogeny constructed of the ITS-sequences of the *Peltigera canina*-group (*Peltigera* section *Peltigera*). Support for each clade is indicated by branch thickness. Each square represents a specimen of the respective genotype, with the colour indicating its habitat and the symbol indicating its substrate. The sequences in grey were downloaded from the NCBI GeneBank (specimens from outside of Estonia). The outgroup (not shown) included *Peltigera kristinssonii* (AY257891), *P. frigida* (AY257893), *P. continentalis* (AY257890), and *P. isidiofora* (KJ095107).

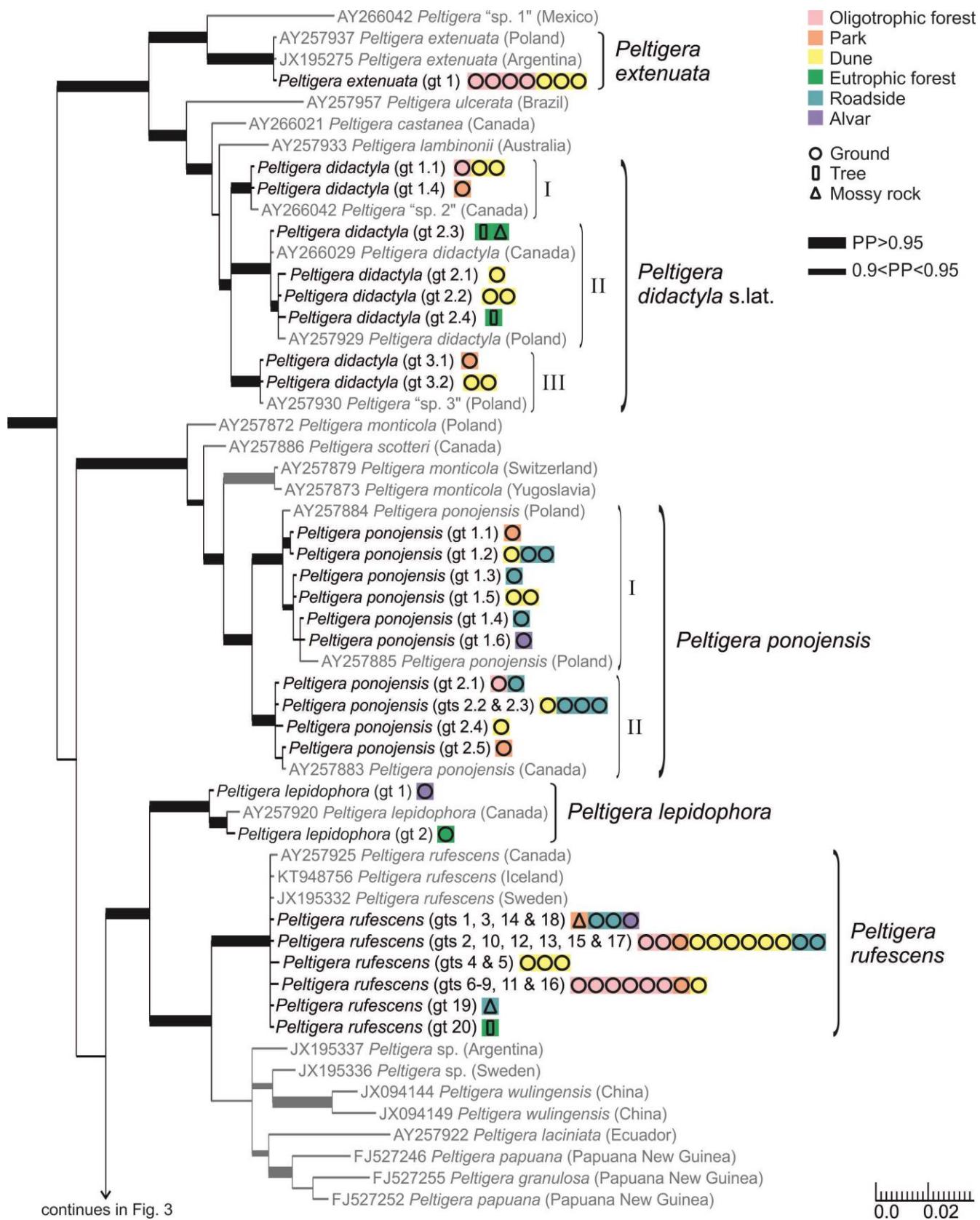


Figure 2. Phylogeny constructed of the ITS-sequences of the *Peltigera rufescens*-group (*Peltigera* section *Peltigera*, the tree is continued in Fig. 3). Support for each clade is indicated by branch thickness. Each square represents a specimen of the respective genotype, with the colour indicating its habitat

and the symbol indicating its substrate. The sequences in grey were downloaded from the NCBI GeneBank (specimens from outside of Estonia). The outgroup (not shown) included *Peltigera canina* ([AY257890](#)), *P. "neocanina"* ([AY257955](#)), *P. continentalis* ([AY257980](#)), *P. kristinssonii* ([AY257891](#)), and *P. frigida* ([AY257893](#)).

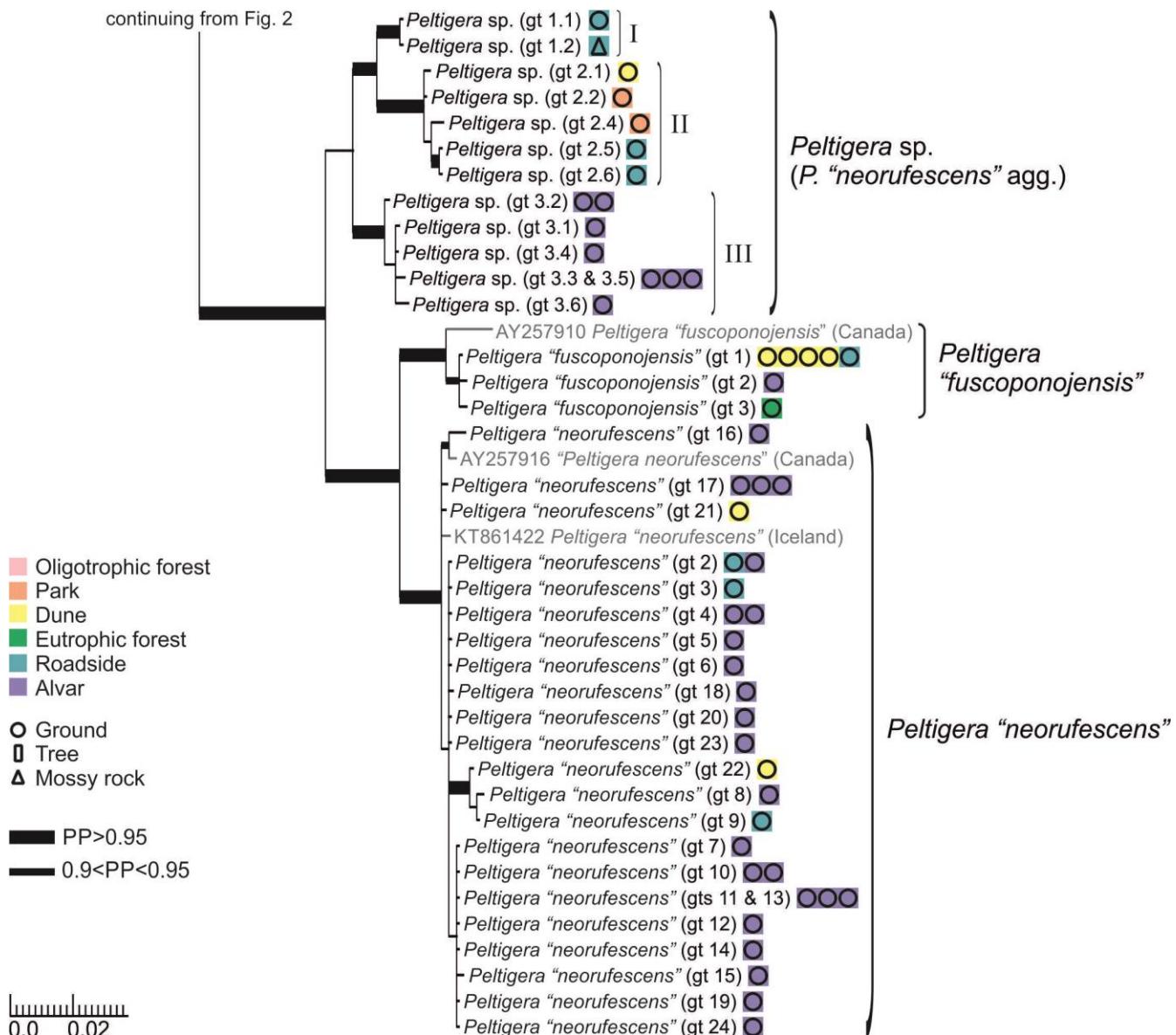


Figure 3. Part of the phylogeny constructed of the ITS-sequences of the *Peltigera rufescens*-group (*Peltigera* section *Peltigera*, the tree is continued from Fig. 2). Support for each clade is indicated by branch thickness. Each square represents a specimen of the respective genotype, with the colour indicating its habitat and the symbol indicating its substrate. The sequences in grey were downloaded from the NCBI GeneBank (specimens from outside of Estonia).

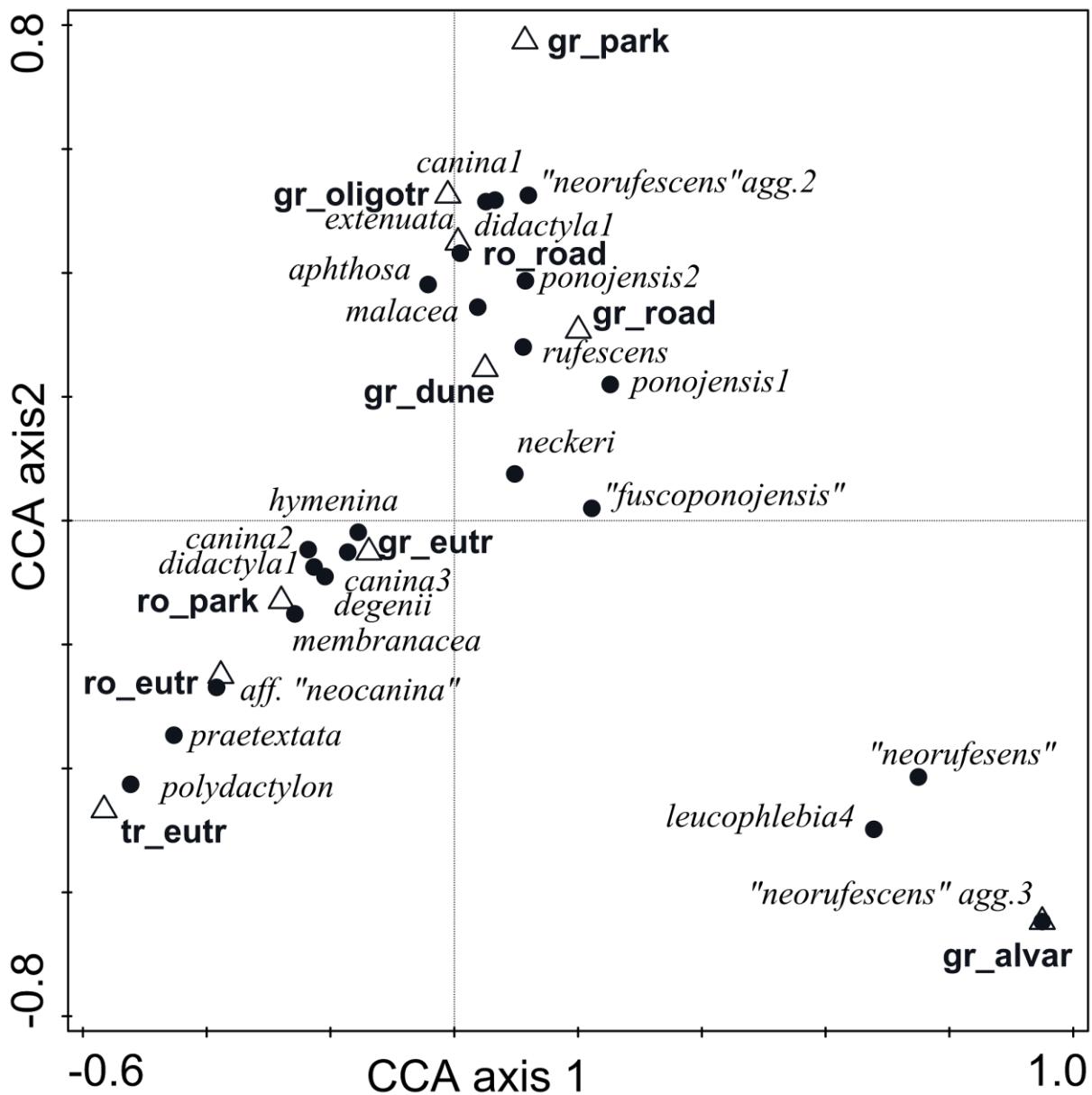


Figure 4. *Peltigera* taxa (dots) and environmental variables (triangles) in the bi-plot of the canonical correspondence analysis (CCA) of the first and second axes. The *Peltigera* species typically found in alvar habitats are situated below on the right and the species preferring tree bases and logs in eutrophic forests are below on the left. Some species growing both on tree bases in woody habitats and on soil in open dune grasslands are in the middle while the ground-dwelling *Peltigera* species preferring xeric habitats cluster in the upper part of the diagram. Abbreviations: 'gr\_alvar' = ground in alvars, 'gr\_park' = ground in park stands, 'gr\_oligotr' = ground in oligotrophic forests, 'gr\_road' = ground in roadside grasslands, 'gr\_dune' = ground on dunes, 'gr\_eutr' = ground in eutrophic forests, 'ro\_eutr' = rocks in eutrophic forests, 'ro\_park' = rocks in park stands, 'tr\_eutr' = trees in eutrophic forests. The statistically important variables in the forward selection of environmental variables are 'gr\_alvar' and 'tr\_eutr'.

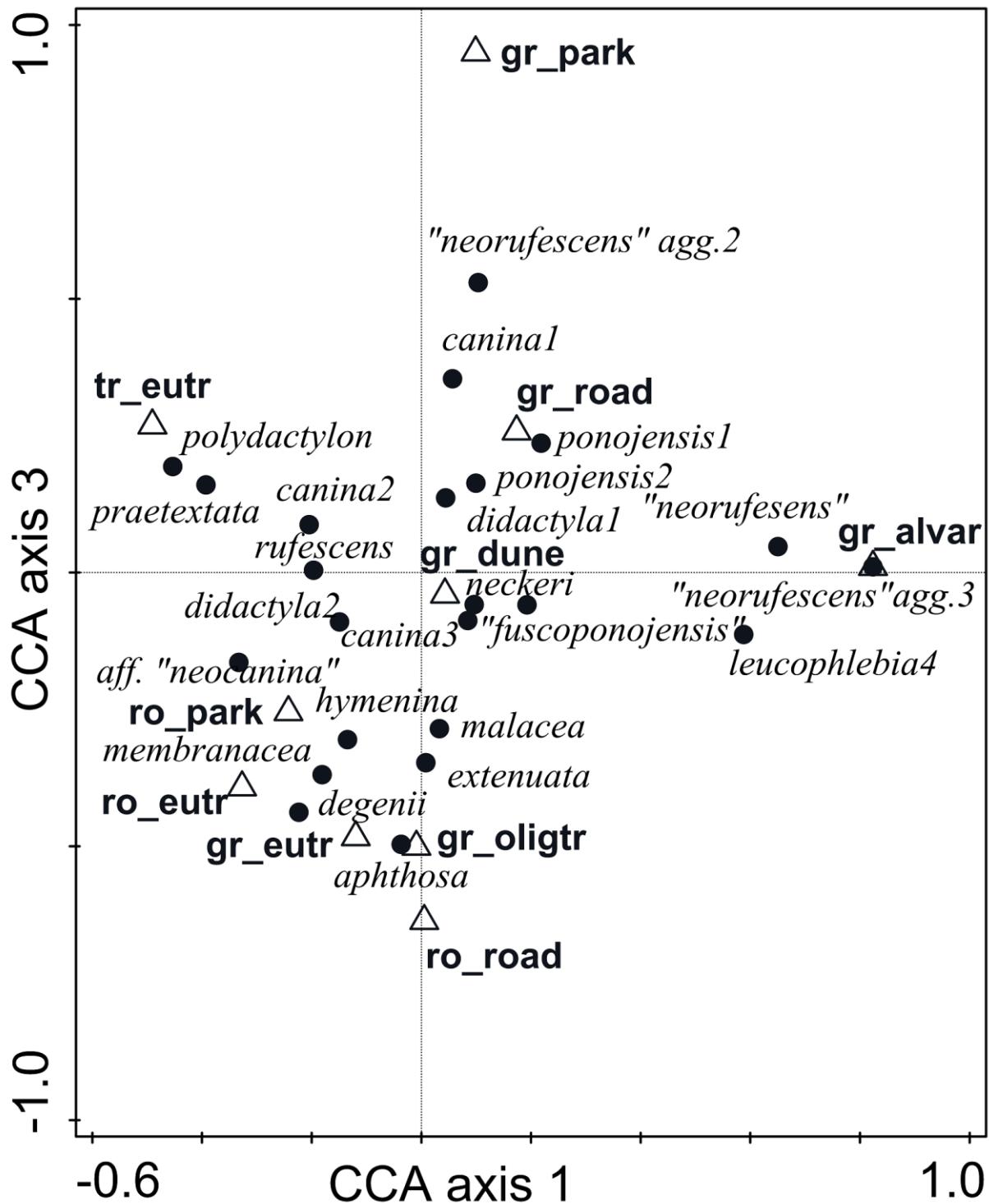


Figure 5. *Peltigera* taxa (dots) and environmental variables (triangles) in the bi-plot of the canonical correspondence analysis (CCA) of the first and third axes. Differences in the habitat preferences of *Peltigera* species from xeric habitats are shown with the *Peltigera* species from oligotrophic pine forests in the lower part of the diagram and the species from more open habitats in the upper part. Abbreviations as in Fig. 4.

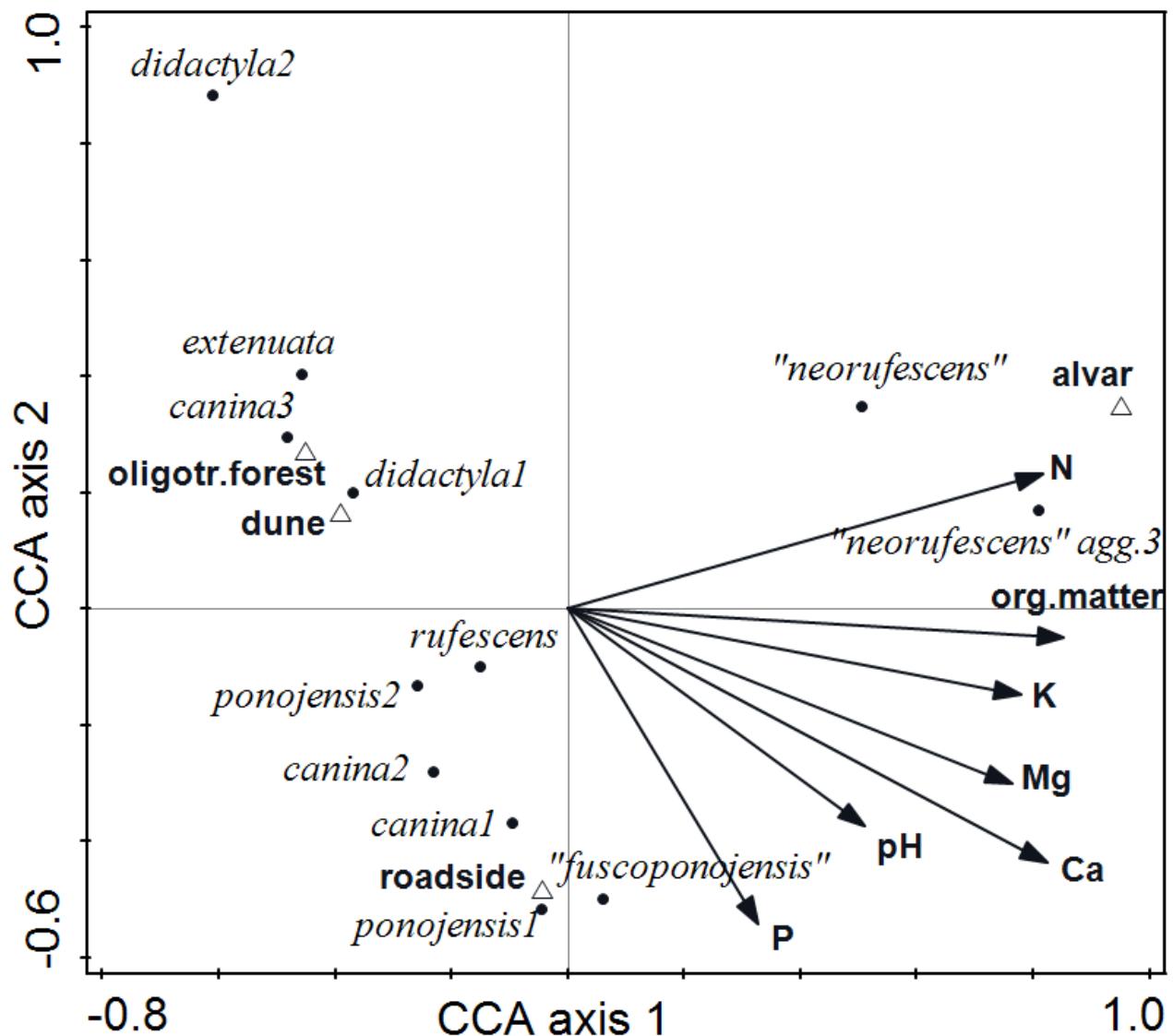


Figure 6. Terricolous *Peltigera* taxa (section *Peltigera*) (dots) and environmental variables (nominal variables as triangles) in the bi-plot of the canonical correspondence analysis (CCA) of the first and second axes. The species typical of alvar soils are on the right; the species from roadside grasslands and other nutrient rich sites are in the lower part, while species of acidic nutrient-poor soils are above on the left. Oligotr. forest = oligotrophic forest, 'N' = soil N content, 'K' = soil K content, 'Mg' = soil Mg content, 'Ca' = soil Ca content, 'P' = soil P content, 'Org. matter' = soil organic matter content, 'pH' = soil pH.

Electronic supplementary material: Fungal Ecology

Inga Jüriado<sup>a, b,\*</sup>, Ulla Kaasalainen<sup>c</sup> and Jouko Rikkinen<sup>b, c</sup>

Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of *Peltigera* (Lecanorales, Ascomycota) in Estonia

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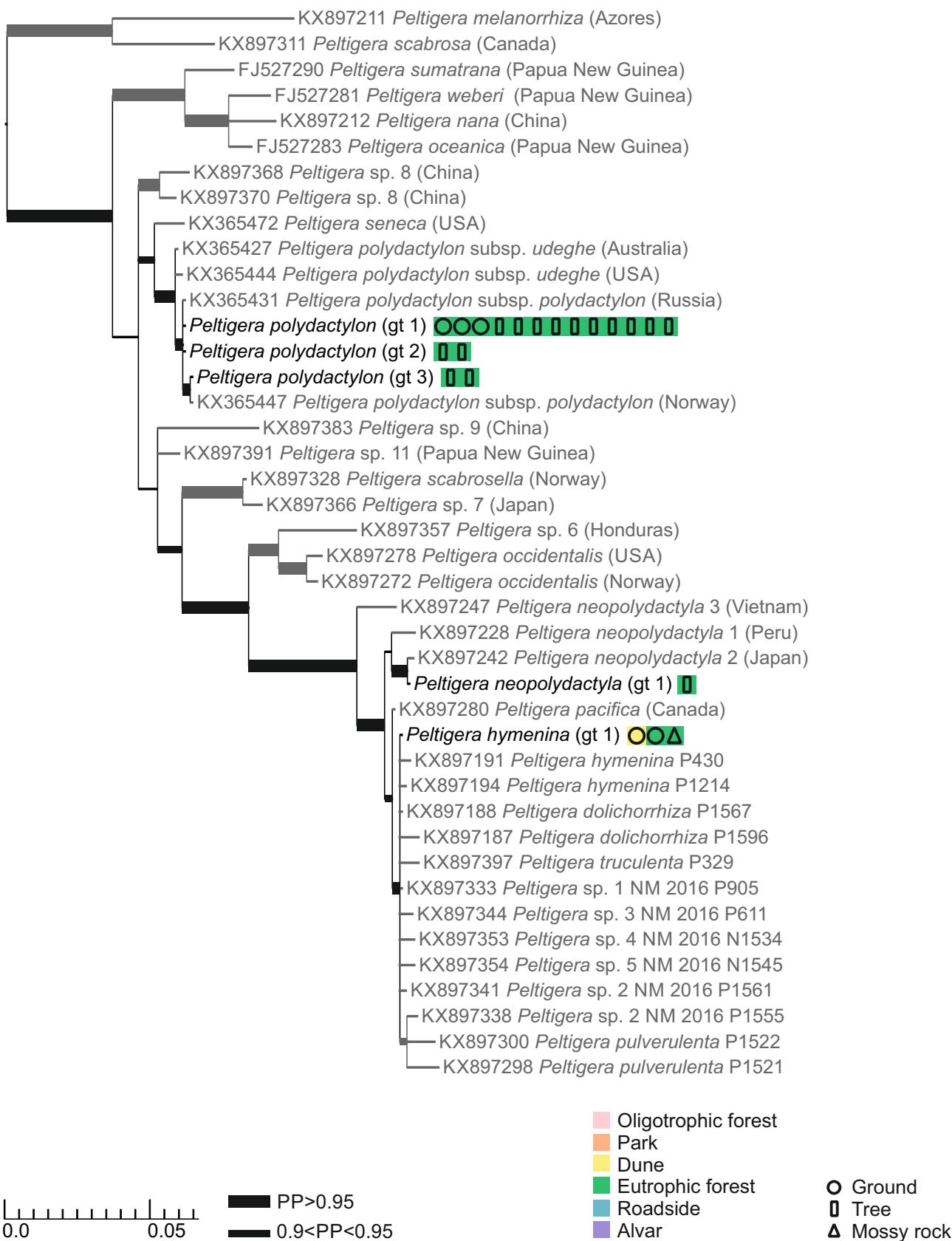


Figure S1. Phylogeny constructed of the ITS-sequences of the polydactyloid and dolichorhizzoid group (Magain et al. 2017) within the *Peltigera* section *Polydactylon*. The support for each clade is reflected in the thickness of the branch. Each square represents a specimen of the respective genotype indicating the habitat (color) and substrate (symbol). Grey specimens are not from Estonia but downloaded from the NCBI GeneBank.

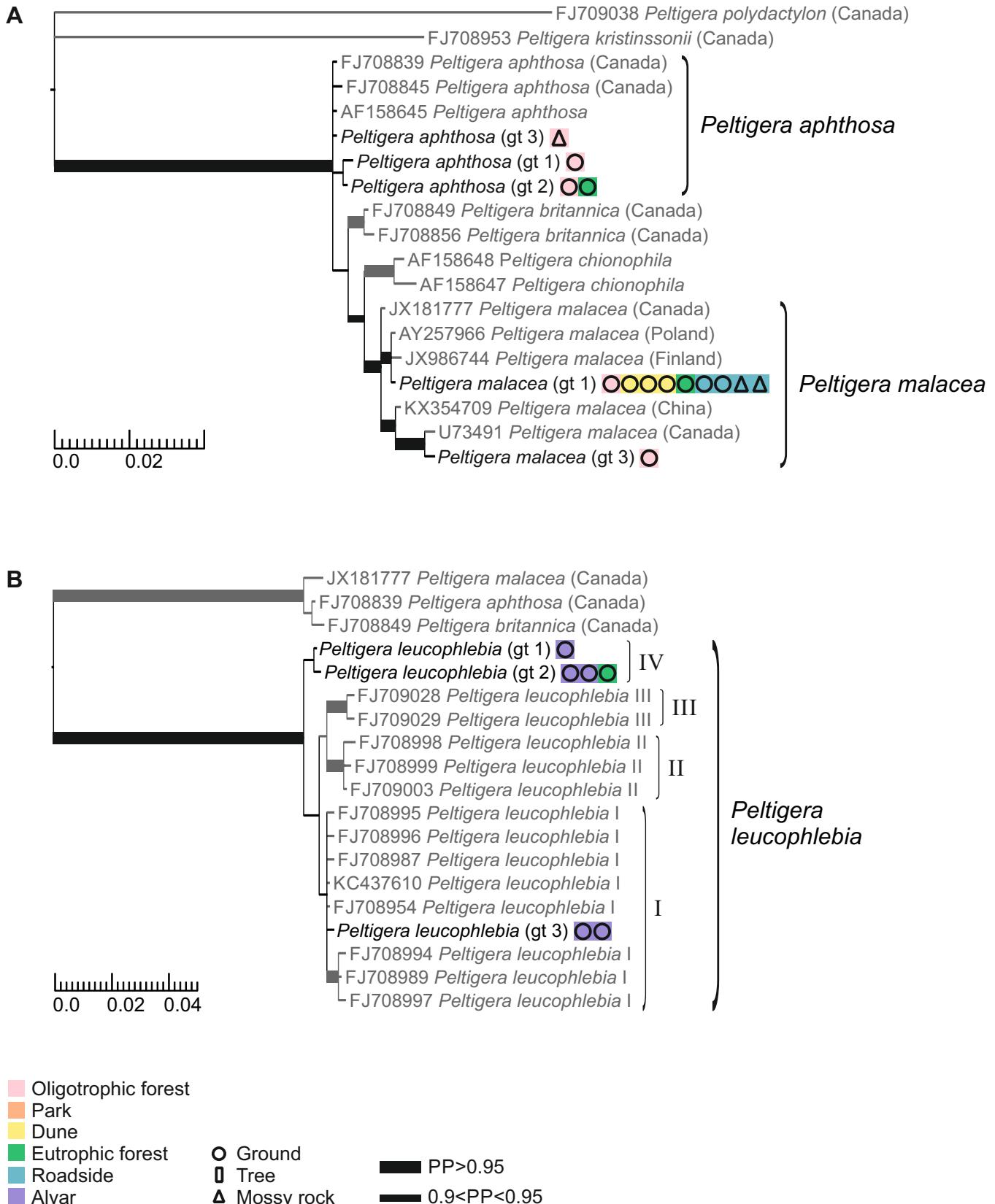


Figure S2. Phylogeny constructed of the ITS-sequences of the *Peltigera* section A) *Peltidea* and B) *Chloropeltigera*. The support for each clade is reflected in the thickness of the branch. Each square represents a specimen of the respective genotype indicating the habitat (color) and substrate (symbol). Grey specimens are not from Estonia but downloaded from the NCBI GeneBank.

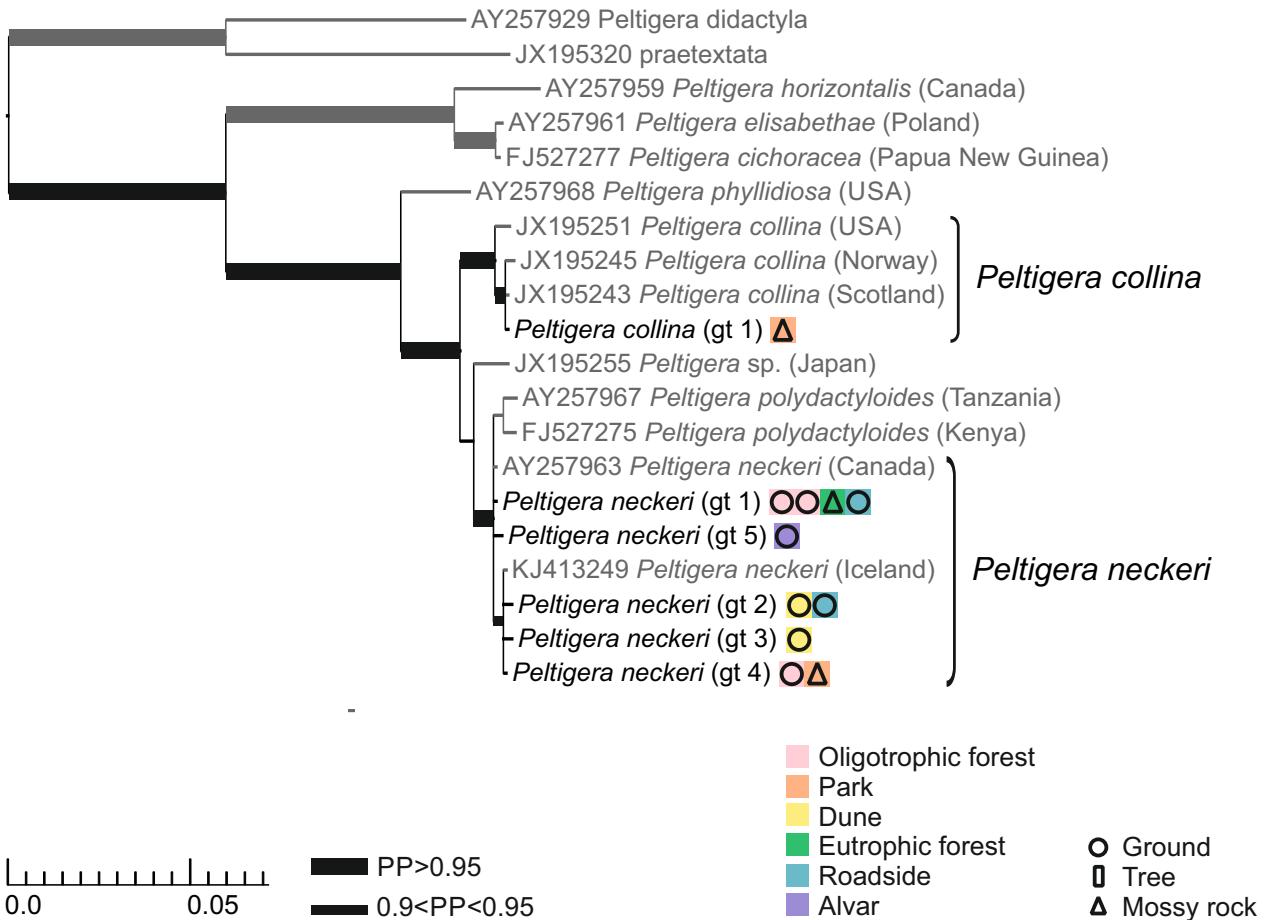
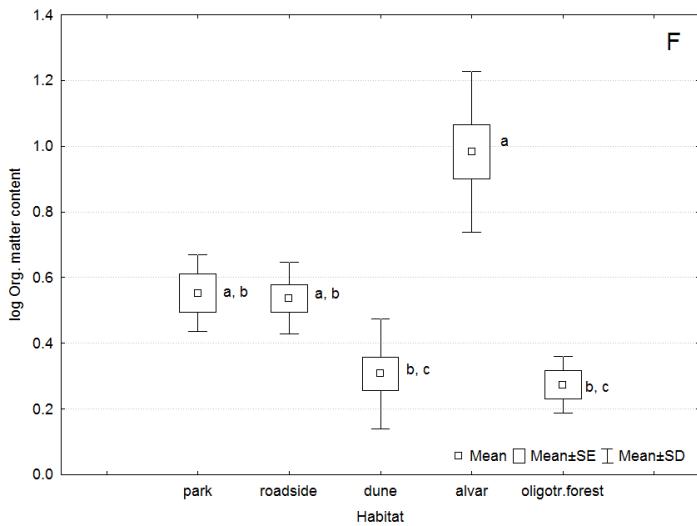
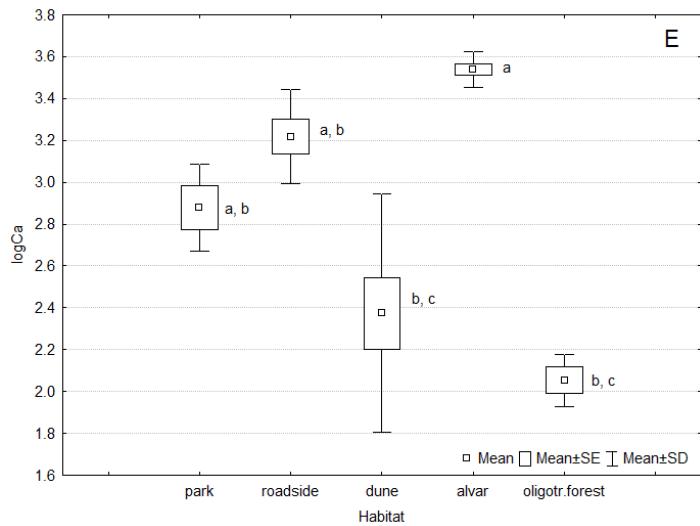
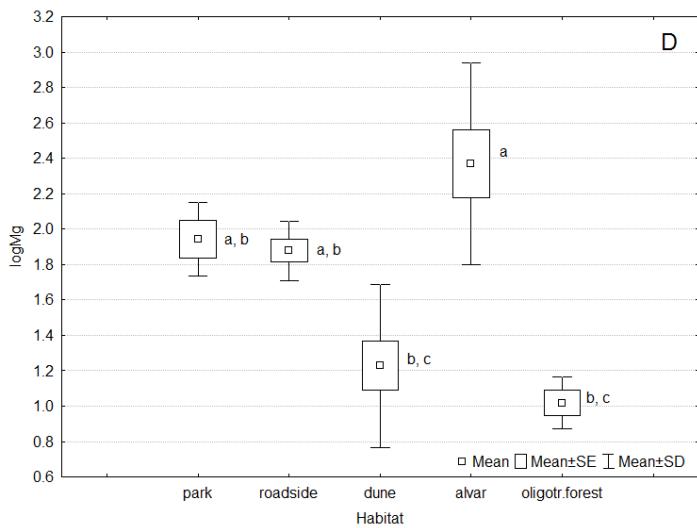
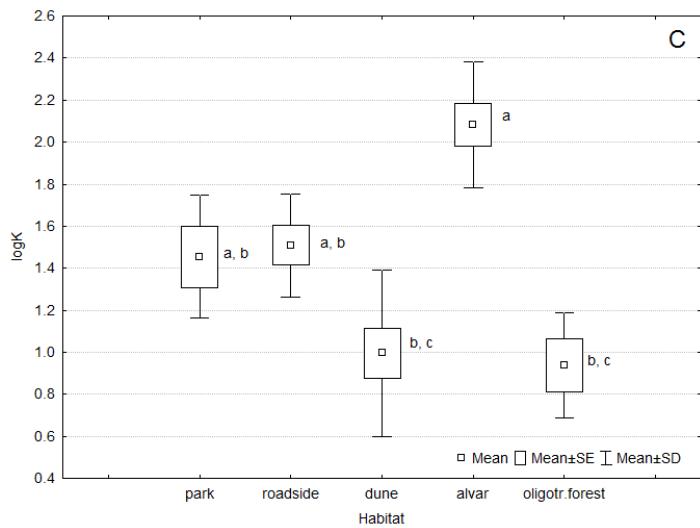
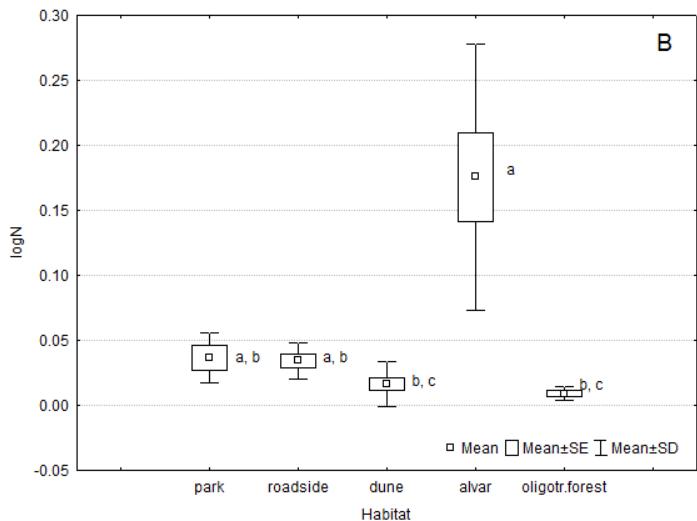
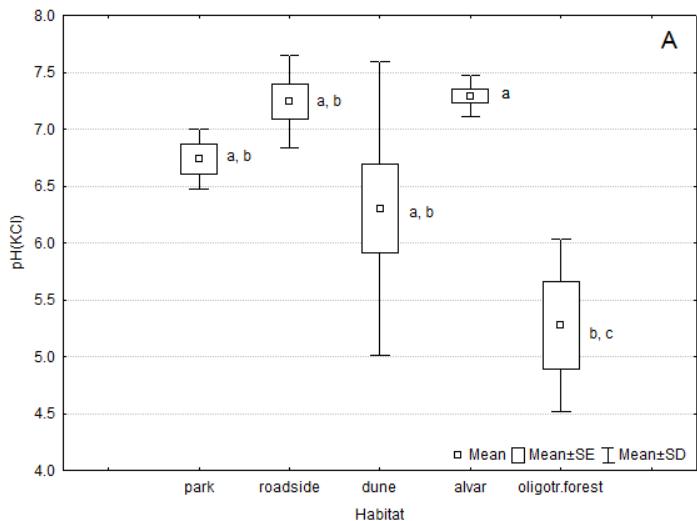
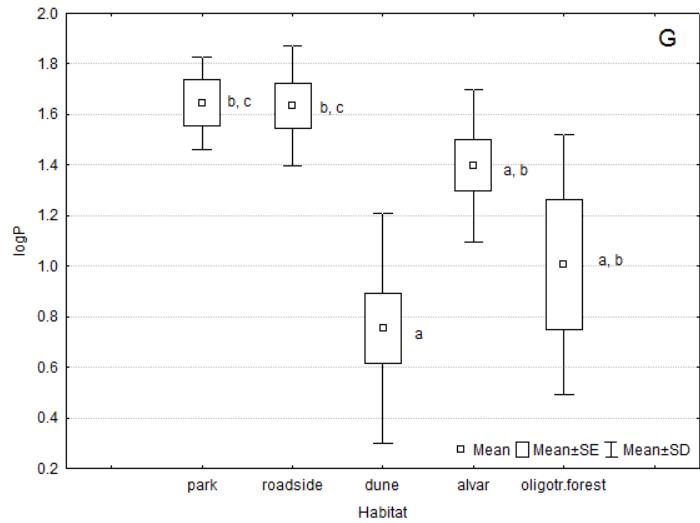


Figure S3. Phylogeny constructed of the ITS-sequences of the *Peltigera* section *Horizontales*. The support for each clade is reflected in the thickness of the branch. Each square represents a specimen of the respective genotype indicating the habitat (color) and substrate (symbol). Grey specimens are not from Estonia but downloaded from the NCBI GeneBank.





**Figure S4A–G.** Mean values of pH soil, N, K, Mg, Ca, K and P organic matter content of studied habitat types. Kruskal-Wallis test for soil pH (**A**)  $H (4, N = 35) = 11.293, p = 0.0023$ ; for soil N (**B**)  $H = 25.685, p < 0.0001$ ; for soil K (**C**)  $H (4, N = 35) = 25.126, p < 0.0001$ ; for soil Mg (**D**)  $H (4, N = 35) = 22.253, p = 0.0002$ ; for soil Ca (**E**)  $H (4, N = 35) = 27.814, p < 0.0001$ ; organic matter (**F**)  $H (4, N = 35) = 25.597, p < 0.0001$  and P (**G**)  $H (4, N = 35) = 18.365, p = 0.001$ ). Homogeneity groups of multiple comparisons are presented with letters.

Electronic supplementary material: Fungal Ecology

Inga Jüriado, Ulla Kaasalainen and Jouko Rikkinen. Specialist taxa restricted to threatened habitats contribute significantly to the regional diversity of *Peltigera* (Lecanorales, Ascomycota) in Estonia.

Table S1. List of the *Peltigera* taxa found in Estonia; GenBank accession numbers and number of ITS clade according to the phylogenetic analyses (see Figures 1–3 and S1–S3). Information about collection site (county and locality in Estonia), substratum and habitat type, collector and specimen ID in TU (University of Tartu, Natural History Museum). Abbreviations: ‘C’ = county, ‘NP’ = national park, ‘LKA’, ‘MKA’ = nature reserves, ‘gr\_alvar’ = ground in alvars, ‘gr\_park’ = ground in park stands, ‘gr\_oligotr’ = ground in oligotrophic forests, ‘gr\_road’ = ground in roadside grasslands, ‘gr\_dune’ = ground on dunes, ‘gr\_eutr’ = ground in eutrophic forests, ‘ro\_eutr’ = rocks in eutrophic forests, ‘ro\_park’ = rocks in park stands, ‘tr\_eutr’ = trees in eutrophic forests.

GenBank accession no	Taxa	Clade	County /Locality	Substratum /Habitat	Collector / Specimen ID
<u>LT852805</u>	<i>Peltigera aphthosa</i>		Põlva C., Ihamaru LKA	gr_oligotr	E. Oja
<u>LT852806</u>	<i>Peltigera aphthosa</i>		Valga C., Otepää Parish	gr_oligotr	V. Liiv (TU73090)
<u>LT852807</u>	<i>Peltigera canina</i>	I	Võru C., Hargla	gr_eutr	I. Jüriado
<u>LT852808</u>	<i>Peltigera canina</i>	I	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852809</u>	<i>Peltigera canina</i>	I	Võru C., Võru	gr_road	I. Jüriado
<u>LT852810</u>	<i>Peltigera canina</i>	I	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852811</u>	<i>Peltigera canina</i>	I	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852812</u>	<i>Peltigera canina</i>	I	Ida-Viru C., Rannapungerja	gr_oligotr	I. Jüriado
<u>LT852813</u>	<i>Peltigera canina</i>	I	Ida-Viru C., Rannapungerja	gr_oligotr	I. Jüriado
<u>LT852814</u>	<i>Peltigera canina</i>	I	Ida-Viru C., Lohusuu	gr_oligotr	I. Jüriado
<u>LT852815</u>	<i>Peltigera canina</i>	I	Ida-Viru C., Lohusuu	gr_oligotr	I. Jüriado
<u>LT852816</u>	<i>Peltigera canina</i>	II	Võru C., Hargla	gr_park	I. Jüriado

<u>LT852817</u>	<i>Peltigera canina</i>	II	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852818</u>	<i>Peltigera canina</i>	II	Tartu C., Järveselja	ro_park	I. Jüriado
<u>LT852819</u>	<i>Peltigera canina</i>	II	Tartu C., Järveselja	gr_road	I. Jüriado
<u>LT852820</u>	<i>Peltigera canina</i>	II	Tartu C., Järveselja	gr_road	I. Jüriado
<u>LT852821</u>	<i>Peltigera canina</i>	II	Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado
<u>LT852822</u>	<i>Peltigera canina</i>	II	Pärnu C., Kihnu	gr_eutr	A. Suija
<u>LT852823</u>	<i>Peltigera canina</i>	II	Põlva C., Ihamaru LKA	tr_eutr	E. Oja
<u>LT852824</u>	<i>Peltigera canina</i>	II	Hiiu C., Tõnupsi	gr_dune	M.-L. Kämärä
<u>LT852825</u>	<i>Peltigera canina</i>	II	Ida-Viru., Lohusuu	gr_oligotr	I. Jüriado
<u>LT852826</u>	<i>Peltigera canina</i>	II	Lääne-Viru C., Lahemaa NP, Karula	ro_eutr	I. Jüriado (TU58785)
<u>LT852827</u>	<i>Peltigera canina</i>	II	Ida-Viru C., Puhatu LKA	tr_eutr	A. Suija (TU39796)
<u>LT852828</u>	<i>Peltigera canina</i>	III	Võru C., Vastse-Roosa	gr_oligotr	I. Jüriado
<u>LT852829</u>	<i>Peltigera canina</i>	III	Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852830</u>	<i>Peltigera canina</i>	III	Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852831</u>	<i>Peltigera canina</i>	III	Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852832</u>	<i>Peltigera canina</i>	III	Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852833</u>	<i>Peltigera canina</i>	III	Saare C., Harilaid	gr_dune	I. Jüriado
<u>LT852834</u>	<i>Peltigera canina</i>	III	Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT852835</u>	<i>Peltigera canina</i>	III	Tartu C., Võnnu	ro_park	I. Jüriado
<u>LT852836</u>	<i>Peltigera canina</i>	III	Tartu C., Võnnu	ro_park	I. Jüriado
<u>LT852837</u>	<i>Peltigera canina</i>	III	Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado

<u>LT852838</u>	<i>Peltigera canina</i>	III	Saare C., Kihnu	gr_eutr	A. Suija
<u>LT852839</u>	<i>Peltigera canina</i>	III	Saare C., Kihnu	gr_eutr	P. Degtjarenko
<u>LT852840</u>	<i>Peltigera canina</i>	III	Hiiu C., Luidja	gr_dune	M.-L. Kämärä
<u>LT852841</u>	<i>Peltigera canina</i>	III	Saare C., Kiipsaare	gr_dune	M.-L. Kämärä
<u>LT852842</u>	<i>Peltigera canina</i>	III	Hiiu C., Tõnupsi	gr_dune	M.-L. Kämärä
<u>LT852843</u>	<i>Peltigera canina</i>	III	Rapla C., Pakamägi	tr_eutr	E. Oja
<u>LT852844</u>	<i>Peltigera canina</i>	III	Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT852845</u>	<i>Peltigera canina</i>	III	Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT852846</u>	<i>Peltigera canina</i>	III	Ida-Viru C., Smolnitsa MK	tr_eutr	I. Jüriado (TU46221)
<u>LT852847</u>	<i>Peltigera canina</i>	III	Ida-Viru C., Agusalu MKA	tr_eutr	A. Suija (TU39795)
<u>LT852848</u>	<i>Peltigera canina</i>	III	Põlva C., Suur-Taevaskoda	ro_eutr	T. Randlane
<u>LT852849</u>	<i>Peltigera islandica</i>		Tartu C., Kambja Parish, Sulu village	gr_road	I. Jüriado
<u>LT852850</u>	<i>Peltigera collina</i>		Saare C., Väike-Rahula	ro_park	I. Jüriado (TU45667)
<u>LT852851</u>	<i>Peltigera degenii</i>		Lääne-Viru C., Lahemaa NP, Palmse	ro_park	I. Jüriado (TU58786)
<u>LT852852</u>	<i>Peltigera degenii</i>		Harju C., Lahemaa NP, Kalme	gr_eutr	A. Suija (TU45213)
<u>LT852853</u>	<i>Peltigera degenii</i>		Lääne-Viru C., Lahemaa NP, Palmse	ro_park	T. Randlane
<u>LT852854</u>	<i>Peltigera didactyla</i>	I	Võru C., Vastse-Roosa	gr_oligotr	I. Jüriado
<u>LT852855</u>	<i>Peltigera didactyla</i>	I	Ida-Viru C., Kauksi	gr_dune	I. Jüriado
<u>LT852856</u>	<i>Peltigera didactyla</i>	I	Ida-Viru C., Kauksi	gr_dune	I. Jüriado
<u>LT852857</u>	<i>Peltigera didactyla</i>	I	Ida-Viru C., Alajõe	gr_park	J. Liira
<u>LT852858</u>	<i>Peltigera didactyla</i>	II	Saare C., Harilaid	gr_dune	I. Jüriado

<u>LT852859</u>	<i>Peltigera didactyla</i>	II	Hiiu C., Luidja	gr_dune	M.-L. Kämärä
<u>LT852860</u>	<i>Peltigera didactyla</i>	II	Ida-Viru C., Kauksi	gr_dune	I. Jüriado
<u>LT852861</u>	<i>Peltigera didactyla</i>	II	Valga C., Soontaga LKA	tr_eutr	E. Oja
<u>LT852862</u>	<i>Peltigera didactyla</i>	II	Põlva C., Väike-Taevaskoja	ro_eutr	T. Randlane
<u>LT852863</u>	<i>Peltigera didactyla</i>	II	Põlva C., Ihamaru LKA	tr_eutr	E. Oja
<u>LT852864</u>	<i>Peltigera didactyla</i>	III	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852865</u>	<i>Peltigera didactyla</i>	III	Saare C., Harilaid	gr_dune	I. Jüriado
<u>LT852866</u>	<i>Peltigera didactyla</i>	III	Saare C., Harilaid	gr_dune	I. Jüriado
<u>LT852867</u>	<i>Peltigera extenuata</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT852868</u>	<i>Peltigera extenuata</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT852869</u>	<i>Peltigera extenuata</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT852870</u>	<i>Peltigera extenuata</i>		Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT852871</u>	<i>Peltigera extenuata</i>		Hiiu C., Tõrvanina	gr_dune	M.-L. Kämärä
<u>LT852872</u>	<i>Peltigera extenuata</i>		Hiiu C., Tõrvanina	gr_dune	M.-L. Kämärä
<u>LT852873</u>	<i>Peltigera extenuata</i>		Hiiu C., Tõrvanina	gr_dune	M.-L. Kämärä
<u>LT852874</u>	<i>Peltigera fuscoponojensis</i>		Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852875</u>	<i>Peltigera fuscoponojensis</i>		Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852876</u>	<i>Peltigera fuscoponojensis</i>		Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852877</u>	<i>Peltigera fuscoponojensis</i>		Saare C., Karala	gr_dune	I. Jüriado
<u>LT852878</u>	<i>Peltigera fuscoponojensis</i>		Saare C., Katri	gr_alvar	I. Jüriado
<u>LT852879</u>	<i>Peltigera fuscoponojensis</i>		Tartu C., Melliste	gr_road	I. Jüriado

<u>LT852880</u>	<i>Peltigera fuscoponojensis</i>		Lääne-Viru C., Lahemaa NP, Käsmu	gr_eutr	T. Randlane
<u>LT852881</u>	<i>Peltigera hymenina</i>		Pärnu C., Häädemeeste	gr_eutr	I. Jüriado
<u>LT852882</u>	<i>Peltigera hymenina</i>		Hiiu C., Tõrvanina	gr_dune	M.-L. Kämärä
<u>LT852883</u>	<i>Peltigera hymenina</i>		Lääne-Viru C., Lahemaa NP, Vihula Parish	ro_eutr	I. Jüriado (TU71624)
<u>LT852884</u>	<i>Peltigera lepidophora</i>		Rapla C., Lipstu	gr_eutr	I. Jüriado, A. Suija (TU66438)
<u>LT852885</u>	<i>Peltigera lepidophora</i>		Jõgeva C., Sopimetsa LKA	gr_alvar	A. Suija (TU45690)
<u>LT852886</u>	<i>Peltigera leucophlebia</i>	IV	Rapla C., Tõrma	gr_alvar	A. Suija (TU42656)
<u>LT852887</u>	<i>Peltigera malacea</i>		Saare C., Odalätsi	gr_dune	I. Jüriado
<u>LT852888</u>	<i>Peltigera malacea</i>		Saare C., Odalätsi	gr_dune	I. Jüriado
<u>LT852889</u>	<i>Peltigera malacea</i>		Saare C., Odalätsi	gr_dune	I. Jüriado
<u>LT852890</u>	<i>Peltigera malacea</i>		Harju C., Lahemaa NP, Kaberneeme	gr_eutr	A. Suija
<u>LT852891</u>	<i>Peltigera malacea</i>		Järva C., Kahala	ro_road	A. Suija
<u>LT852892</u>	<i>Peltigera malacea</i>		Järva C., Koigi Parish	ro_road	A. Suija (TU75719)
<u>LT852893</u>	<i>Peltigera malacea</i>		Harju C., Väike-Pakri	gr_road	E. Leppik, A. Suija (TU67659)
<u>LT852894</u>	<i>Peltigera malacea</i>		Põlva C., Piusa	gr_oligotr	A. Suija (TU68244)
<u>LT852895</u>	<i>Peltigera malacea</i>		Tartu C., Lohkva	gr_road	T. Randlane
<u>LT852896</u>	<i>Peltigera membranacea</i>		Lääne-Viru C., Lahemaa NP, Mohni	gr_eutr	I. Jüriado (TU58684)
<u>LT852897</u>	<i>Peltigera membranacea</i>		Lääne-Viru C., Lahemaa NP, Mohni	gr_eutr	I. Jüriado (TU58678)
<u>LT852898</u>	<i>Peltigera membranacea</i>		Lääne-Viru C., Lahemaa NP, Mohni	gr_eutr	I. Jüriado (TU58679)
<u>LT852899</u>	<i>Peltigera membranacea</i>		Lääne-Viru C., Lahemaa NP, Mohni	ro_eutr	I. Jüriado (TU58685)

<u>LT852900</u>	<i>Peltigera neckeri</i>		Võru C., Vastse-Roosa	gr_oligotr	I. Jüriado
<u>LT852901</u>	<i>Peltigera neckeri</i>		Võru C., Vastse-Roosa	gr_oligotr	I. Jüriado
<u>LT852902</u>	<i>Peltigera neckeri</i>		Võru C., Vastse-Roosa	gr_oligotr	I. Jüriado
<u>LT852903</u>	<i>Peltigera neckeri</i>		Lääne C., Noarootsi Parish, Põõsaspea	gr_road	T. Randlane
<u>LT852904</u>	<i>Peltigera neckeri</i>		Tartu C., Kambja Parish, Sulu village	gr_road	I. Jüriado
<u>LT852905</u>	<i>Peltigera neckeri</i>		Saare C., Kiipsaare	gr_dune	M.-L. Kämärä
<u>LT852906</u>	<i>Peltigera neckeri</i>		Lääne C., Keibu	gr_dune	M.-L. Kämärä
<u>LT852907</u>	<i>Peltigera neckeri</i>		Lääne C., Osmussaar	gr_road	I. Jüriado, A. Suija (TU55488)
<u>LT852908</u>	<i>Peltigera neckeri</i>		Hiiu C., Sarve MKA	gr_alvar	E. Leppik, I. Jüriado (TU55487)
<u>LT852909</u>	<i>Peltigera neckeri</i>		Jõgeva C., Josua	ro_eutr	T. Randlane
<u>LT852910</u>	<i>Peltigera neocanina</i>		Võru C., Hargla	gr_eutr	I. Jüriado
<u>LT852911</u>	<i>Peltigera neocanina</i>		Võru C., Hargla	gr_eutr	I. Jüriado
<u>LT852912</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Lasila	tr_eutr	I. Jüriado
<u>LT852913</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Lasila	tr_eutr	I. Jüriado
<u>LT852914</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado
<u>LT852915</u>	<i>Peltigera aff. neocanina</i>		Rapla C., Lokuta	ro_eutr	E. Oja
<u>LT852916</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado
<u>LT852917</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Lasila	tr_eutr	I. Jüriado
<u>LT852918</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., NP, Mohni	gr_eutr	I. Jüriado (TU58683)
<u>LT852919</u>	<i>Peltigera aff. neocanina</i>		Lääne-Viru C., Lahemaa NP, Palmse	ro_park	T. Randlane
<u>LT852920</u>	<i>Peltigera aff. neocanina</i>		Põlva C., Taevaskoja	ro_eutr	T. Randlane

<u>LT852921</u>	<i>Peltigera neopolydactyla</i>		Ida-Viru C., Muraka LKA	tr_eutr	P. Lõhmus (TU47418)
<u>LT852922</u>	<i>Peltigera neorufescens</i>		Võru C., Võru	gr_road	I. Jüriado
<u>LT852923</u>	<i>Peltigera neorufescens</i>		Võru C., Võru	gr_road	I. Jüriado
<u>LT852924</u>	<i>Peltigera neorufescens</i>		Lääne C., Sillukse	gr_alvar	I. Jüriado
<u>LT852925</u>	<i>Peltigera neorufescens</i>		Lääne C., Sillukse	gr_alvar	I. Jüriado
<u>LT852926</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Nõmmküla	gr_alvar	I. Jüriado
<u>LT852927</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Tupenurme	gr_alvar	I. Jüriado
<u>LT852928</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Tupenurme	gr_alvar	I. Jüriado
<u>LT852929</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Tupenurme	gr_alvar	I. Jüriado
<u>LT852930</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852931</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852932</u>	<i>Peltigera neorufescens</i>		Saare C., Katri	gr_alvar	I. Jüriado
<u>LT852933</u>	<i>Peltigera neorufescens</i>		Saare C., Tammese	gr_alvar	I. Jüriado
<u>LT852934</u>	<i>Peltigera neorufescens</i>		Saare C., Atla	gr_alvar	I. Jüriado
<u>LT852935</u>	<i>Peltigera neorufescens</i>		Saare C., Atla	gr_alvar	I. Jüriado
<u>LT852936</u>	<i>Peltigera neorufescens</i>		Saare C., Lõo	gr_alvar	I. Jüriado
<u>LT852937</u>	<i>Peltigera neorufescens</i>		Saare C., Lõo	gr_alvar	I. Jüriado
<u>LT852938</u>	<i>Peltigera neorufescens</i>		Saare C., Lõo	gr_alvar	I. Jüriado
<u>LT852939</u>	<i>Peltigera neorufescens</i>		Tartu C., Melliste	gr_road	I. Jüriado
<u>LT852940</u>	<i>Peltigera neorufescens</i>		Saare C., Kaugatoma	gr_alvar	I. Jüriado
<u>LT852941</u>	<i>Peltigera neorufescens</i>		Saare C., Atla	gr_alvar	I. Jüriado

<u>LT852942</u>	<i>Peltigera neorufescens</i>		Saare C., Atla	gr_alvar	I. Jüriado
<u>LT852943</u>	<i>Peltigera neorufescens</i>		Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852944</u>	<i>Peltigera neorufescens</i>		Saare C., Eeriksaare	gr_dune	I. Jüriado
<u>LT852945</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852946</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852947</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852948</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852949</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Tupenurme	gr_alvar	I. Jüriado
<u>LT852950</u>	<i>Peltigera neorufescens</i>		Saare C., Muhu, Tupenurme	gr_alvar	I. Jüriado
<u>LT852951</u>	<i>Peltigera neorufescens</i> agg.	I	Pärnu C., Kilingi-Nõmme	gr_road	I. Jüriado
<u>LT852952</u>	<i>Peltigera neorufescens</i> agg.	I	Harju C., Pakri peninsula	ro_road	T. Randlane
<u>LT852953</u>	<i>Peltigera neorufescens</i> agg.	II	Pärnu C., Kilingi-Nõmme	gr_road	I. Jüriado
<u>LT852954</u>	<i>Peltigera neorufescens</i> agg.	II	Pärnu C., Kilingi-Nõmme	gr_road	I. Jüriado
<u>LT852955</u>	<i>Peltigera neorufescens</i> agg.	II	Tartu C., Nõgiaru	gr_park	T. Randlane
<u>LT852956</u>	<i>Peltigera neorufescens</i> agg.	II	Hiiu C., Tõrvanina	gr_dune	M.-L. Kämärä
<u>LT852957</u>	<i>Peltigera neorufescens</i> agg.	II	Ida-Viru C., Rannapungerja	gr_park	I. Jüriado
<u>LT852958</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852959</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Tammese	gr_alvar	I. Jüriado
<u>LT852960</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Atla	gr_alvar	I. Jüriado
<u>LT852961</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Tammese	gr_alvar	I. Jüriado
<u>LT852962</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Atla	gr_alvar	I. Jüriado

<u>LT852963</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Atla	gr_alvar	I. Jüriado
<u>LT852964</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852965</u>	<i>Peltigera neorufescens</i> agg.	III	Saare C., Muhu, Üügu	gr_alvar	I. Jüriado
<u>LT852966</u>	<i>Peltigera polydactylon</i>		Tartu C., Järveselja	gr_eutr	I. Jüriado
<u>LT852967</u>	<i>Peltigera polydactylon</i>		Tartu C., Järveselja	gr_eutr	I. Jüriado
<u>LT852968</u>	<i>Peltigera polydactylon</i>		Tartu C., Järveselja	gr_eutr	I. Jüriado
<u>LT852969</u>	<i>Peltigera polydactylon</i>		Tartu C., Järveselja	tr_eutr	I. Jüriado
<u>LT852970</u>	<i>Peltigera polydactylon</i>		Tartu C., Järveselja	tr_eutr	I. Jüriado
<u>LT852971</u>	<i>Peltigera polydactylon</i>		Tartu C., Välggi LKA	tr_eutr	E. Oja
<u>LT852972</u>	<i>Peltigera polydactylon</i>		Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT852973</u>	<i>Peltigera polydactylon</i>		Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT852974</u>	<i>Peltigera polydactylon</i>		Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT852975</u>	<i>Peltigera polydactylon</i>		Pärnu C., Vihtra	tr_eutr	J. Liira
<u>LT852976</u>	<i>Peltigera polydactylon</i>		Ida-Viru C., Agusalu MKA	tr_eutr	E. Oja
<u>LT852977</u>	<i>Peltigera polydactylon</i>		Põlva C., Ihamaru LKA	tr_eutr	E. Oja
<u>LT852978</u>	<i>Peltigera polydactylon</i>		Ida-Viru C., Puhatu LKA	tr_eutr	L. Marmor (TU39232)
<u>LT852979</u>	<i>Peltigera polydactylon</i>		Ida-Viru C., Puhatu LKA	tr_eutr	A. Suija (TU39798)
<u>LT852980</u>	<i>Peltigera polydactylon</i>		Lääne-Viru C., Lahemaa NP, Palmse	tr_eutr	T. Randlane
<u>LT852981</u>	<i>Peltigera ponjensis</i>	I	Võru C., Võru	gr_road	I. Jüriado
<u>LT852982</u>	<i>Peltigera ponjensis</i>	I	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852983</u>	<i>Peltigera ponjensis</i>	I	Viljandi C., Kõpu	gr_road	I. Jüriado

<u>LT852984</u>	<i>Peltigera ponojensis</i>	I	Saare C., Karala	gr_dune	I. Jüriado
<u>LT852985</u>	<i>Peltigera ponojensis</i>	I	Saare C., Karala	gr_dune	I. Jüriado
<u>LT852986</u>	<i>Peltigera ponojensis</i>	I	Saare C., Pidula	gr_dune	I. Jüriado
<u>LT852987</u>	<i>Peltigera ponojensis</i>	I	Pärnu C., Rannametsa	gr_road	I. Jüriado
<u>LT852988</u>	<i>Peltigera ponojensis</i>	I	Pärnu C., Rannametsa	gr_road	I. Jüriado
<u>LT852989</u>	<i>Peltigera ponojensis</i>	II	Võru C., Hargla	gr_park	I. Jüriado
<u>LT852990</u>	<i>Peltigera ponojensis</i>	II	Saare C., Järve	gr_dune	I. Jüriado
<u>LT852991</u>	<i>Peltigera ponojensis</i>	II	Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT852992</u>	<i>Peltigera ponojensis</i>	II	Pärnu C., Rannametsa	gr_road	I. Jüriado
<u>LT852993</u>	<i>Peltigera ponojensis</i>	II	Saare C., Pidula	gr_dune	M.-L. Kämärä
<u>LT852994</u>	<i>Peltigera ponojensis</i>	II	Ida-Viru C., Raadna	gr_road	I. Jüriado
<u>LT852995</u>	<i>Peltigera ponojensis</i>	II	Ida-Viru C., Raadna	gr_road	I. Jüriado
<u>LT852996</u>	<i>Peltigera praetextata</i>		Viljandi C., Köpu	ro_park	I. Jüriado
<u>LT852997</u>	<i>Peltigera praetextata</i>		Tartu C., Järvelja	tr_eutr	I. Jüriado
<u>LT852998</u>	<i>Peltigera praetextata</i>		Tartu C., Järvelja	tr_eutr	I. Jüriado
<u>LT852999</u>	<i>Peltigera praetextata</i>		Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado
<u>LT853000</u>	<i>Peltigera praetextata</i>		Lääne-Viru C., Suurekivi	tr_eutr	I. Jüriado
<u>LT853001</u>	<i>Peltigera praetextata</i>		Tartu C., Elva-Vitipalu MKA	tr_eutr	E. Oja
<u>LT853002</u>	<i>Peltigera praetextata</i>		Ida-Viru C., Muraka LKA	tr_eutr	E. Oja
<u>LT853003</u>	<i>Peltigera praetextata</i>		Harju C., Väike-Pakri	ro_eutr	A. Suija (TU42658)
<u>LT853004</u>	<i>Peltigera rufescens</i>		Võru C., Hargla	gr_park	I. Jüriado

<u>LT853005</u>	<i>Peltigera rufescens</i>		Võru C., Hargla	gr_park	I. Jüriado
<u>LT853006</u>	<i>Peltigera rufescens</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT853007</u>	<i>Peltigera rufescens</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT853008</u>	<i>Peltigera rufescens</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT853009</u>	<i>Peltigera rufescens</i>		Võru C., Varstu Parish, Singa	gr_oligotr	I. Jüriado
<u>LT853010</u>	<i>Peltigera rufescens</i>		Võru C., Võru	gr_road	I. Jüriado
<u>LT853011</u>	<i>Peltigera rufescens</i>		Lääne C., Hanila	gr_road	I. Jüriado
<u>LT853012</u>	<i>Peltigera rufescens</i>		Lääne C., Hanila	gr_road	I. Jüriado
<u>LT853013</u>	<i>Peltigera rufescens</i>		Saare C., Järve	gr_dune	I. Jüriado
<u>LT853014</u>	<i>Peltigera rufescens</i>		Saare C., Järve	gr_dune	I. Jüriado
<u>LT853015</u>	<i>Peltigera rufescens</i>		Saare C., Pidula	gr_dune	I. Jüriado
<u>LT853016</u>	<i>Peltigera rufescens</i>		Saare C., Pidula	gr_dune	I. Jüriado
<u>LT853017</u>	<i>Peltigera rufescens</i>		Saare C., Pidula	gr_dune	I. Jüriado
<u>LT853018</u>	<i>Peltigera rufescens</i>		Saare C., Pidula	gr_dune	I. Jüriado
<u>LT853019</u>	<i>Peltigera rufescens</i>		Saare C., Katri	gr_alvar	I. Jüriado
<u>LT853020</u>	<i>Peltigera rufescens</i>		Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT853021</u>	<i>Peltigera rufescens</i>		Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT853022</u>	<i>Peltigera rufescens</i>		Pärnu C., Rannametsa	gr_oligotr	I. Jüriado
<u>LT853023</u>	<i>Peltigera rufescens</i>		Saare C., Pidula	gr_dune	M.-L. Kämärä
<u>LT853024</u>	<i>Peltigera rufescens</i>		Ida-Viru C., Kauksi	gr_dune	I. Jüriado
<u>LT853025</u>	<i>Peltigera rufescens</i>		Ida-Viru C., Kauksi	gr_dune	I. Jüriado

<u>LT853026</u>	<i>Peltigera rufescens</i>		Ida-Viru C., Kauksi	gr_dune	I. Jüriado
<u>LT853027</u>	<i>Peltigera rufescens</i>		Ida-Viru C., Raadna	gr_road	I. Jüriado
<u>LT853028</u>	<i>Peltigera rufescens</i>		Ida-Viru C., Lohusuu	gr_oligotr	I. Jüriado
<u>LT853029</u>	<i>Peltigera rufescens</i>		Tartu C., Rõngu	ro_park	T. Randlane
<u>LT853030</u>	<i>Peltigera rufescens</i>		Harju C., Lahemaa NP, Kaberneeme	ro_road	A. Suija
<u>LT853031</u>	<i>Peltigera leucophlebia</i>	I	Hiiu C., Kadakalaid	gr_alvar	I. Jüriado, A. Suija (TU29593)
<u>LT853032</u>	<i>Peltigera leucophlebia</i>	I	Harju C., Suur-Pakri	gr_alvar	E. Leppik, A. Suija (TU67862)
<u>LT853033</u>	<i>Peltigera leucophlebia</i>	IV	Lääne-Viru C., Varangu	gr_eutr	M. Leis (TU36673)
<u>LT853034</u>	<i>Peltigera leucophlebia</i>	IV	Hiiu C., Vohilaid	gr_alvar	I. Jüriado, A. Suija (TU29124)
<u>LT853035</u>	<i>Peltigera leucophlebia</i>	IV	Saare C., Paadla	gr_alvar	E. Oja
<u>LT853036</u>	<i>Peltigera aphthosa</i>		Lääne-Viru C., Lahemaa NP, Käsmu peninsula	ro_oligotr	A. Suija (TU45233)
<u>LT853037</u>	<i>Peltigera aphthosa</i>		Harju C., Põhja-Kõrvemaa, Paukjärve	gr_oligotr	A. Palo
<u>LT853038</u>	<i>Peltigera malacea</i>		Harju C., Põhja-Kõrvemaa, Paukjärve	gr_oligotr	A. Palo
<u>LT853039</u>	<i>Peltigera polydactylon</i>		Põlva C., Ihamaru LKA	tr_eutr	E. Oja
<u>LT853040</u>	<i>Peltigera polydactylon</i>		Tartu C., Padakörve LKA	tr_eutr	E. Oja
<u>LT853041</u>	<i>Peltigera canina</i>	III	Ida-Viru C., Muraka LKA, Kaukavere	gr_eutr	P. Lõhmus (TU47639)
<u>LT853042</u>	<i>Peltigera canina</i>	II	Pärnu C., Kihnu	gr_road	P. Degtjarenko
<u>LT853043</u>	<i>Peltigera canina</i>	II	Järva C., Kolu	tr_eutr	E. Oja
<u>LT853044</u>	<i>Peltigera canina</i>	II	Tartu C., Välgi LKA	tr_eutr	E. Oja
<u>LT853045</u>	<i>Peltigera canina</i>	II	Tartu C., Järveselja	gr_park	T. Randlane

<u>LT853046</u>	<i>Peltigera canina</i>	III	Saare C., Muhu, Koguva	ro_road	I. Jüriado
<u>LT853047</u>	<i>Peltigera canina</i>	III	Põlva C., Valgesoo	gr_oligotr	P. Degtjarenko
<u>LT853048</u>	<i>Peltigera canina</i>	III	Võru C., Karisöödi	tr_eutr	A. Palo
<u>LT853049</u>	<i>Peltigera canina</i>	III	Saare C., Korese	alvar	E. Oja
<u>LT853050</u>	<i>Peltigera praetextata</i>		Põlva C., Ihamaru LKA	tr_eutr	E. Oja
<u>LT853051</u>	<i>Peltigera praetextata</i>		Tartu C., Järvselja	gr_road	I. Jüriado
<u>LT853052</u>	<i>Peltigera praetextata</i>		Lääne C., Puhtu	tr_eutr	I. Jüriado
<u>LT853053</u>	<i>Peltigera praetextata</i>		Lääne-Viru C., Kunda	tr_eutr	A. Palo
<u>LT853054</u>	<i>Peltigera praetextata</i>		Lääne-Viru C., Padaorg	tr_eutr	A. Palo
<u>LT853055</u>	<i>Peltigera ponogensis</i>	II	Pärnu C., Häädemeeste	gr_road	I. Jüriado
<u>LT853056</u>	<i>Peltigera ponogensis</i>	I	Saare C., Korese	gr_alvar	E. Oja

Table S2. Alignment information, including both the newly generated sequences (each identical genotype included only once) and the sequences downloaded from the NCBI Genbank. Bare numbers were calculated by excluding the outgroup\* sequences; the numbers including the outgroup sequences are given in the parentheses. Variable sites include gaps as a fifth state.

<i>Peltigera</i> section	Number of sequences	Alignment length	Variable sites	*outgroup
<i>Peltidea</i>	17 (19)	571 (616)	63 (245)	FJ709038 <i>Peltigera polydactylon</i> , FJ708953 <i>P. kristinssonii</i>
<i>Horizontales</i>	18 (20)	668 (683)	199 (312)	AY257929 <i>Peltigera didactyla</i> , JX195320 <i>P. praetextata</i>
<i>Polydactylon</i>	40 (42)	714 (728)	323 (382)	KX897211 <i>Peltigera melanorrhiza</i> , KX897311 <i>P. scabrosa</i>
<i>Chloropeltigera</i>	16 (19)	532 (554)	38 (168)	FJ708839 <i>Peltigera aphthosa</i> , JX181777 <i>P. malacea</i> , FJ708849 <i>P. britannica</i>
<i>Peltigera</i> , group <i>canina</i>	50 (54)	679 (713)	282 (376)	AY257891 <i>Peltigera kristinssonii</i> , AY257893 <i>P. frigida</i> , AY257890 <i>P. continentalis</i> , KJ095107 <i>P. isidiofora</i>
<i>Peltigera</i> , group <i>rufescens</i>	96 (101)	764 (791)	462 (512)	AY257890 <i>Peltigera canina</i> , AY257955 <i>P. "neocanina"</i> , AY257980 <i>P. continentalis</i> , AY257891 <i>P. kristinssonii</i> , AY257893 <i>P. frigida</i>