Can changes in soil biochemistry and plant stoichiometry explain loss of animal diversity of heathlands?

J.J. Vogels [a,b,*], W.C.E.P. Verberk [b], L.P.M. Lamers [c], & H. Siepel [b,d]

[a] Bargerveen Foundation, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands
[b] Department of Animal Ecology and Physiology, Radboud University Nijmegen, The Netherlands
[c] Department of Aquatic Ecology and Environmental Biology, Radboud University Nijmegen, The Netherlands
[d] Plant Ecology and Nature Conservation Group, Wageningen University, The Netherlands

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ABSTRACT

Increased atmospheric deposition rates of nitrogen (N) and sulphur (S) are known to affect soil biogeochemistry and cause a decline in plant biodiversity of heathlands. Concomitant declines of heathland invertebrates are mainly attributed to changes in vegetation composition and altered habitat structure. While there may also be effects on animals through altered plant chemistry, these have received little attention up to now. Here, we remedy this by quantifying soil nutrient and acid buffering status, vegetation composition and structure, plant nutrient stoichiometry, and densities and species richness of Diptera and Carabidae in two large heathland systems. Soil acid buffering status appeared to be a key driver for plant P availability. Sod-cutting was found to further increase plant N:P ratios, suggesting increased P-limitation. Vegetation N:P ratio was negatively linked to invertebrate density and species richness, and was found to impact fauna more strongly than vegetation structure and plant species richness. The relationship between invertebrates and plant C:N ratio was weaker and less consistent, suggesting that for invertebrates, plant P is generally more limiting than N. Our results imply that the role of plant stoichiometry is underestimated in explaining declines of heathland invertebrates, and we here provide a novel mechanistic model including this pathway. Management should therefore not only focus on restoring habitat structural complexity, attention should be paid to restoring plant stoichiometry. This can be achieved through restoring biogeochemical soil conditions, especially by mitigating soil acidification, while measures solely focusing on removal of accumulated N by means of sod-cutting should be avoided.

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1. Introduction

Heathland landscapes in Northwest Europe are under considerable pressure from land use change (Diemont, 1996) and atmospheric pollution by nitrous oxides (NO_x), ammonia/ammonium (NH_y) and sulphur dioxide (SO_2) (Cowling, 1982; Elser, 2011), which greatly surpass the critical loads for these systems (Bobbink et al., 2010; Bobbink and Roelofs, 1995). High deposition of N and S compounds has strongly altered soil chemistry of heathlands and acidic grasslands, not only by increasing ammonium (NH_4^+) and nitrate (NO_3^-) availability, but also by accelerating soil acidification, which has resulted in increased mobilization of aluminium (Al) and the accumulation of NH_4^+ (Bobbink et al., 1998; Houdijk et al., 1993). As a result, vegetation has shifted towards grass dominance at the expense of herbaceous species (Bobbink et al., 1998; Bobbink and Roelofs, 1995; De Graaf et al., 1997; De Graaf et al., 1998; Heil and Bruggink, 1987; Heil and Diemont, 1983; Houdijk et al., 1993; Roelofs,

1986), with a concomitant overall loss of plant biodiversity (De Graaf et al., 2009; Kleijn et al., 2008; Roem et al., 2002). Restoration management of heathlands generally involves removal of the N-rich top layer (sod-cutting), to reduce the competitive advantage of fast-growing tall-grasses in favour of dwarf shrubs and herbaceous vegetation (Diemont, 1996).

The simultaneous decline of heathland animal diversity is commonly attributed to the loss of plant biodiversity and grass encroachment following eutrophication and acidification. Mechanisms thought to underlie the vegetation-driven negative effects on fauna include changes in microclimatic conditions (Schirmel et al., 2011; Vanreusel and Van Dyck, 2007; Wallis de Vries and van Swaay, 2006), loss of open habitat (Öckinger et al., 2006; van Turnhout, 2005), and a decrease of nectar and host plants (Öckinger et al., 2006; Vanreusel et al., 2007; Wallis DeVries, 2004). However, much less attention has been paid to the question whether eutrophication and acidification might also affect heathland animals directly through deposition-mediated shifts in plant macronutrient stoichiometry. In nutrient-poor terrestrial environments, increased N deposition can lead to substantial increases in plant-available N relative to phosphorus (P) and can, thus, potentially increase the N:P ratio of plant biomass. Pitcairn et al. (2001) found a significant

* Corresponding author at: Bargerveen Foundation, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands.
  E-mail address: j.vogels@science.ru.nl (J.J. Vogels).

positive relationship between foliar N content of *Calluna vulgaris* and annual N deposition levels. In the poorly buffered heathland ecosystem, however, soil acidification could also affect plant N:P stoichiometry in a different way, as under increasing acidity, plant P availability will generally decrease through stronger formation of Al- and Fe-bound P (Blume et al., 2016). Shoot P concentrations of plants can also be significantly lowered as a result of Al toxicity (De Graaf et al., 1997; Foy et al., 1978). In addition, reduced mycorrhizal infection as a result of acidification and/or increased soil NH_4^+ concentrations will significantly lower P uptake rates (Pearson and Stewart, 1993). Both the increase in foliar N content due to higher N inputs and the lower P availability related to soil acidification can increase plant N:P ratios, and reinforce one another. Stoichiometric studies of heathlands have primarily focused on the effects of changes in plant stoichiometry on interspecific plant competition and plant community structure (Britton and Fisher, 2007; Roem and Berendse, 2000; Roem et al., 2002; Von Oheimb et al., 2010). Increased P-limitation in heathlands has been found to decrease plant species richness (Roem and Berendse, 2000), with many herbaceous and/or graminoid plant species with relatively low mean N:P ratios declining or disappearing in stands on soils with low P-availability. Plants with high mean N:P ratio and/or plants that show a higher plasticity in tissue N:P ratio (e.g. *C. vulgaris*, *Molinia caerulea*) show much lower declines or may even increase in cover. Thus, increased P-limitation for plants can lead to 1) reduced plant species richness due to the disappearance of plant species that require high P availability, and 2) shifts towards increased N:P ratios in more tolerant plant species. The question whether increased heathland vegetation N:P ratios may also significantly impact higher trophic levels has, however, still largely been unexplored.

Interestingly, Elser et al. (2000) showed that terrestrial herbivore N:P ratios are significantly lower than autotroph N:P ratios, indicating that for herbivores in terrestrial ecosystems shortage of P rather than N is more likely. Animals exhibit compensatory feeding behaviour when faced with nutritionally imbalanced foods (Behmer, 2009; Berner et al., 2005; Mayntz et al., 2005; Raubenheimer and Simpson, 1993). Compensatory feeding alleviates fitness reductions of ingesting nutritionally imbalanced foods, thereby obscuring the importance of a balanced diet for consumers (Berner et al., 2005). Studies on compensatory feeding have focused mainly on behavioural responses for dietary carbohydrate and protein and the majority of stoichiometric studies feature C:N ratios. Evidence for compensatory feeding for low levels of dietary P is weak, even though increased dietary P content can significantly enhance fitness (Cease et al., 2016; Perkins et al., 2004; Visanuvimol and Bertram, 2010, 2011). Possibly, increasing food intake to compensate low P content is not as tightly regulated as for carbohydrates and protein. Consequently, an increase in plant N:P ratio will further exacerbate low dietary P content, as compensatory feeding will be less in herbivores feeding on plants with elevated N (protein) content, further reducing their P-intake (Berner et al., 2005).

Animals may be affected by increases in vegetation N:P ratio in multiple ways (Elser et al., 2009; Elser et al., 2010). Most straightforward, if increased P-limitation for plants results in a loss of plants having relatively low N:P ratios, species that specialize on these plants will be affected. However, if N:P ratios of plants that remain also increase, all herbivorous species are expected to be subject to increased P-limitation, also adversely affecting generalist herbivore growth rates, densities and community structure (DeMott and Gulati, 1999). Detritivorous species can also be considered to be generalist species; they feed on decomposing litter and fungal hyphae and will also be impacted by altered vegetation N:P ratio, as the N:P ratio of fresh litter is largely determined by that of living tissue. Finally, the impacts of increased vegetation N:P ratios could also cascade towards higher trophic levels, reducing carnivore diversity. This could simply result from reduced prey availability, but also from stoichiometric imbalances in their prey (see e.g. Jensen et al., 2011; Mayntz et al., 2005; Mayntz and Toft, 2001; Raubenheimer et al., 2007).

In this study, we therefore explored whether plant macronutrient stoichiometry, as related to soil chemistry, can explain changes in community composition and diversity of animals of lowland heathlands. We assessed how these stoichiometric impacts compare to the effect of vegetation structure and composition using a multimodel inference approach as proposed by Burnham and Anderson (2002). We first investigated how soil chemistry is related to both C:N and N:P ratio of the vegetation, and to vegetation composition. Modelling included contrasting hypotheses that were based on soil chemical parameters found to be most important in predicting vegetation diversity and richness in previous studies dealing with N and acid deposition in heathland ecotypes (Bobbink et al., 1998; De Graaf et al., 2009; De Graaf et al., 1997; De Graaf et al., 1998; Kleijn et al., 2008; Roelofs, 1986; Roem and Berendse, 2000; Roem et al., 2002). We tested whether vegetation responses were related to either increased soil N availability (H1), increased soil acidity (H2), reduced soil P availability (H3), and their combinations: N availability in relation to acidity (H4); N in relation to P availability (H5); acidity in relation to P availability (H6); or combined effects of N, P availability and acidity (H7; Table 1). Soil chemical parameters used were: NO_3^-, NH_4^+, NH_4:NO_3-ratio for N availability hypotheses, plant available P for P availability hypotheses and pH, Al^{3+}, Ca^{2+} and Al:Ca-ratio for soil acidity hypotheses. In order to test whether changes in vegetation N:P ratio were mainly the result of changes in species composition (e.g. loss of low N:P ratio species) or whether intraspecific changes in plant N:P ratio also contributed, we contrasted the results for the N:P-ratio of the vegetation as a whole with those obtained when using the N:P ratio of the most common plant species, *C. vulgaris*. Next, we related animal taxon richness and abundance data (Diptera and carabid beetles) to vegetation C:N and N:P stoichiometry, structure and composition. We chose Diptera and carabid beetles because they represent widespread species groups in heathland ecosystems, are typically present in high abundance, encompass different trophic levels and, for carabid beetles, trophic level as well as other relevant autecological information are available at species level (Turin, 2000). We tested whether animal responses were related to either plant nutrient ratios (H1-F); 2) plant species richness (H2-F); plant species richness and vegetation structure (H3-F); or combinations of plant macronutrient ratio, vegetation structure and/or plant species richness (H4-F; Table 2). Subsequently, we explored the effect of different management types on vegetation community structure and plant C:N and N:P stoichiometry. The study was carried out in the Netherlands, which is one of the regions in Europe that has very high atmospheric N and acid deposition rates (EMEP, 2015).

2. Material and methods

2.1. Research locations

In order to account for regional variation, this study was performed in two large open heathland reserves in the Netherlands, the Dwingelderveld heathland reserve (Lat: 52.796°, Lon: 6.393°) and the Strabrechtse Heide heathland reserve (Lat: 51.403°, Lon: 5.619°). In both areas, 30 sites covering an area of 10 m × 10 m were selected for soil and plant chemistry sampling, vegetation relevés and sampling of Diptera and Carabidae, giving a total of 60 sites. Plant communities in the selected sites consisted of *Genisto-Callunetum* (n = 42), *Ericion tetralicis* (n = 15) and *Nardo-Galion* (n = 3) communities on loamy soils or long-term (>25 years) abandoned crop fields on sandy soils.

2.2. Management

Of all sites, management practice carried out over a period of 30 years and information of historical land use were provided by the managers of both reserves. Management of the heather dominated sites included sod-cutting (topsoil removal), grazing, a combination of both, controlled burning, or no management for at least 30 years.

Table 1

Overview and summary description of all models used in predicting vegetation C:N and N:P ratio, *Calluna* N:P ratio, N:P ratio of other plants, total plant species richness, herb species richness and cover of ericaceous shrubs or grasses.

Hypothesis	Hypothesis description	Model #	Variables in model
H1	N-availability	Model 1	NO_3 concentration
		Model 2	NH_4 concentration
		Model 3	NO_3 and NH_4 concentration
		Model 4	NH_4:NO_3 ratio
H2	Soil acidity	Model 5	pH
		Model 6	pH + Ca concentration
		Model 7	pH + Al concentration
		Model 8	pH + Al:Ca ratio
H3	P-availability	Model 9	Plant available P
H4	Soil acidity + N-availability	Model 10	Acidity + NH_4 concentration
		Model 11	Acidity + NO_3 and NH_4 concentration
		Model 12	Acidity + NH_4:NO_3 ratio
		Model 13	Al:Ca ratio + NH_4:NO_3 ratio
H5	N and P-availability	Model 14	NO_3 concentration + plant available P
		Model 15	NH_4 + plant available P
		Model 16	NO_3 + NH_4 + plant available P
		Model 17	NH_4:NO_3 ratio + plant available P
H6	Soil acidity + P-availability	Model 18	pH + plant available P
		Model 19	Ca + plant available P
		Model 20	Al concentration + plant available P
H7	Soil acidity + N + P-availability	Model 21	NO_3 + Ca + Al concentration + plant available P
		Model 22	Al:Ca ratio + NH4:NO3 ratio + plant available P
0	Null model	Model 23	Intercept only

Notes: for all tested plant and vegetation response variables, the same models were used. All models were of the formulation "response ~ variable A + variable B + … + (1|area)", where area is either Dwingelderveld or Strabrechtse Heide heathland reserve. The hypotheses and numbers refer to the 7 different hypotheses formulated in in the introduction. Model 23 is a predictorless null-model (response ~ (1|area), used in evaluating the top ranking models explanatory power.

Other sites (mainly *Nardo-Galion* communities) were managed by extensive grazing. Some of these sites were known to have a history of extensive farming, but were left fallow for several (>25) years (see Table C.1 for a complete overview).

2.3. Soil chemistry

In May 2009, five soil cores (5.5 cm diameter) of the upper 5 cm were sampled at each site. Soil cores were kept cool during transport and stored in a freezer before chemical analysis. Soil exchangeable nutrients and ions were determined using sodium chloride (NaCl) extraction (van den Berg et al., 2003). After 1 h the pH of the solution was measured using a combined pH electrode with an Ag/AgCl internal reference (Orion Research, Beverly, CA, USA), and a TIM800 pH meter. Soil extracts were obtained using rhizon soil water samplers placed in a bottle with soil extract and connected to a vacuumed-bottle. After 12 h, 10 ml extract was transferred in a 10 ml tube and stored at 4 °C for later analysis of dissolved ions. 20 ml of extract was transferred in a 20 ml flask and stored at −20 °C for later analysis of NO_3^- and NH_4^+. Plant available phosphorus (P_{Olsen}) was determined using extraction with sodium bicarbonate (Olsen et al., 1954).

Table 2

Overview and summary description of all models used in predicting vegetation different trophic groups of Diptera (density) and Carabid beetles (both species richness and activity-density).

Hypothesis	Hypothesis description	Model #	Variables in model
H1F	Plant macrostoichiometry	Model 1	C:N ratio
		Model 2	N:P ratio
		Model 3	C:N + N:P ratio
H2F	Plant SR	Model 4	Plant species richness
		Model 5	Herb species richness
H3F	Plant SR + structure	Model 6	Ericaceous shrub cover
		Model 7	Graminoid cover
		Model 8	Plant species richness + ericaceous shrub cover
		Model 9	Plant species richness + graminoid cover
		Model 10	Herb species richness + ericaceous shrub cover
		Model 11	Herb species richness + graminoid cover
H4F	plant macrostoichiometry + richness/structure null model	Model 12	C:N ratio + Plant species richness
		Model 13	N:P ratio + plant species richness
		Model 14	C:N + N:P ratio + plant species richness
		Model 15	C:N ratio + ericaceous shrub cover
		Model 16	N:P ratio + ericaceous shrub cover
		Model 17	C:N + N:P ratio + ericaceous shrub cover
		Model 18	C:N ratio + graminoid cover
		Model 19	N:P ratio + graminoid cover
		Model 20	C:N + N:P ratio + graminoid cover
		Model 21	C:N ratio + herb species richness
		Model 22	N:P ratio + herb species richness
		Model 23	C:N + N:P ratio + herb species richness
0F		Model 24	Intercept only

Notes: for all tested animal response variables, the same models were used. All models were of the formulation "response ~ variable + variable B + … + (1|area)", where area is either Dwingelderveld or Strabrechtse Heide heathland reserve. The hypotheses and numbers refer to the 4 different hypotheses formulated in in the introduction. Model 24 is a predictorless null-model (response ~ (1|area), used in evaluating the top ranking models explanatory power.

Ca, P, Al, S concentrations in the NaCl extracts and P in the Olsen extracts were measured by inductively coupled plasma emission spectrometry (IRIS Intrepid II XDL, Thermo Electron Corporation, Franklin, USA). The concentrations of NO_3^- and NH_4^+ were determined with an Auto Analyser III (Bran & Luebbe, Norderstedt, Germany), using hydrazine sulphate (Kamphake et al., 1967) and salicylate (Grasshoff and Johannsen, 1972) respectively. K was determined by a Technicon Flame Photometer (Technicon Autoanalyser Methodology: N20b, 1966). All soil chemistry data derived from each site was pooled prior to statistical analysis.

2.4. Plant chemistry

In May 2009, vegetation was sampled for chemical analyses. At each site, five samples were taken, consisting of 2-year shoots of *C. vulgaris* when present within the site perimeter, and/or a representative mixture of other dominant species present (including *Erica tetralix*, *Empetrum nigrum*, *Trichophorum cespitosum*, *Carex pilulifera*, *Juncus squarrosus*, *M. caerulea*, *Deschampsia flexuosa*, *Festuca ovina* and/or *Nardus stricta*). Plant samples were dried at 60 °C for 48 h, finely ground and stored for later analysis. Chemical composition of each separate sample was determined through chemical digestion of 200 mg of ground plant material using a microwave (Milestone, type MLS 1200 Mega) after addition of 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%). Elemental composition was measured by inductively coupled plasma emission spectrometry as described above. For plant C and N contents, 3 mg of finely ground dry plant material was analysed on a CNS elemental analyser (Model EA NA1500, Carlo Erba - Thermo Fisher Scientific).

2.5. Fauna sampling

Diptera were sampled using emergence traps (one trap per site). These traps are pyramid-shaped metal constructions, covering 60 cm × 60 cm of bare soil, and are covered by black cloth. On top of the trap, a transparent collecting jar is attached to create a single source of light attracting emerging invertebrates into the collecting jar. This sampling method can be used quantitatively, as sampling intensity is based on the surface of ground covered by the trap (Southwood and Henderson, 2000). The collecting jar was filled with a layer of 4% formaldehyde solution to prevent decomposition of the collected specimens. To minimize the influence of trapping on emergence rates, emergence traps were randomly relocated within the 10 m × 10 m × 10 m triangular perimeter of the pitfall traps at each sampling site at the end of each sampling interval. Carabid beetles (Coleoptera: Carabidae) were sampled using pitfall trapping. At each location, three plastic jars (8.5 cm diameter) were placed in the ground in a triangular pattern with a distance of 10 m between traps and filled with a layer of 4% formaldehyde solution to prevent decomposition of the collected specimens. In contrast to emergence trapping for Diptera, pitfall trapping is known to poorly represent actual densities of the species trapped (Southwood and Henderson, 2000; Topping and Sunderland, 1992) as the numbers of a given species trapped is related to the local activity of this species, which could also be influenced by external factors such as vegetation density (Melbourne, 1999). Total numbers of trapped individuals of carabid beetles are therefore referred to as activity densities, rather than actual densities.

Fauna sampling started at the beginning of May 2008 and ended at the end of September 2008 for Diptera, with continuous sampling intervals of 3 weeks. In order to ensure trapping of species with late or early seasonal activity, carabid beetles were also sampled additionally in three non-continuous, three week sampling intervals in late autumn of the same year, and winter and early spring of the following year. At the end of every sampling interval, all trapped individuals were collected and transferred to a 70% alcohol solution, and all traps were refilled with formaldehyde solution. All trapped individuals of carabid beetles were identified to the species level using Boeken et al. (2002). Diptera were identified only to family level, as this proved sufficient in providing information on trophic status of this group (see Table E.2). Trophic level assignment of Diptera was based on information provided by Beuk (2002). Carabid beetle trophic level assignment, as well as habitat preference and degree of habitat specialization (see Table E.1) were determined per species, based on information provided by Turin (2000).

2.6. Vegetation composition and structure

In June 2009, vegetation composition was recorded at each site. Vegetation relevés of the whole site perimeter were recorded using the scale of Braun-Blanquet. The vegetation relevé data was used to quantify vegetation species richness and structure, using total vascular plant species richness, herbaceous plant species richness, and total cover percentage of ericaceous shrubs and of graminoids as predictor variables.

2.7. Statistical analyses

The relationships between soil chemical variables and plant macronutrient stoichiometry (C:N and N:P ratios), structure and composition, and between plant response variables and invertebrate densities and/or species richness were investigated using a multimodel inference approach following Aikaike's Information Criterion (ΔAIC_c) corrected for small sample sizes (see Burnham and Anderson, 2002; Mundry and Nunn, 2009). In order to correct for area effects on response variable outcome, heathland reserve (Dwingelderveld and Strabrechtse Heide) was included as a random factor in all regression models, and thus (generalized) linear mixed-effects models were used for all regression analyses. Three sites were excluded from the analysis, resulting in a total of 57 sites used in the analyses. A detailed description of site exclusion criteria, collinearity between predictor variables and types of models used is given in Appendix A.

We first specified 22 candidate models, representing the different hypotheses about the relation between soil chemical status on plant parameters used in the invertebrate response models (Table 1). In addition, in order to test whether changes in vegetation mean N:P ratio were due to changes in vegetation composition or also due to intraspecific changes, we additionally tested the models on predicting mean N:P ratio of *C. vulgaris*, and mean N:P ratio of mixed signature vegetation samples (not containing *C. vulgaris*). In order to further elucidate the nutrient (N or P) most important in determining plant N:P ratio, we calculated Pearson correlation coefficients of plant N and P content with plant N:P ratio. Next, we specified 23 candidate models representing the 4 different hypotheses about the relation between invertebrate response and plant chemistry, richness and vegetation structure (Table 2). Invertebrate response variables were categorised according to taxonomical status (Diptera families and Carabid beetles) and trophic level. For both analyses, we also included a null model (response ~ intercept) in order to obtain a measure of explanatory power for the best fitting models. Calculated AICc weights (w_i) were used to assess the level of fit of each model. Evidence Ratio (ER) values were also calculated ($ER = w_{i(trm)} / w_{i(j)}$ for all j models, $w_{i(trm)} = AIC_c$ weight (w_i) of the top ranking model). For all analyses, the best models (defined as models with $w_i > 0.1$) are presented, as well as the model averaged results of these sets of models, which provide parameter estimates of all predictor variables, F-values and significance levels.

In order to obtain a general overview of between-site similarities and dissimilarities in vegetation composition, vegetation relevé data was used to obtain a set of groups of similar sites, using standard hierarchical clustering of sites (complete linkage method) based on calculated Bray-Curtis dissimilarity indices on number transformed (on a scale of 1 to 10) Braun-Blanquet scores. For a detailed description of methods used, see Appendix A. Subsequently, these results were contrasted to management history and other site characteristics by summarizing the types of management performed and other site characteristics for each cluster.

All statistical analyses were performed using the software program R version 3.2.0 (R Core Team, 2015), using the packages vegan (Oksanen

et al., 2015) for hierarchical clustering and correspondence analysis, lme4 (Bates et al., 2014) for all LMMs, and glmmADMB (Fournier et al., 2012; Skaug et al., 2015) for all GLMMs.

3. Results

3.1. Relation between soil-chemistry and vegetation

3.1.1. Vegetation C:N ratio

Vegetation C:N ratio was best explained by models reflecting hypotheses 7 (combined effects) and 5 (N and P-availability) and included soil exchangeable NO_3^-, Ca^{2+}, Al^{3+} and Olsen-P (Table 3). Model-averaged parameter estimations of these models show a highly significant negative relation between soil exchangeable NO_3^- and plant C:N ratio (Table 4). Olsen-P showed a weaker, near-significant negative relationship with plant C:N ratio, and soil exchangeable Al^{3+} showed a weak, near-significant positive relationship with plant C:N ratio, suggesting a role for these parameters in influencing plant C:N ratio. Soil exchangeable Ca^{2+} showed a very weak, non-significant negative relationship with plant C:N ratio.

3.1.2. Vegetation, Calluna and other plants tissue N:P ratio

Vegetation N:P ratio was best explained by models reflecting hypotheses 7 (combined effects) and 6 (acidity and P-availability) and included soil exchangeable NO_3^-, Ca^{2+}, Al^{3+} and Olsen-P (Table 3). Model-averaged parameter estimations of these models show a highly significant positive relation between soil exchangeable Al^{3+} and plant N:P ratio, and a highly significant negative relation between Olsen-P and plant N:P ratio (Table 4). Ca^{2+} and NO_3^- showed only very weak, non-significant negative relationships with plant N:P ratio.

The N:P ratio of *Calluna*, as well as from other plants, was also best explained by models reflecting hypotheses 7 and 6, and model-averaged parameter estimations were highly similar to those of vegetation N:P ratio (Tables 4 and 5). Vegetation N:P ratio was correlated to both vegetation P content and N content, but the correlation was much stronger for P content (Pearson $r = -0.82$; $n = 57$ for P content; Pearson $r = -0.37$; n = 57 for N content).

3.1.3. Plant and herb species richness

Plant species richness was best explained by models reflecting hypotheses 5 (N- and P-availability), 4 (N-availability and acidity) and 6 and included soil exchangeable NO_3^-, NH_4^+, Olsen-P and $pH_{(NaCl)}$ (Table 3). Model-averaged parameter estimates showed significant positive relationships with P_{olsen} and $pH_{(NaCl)}$, and significant negative relationships with NH_4^+ (Table 4). NO_3^- was positively related to plant species richness, but highly variable and not significant.

Herb species richness was best explained by a single model ($w_i = 0.900$) reflecting hypothesis 4, which included pH and soil exchangeable NO_3^- and NH_4^+ (Table 3). Parameter estimation of this model shows highly significant positive relations of soil $pH_{(NaCl)}$ and soil exchangeable NO_3^- with herb species richness (Table 4). The negative relation between soil exchangeable NH_4^+ and herb species richness was much weaker and not significant.

3.1.4. Cover of ericaceous shrubs

Cover of ericaceous shrubs was best explained by a single model ($w_i = 0.858$) reflecting hypothesis 5, which included soil exchangeable NO_3^- and NH_4^+ and Olsen-P (Table 3). Parameter estimation of this model shows a highly significant positive relation between soil exchangeable NH_4^+ and cover of ericaceous shrubs and a highly significant negative relation between Olsen-P and cover of ericaceous shrubs (Table 4). The negative relation between soil exchangeable NO_3^- and cover of ericaceous shrubs was much weaker and not significant.

3.1.5. Cover of graminoids

Cover of graminoids was best explained by models reflecting hypotheses 7 and 5 and included soil exchangeable Ca^{2+}, Al^{3+}, Olsen-P and soil exchangeable NO_3^- and NH_4^+ (Table 3). Model-averaged parameter estimations of these models show a highly significant positive relation between Olsen-P and cover of graminoids, and a significant negative relation between soil exchangeable NH_4^+ and cover of graminoids (Table 4). Soil exchangeable Al^{3+} showed a negative, near significant relation with graminoid cover, suggesting a role for this parameter in influencing graminoid cover as well. Soil exchangeable

Table 3

Summary of results identifying the top ranking sets of models predicting vegetation C:N and N:P ratio, *Calluna* N:P ratio, N:P ratio of other plants, total plant species richness, herb species richness and cover of ericaceous shrubs or grasses, using Akaike information theory criteria.

Hypothesis	Model number	AICc	ΔAIC	wi	ER	variables in model
Vegetation C:N ratio						
H7	Model 21	371.328	0	0.705	1	NO_3^-, Ca^{2+}, Al^{3+}, Olsen-P
H5	Model 14	373.962	2.633	0.189	3.73	NO_3^-, Olsen-P
Vegetation N:P ratio						
H7	Model 21	338.045	0	0.804	1	NO_3^-, Ca^{2+}, Al^{3+}, Olsen-P
H6	Model 20	340.868	2.823	0.196	4.10	Ca^{2+}, Al^{3+}, Olsen-P
Calluna N:P ratio						
H7	Model 21	273.245	0	0.616	1	NO_3^-, Ca^{2+}, Al^{3+}, Olsen-P
H6	Model 20	276.152	2.907	0.144	4.28	Ca^{2+}, Al^{3+}, Olsen-P
Other plants N:P ratio						
H7	Model 21	271.369	0	0.842	1	NO_3^-, Ca^{2+}, Al^{3+}, Olsen-P
H6	Model 20	274.740	3.371	0.156	5.40	Ca^{2+}, Al^{3+}, Olsen-P
Plant species richness						
H5	Model 16	294.582	0	0.480	1	NO_3^-, NH_4^+, Olsen-P
H4	Model 11	296.141	1.559	0.222	2.18	pH, NO_3^-, NH_4^+
H6	Model 18	296.607	2.205	0.174	2.75	pH, Olsen-P
H5	Model 15	297.681	3.100	0.102	4.71	NH_4^+, Olsen-P
Herb species richness						
H4	Model 11	174.864	0	0.900	1	pH, NO_3^-, NH_4^+
Cover of ericaceous shrubs						
H5	Model 16	507.747	0	0.858	1	NO_3^-, NH_4^+, Olsen-P
Cover of graminoids						
H7	Model 21	497.742	0	0.635	1	Ca^{2+}, Al^{3+}, Olsen-P
H5	Model 16	499.547	1.805	0.258	2.47	NO_3^-, NH_4^+, Olsen-P

Notes: AIC_c is the Akaike information criterion, corrected for small sample size, ΔAIC is the difference between a models AIC_c score and the best model AIC_c score, w_i is the Akaike weight (ranging from 1–0), representing the relative likelihood of the model given the data, and ER is the evidence ratio (calculated as $w_{i(top\ ranking\ model)}/w_{i(j)}$ for all j models), representing the likelihood of a given model to represent the correct model of the data sampled (given as a ratio compared to the "best model"). For all response variables, only the models with $w_i > 0.1$ are represented here. For herb species richness and cover of ericaceous shrubs, this resulted in the presentation of a single model. For all analyses n = 57.

Table 4
Model-averaged parameter estimation of the top ranking plant response - soil chemistry models presented in Table 3.

Parameter	Estimate	Adj. Std. Error	z value	Pr(>|z|)
Vegetation C:N ratio				
NO_3^-	−29.353	8.720	3.366	<0.001***
Ca^{2+}	−0.585	0.645	0.907	0.364
Al^{3+}	2.520	1.296	1.946	0.052.
Olsen-P	−8.533	4.881	1.748	0.080.
Vegetation N:P ratio				
NO_3^-	−0.650	6.166	0.105	0.916
Ca^{2+}	−0.581	0.461	1.260	0.208
Al^{3+}	5.191	0.931	5.574	<0.001***
Olsen-P	−14.188	3.492	4.063	<0.001***
***Calluna* N:P ratio**				
NO_3^-	0.411	6.988	0.059	0.953
Ca^{2+}	−0.113	0.472	0.240	0.810
Al^{3+}	3.115	1.088	2.864	0.004**
Olsen-P	−13.111	3.441	3.810	<0.001***
Other plants N:P ratio				
NO_3^-	−1.742	9.360	0.186	0.852
Ca^{2+}	−0.604	0.666	0.906	0.365
Al^{3+}	6.166	1.317	4.681	<0.001***
Olsen-P	−15.880	5.061	3.138	0.002**
Plant species richness				
NO_3^-	5.473	4.339	1.261	0.207
NH_4^+	−0.920	0.329	2.801	0.005**
Olsen-P	6.552	2.210	2.965	0.003**
pH	4.493	1.466	3.065	0.002**
Herb species richness				
pH	1.834	0.383	4.788	<0.001***
NO_3^-	4.233	1.155	3.666	<0.001***
NH_4^+	−0.081	0.065	1.253	0.210
Cover of ericaceous shrubs				
NO_3^-	−28.461	28.638	0.994	0.320
NH_4^+	5.426	1.554	3.491	<0.001***
Olsen-P	−66.145	16.089	4.111	<0.001***
Cover of graminoids				
NO_3^-	−5.086	28.672	0.177	0.859
Ca^{2+}	1.315	2.150	0.611	0.541
Al^{3+}	−7.612	4.368	1.742	0.081.
Olsen-P	70.583	16.121	4.378	<0.001***
NH_4^+	−3.193	1.445	2.209	0.027*

Notes: Models included in parameter estimation are all models listed in Table 3, with Akaike weight > 0.10. Adjusted standard error (Adj. Std. Error: standard error estimation adjusted for small sample sizes; see par. 4.3 in Burnham and Anderson, 2002), z-values and significance scores were calculated using the conditional averaging method, which means that each predictor variable is only averaged over models in which it appears. In the case of herb species richness and ericaceous shrub cover, no model averaging was actually performed, as only one model was included in Table 4 (indicating a very high chance of this model being the correct model given the data). For all analyses n = 57.

* p < 0.05
** p < 0.01
*** p < 0.001

Ca^{2+} (positive relation) and NO_3^- (negative relation) showed only very weak, non-significant relations with graminoid cover.

3.2. Relation between vegetation and fauna

3.2.1. Density of Diptera trophic groups

Densities of herbivorous and detrivorous Diptera were best explained by models reflecting hypothesis 4F (vegetation macronutrient stoichiometry and plant richness/structure) and included C:N and N:P ratio along with cover of ericaceous shrubs (Table 5). Model-averaged parameter estimations show that densities for herbivorous Diptera were positively related to ericaceous shrub cover, and significantly negatively related to both vegetation C:N and N:P ratio (Table 6).

Densities of detritivorous Diptera were similarly best explained by models reflecting hypothesis 4F, being positively related to ericaceous shrub cover and negatively to vegetation N:P ratio (Tables 5 and 6). In contrast to the herbivorous Diptera, there was a much smaller and non-significant effect of vegetation C:N ratio on detritivorous Diptera densities.

3.2.2. Species richness of Carabidae trophic groups

Species richness of herbivorous and carnivorous Carabid beetles was best explained by models reflecting hypothesis 4F, and included vegetation N:P ratio, C:N ratio and cover of ericaceous shrubs and herb species richness (Table 5). Model-averaged parameter estimations of these models show a significant negative effect of both ericaceous shrub cover and vegetation N:P ratio on herbivorous carabid beetle species richness, whereas vegetation C:N ratio had a non-significant, positive effect (Table 6).

Species richness of carnivorous Carabid beetles was similarly best explained by models that included vegetation N:P ratio, C:N ratio, cover of ericaceous shrubs and herb species richness (Table 5). Model-averaged parameter estimations of all top models how significant effects of all four model parameters, including herbaceous plants species richness (Table 6). Vegetation N:P ratio and ericaceous shrub cover negatively influence carnivorous carabid beetle species richness, while vegetation C:N ratio and herbaceous plants species richness positively influence carnivorous carabid beetle species richness.

3.2.3. Activity-density of Carabidae trophic groups

Activity-density of herbivorous Carabid beetles was also best explained by models reflecting hypothesis 4F, and included vegetation N:P ratio, C:N ratio and cover of graminoids (Table 5). Model-averaged parameter estimations of these models show a significant negative effect of vegetation N:P ratio and a significant positive effect of graminoid cover on herbivorous carabid beetle activity-density (Table 6). Vegetation C:N ratio showed a much weaker, not significant negative effect.

Activity-density of carnivorous Carabid beetles was poorly explained by all 23 models, as the ΔAIC_c between the top ranked models and the null model (0F) was only 0.81 (Table 5). The top ranked models referred to hypotheses 1F (plant macrostoichiometry) and 2F (plant species richness) respectively and included either vegetation N:P ratio ($w_i = 0.117$) or herb species richness ($w_i = 0.104$). The third ranked model was actually the null model (0F), with Akaike weight $w_i = 0.078$. Not surprisingly, model-averaged parameter estimations only showed weakly supported relationships with vegetation N:P ratio (negative) and herb species richness (positive) (Table 6).

A visual overview of the relation between single predictor variables retained in the top ranking models and the corresponding invertebrate response parameter investigated is presented in Fig. D.1.

3.3. Relationships with management

Dissimilarity-based hierarchical clustering of vegetation relevés resulted in the identification of 8 separate clusters (Fig. B.1). These clusters varied between 1 and 18 members, and clustering largely identified clusters of sites from the same reserves (Strabrechtse Heide vs Dwingelderveld) and sites with similar management (sod-cutting, grazing, no management, other management) (Table 7).

Sod-cutting resulted in a remarkable dichotomy of the clusters (Table 7): sites with former sod-cutting management were mainly clustered in clusters E–H, and were mainly absent in clusters A–D. Cluster D incorporated the majority of unmanaged heathland sites, and cluster A–C incorporated mainly sites with other, less frequently occurring management types and/or historical use (relic drift sand, burning, liming after sod-cutting, history of agriculture, formerly afforested).

Box-and-whisker plots of the important variables identified in the AIC_c based model selection approach regarding trophic groups of invertebrates and all animal response variables are given in Figs. 1 and 2 respectively. Vegetation N:P ratio varied greatly between clusters (F = 12.23). The sod-cut dominated clusters E-H show a much higher median N:P ratio than the clusters incorporating sites with other management. Interestingly, the ericaceous shrub dominated sites with no management (cluster D) show lower N:P ratios, similar to the clusters A–C. The same applies for C:N ratio, but the variation in the sod cut sites is generally higher than non-sod-cut sites, resulting in a somewhat

Table 5
Summary of results identifying the top ranking sets of models predicting different trophic groups of Diptera (density) and Carabid beetles (both species richness and activity-density), using Akaike information theory criteria.

Hypothesis	Model number	AICc	ΔAIC	wi	ER	variables in model
Herbivorous Diptera density						
H4F	Model 17	680.112	0	0.634	1	Plant C:N ratio, plant N:P ratio, cover of ericaceous shrubs
H4F	Model 15	682.090	1.978	0.236	2.689	Plant C:N ratio, cover of ericaceous shrubs
Detritivorous Diptera density						
H4F	Model 16	795.368	0	0.453	1	Plant N:P ratio, cover of ericaceous shrubs
H4F	Model 17	795.940	0.572	0.340	1.331	plant C:N ratio, plant N:P ratio, cover of ericaceous shrubs
H4F	Model 15	798.248	2.88	0.107	4.221	Plant C:N ratio, cover of ericaceous shrubs
Herbivorous Carabidae species richness						
H4F	Model 16	220.453	0	0.490	1	Plant N:P ratio, cover of ericaceous shrubs
H4F	Model 17	222.516	2.063	0.175	2.806	Plant C:N ratio, plant N:P ratio, cover of ericaceous shrubs
Carnivorous Carabidae species richness						
H4F	Model 17	315.772	0	0.642	1	Plant C:N ratio, plant N:P ratio, cover of ericaceous shrubs
H4F	Model 23	318.588	2.816	0.157	4.088	plant C:N ratio, plant N:P ratio, herb species richness
Herbivorous Carabidae activity-density						
H4F	Model 19	426.39	0	0.402	1	Plant N:P ratio, cover of graminoids
H4F	Model 20	427.726	1.336	0.206	1.950	plant C:N ratio, plant N:P ratio, cover of graminoids
Carnivorous Carabidae activity-density						
H1F	Model 2	701.583	0	0.117	1	Plant N:P ratio
H2F	Model 5	701.819	0.236	0.104	1.125	Herb species richness
0F	Model 24	702.393	0.81	0.078	1.499	Intercept only

Notes: AIC$_c$ is the Akaike information criterion, corrected for small sample size, ΔAIC is the difference between a models AIC$_c$ score and the best model AIC$_c$ score, w$_i$ is the Akaike weight (ranging from 1–0), representing the relative likelihood of the model given the data, and ER is the evidence ratio (calculated as $w_{i(top\ ranking\ model)}/w_{i(j)}$ for all j models), representing the likelihood of a given model to represent the correct model of the data sampled (given as a ratio compared to the "best model"). For all response variables, only the models with w$_i$ > 0.1 are represented here. An exception was made for carnivorous Carabidae activity-density where the third-ranked null-model is also included, which indicates general poor model fit in all models tested including the best models (with w$_i$ > 0.1). For all analyses n = 57.

lower F-value over all sites considered (F = 7.43). Not surprisingly, ericaceous shrub cover and graminoid cover largely mirror each other, as a high dominance of ericaceous shrubs leaves no room for a high cover of graminoids and vice-versa. Herbaceous plant species richness is generally higher in clusters A–C and H. Mean densities of herbivorous Diptera were low in clusters G–H, and highly variable within clusters D–F.

Table 6
Model-averaged parameter estimation of the top ranking invertebrate response models.

Parameter	Estimate	Adj. Std. Error	z value	Pr(>|z|)
Herbivorous Diptera density				
Plant C:N ratio	−0.050	0.012	4.046	<0.001***
Plant N:P ratio	-0.029	0.013	2.136	0.033*
Cover of ericaceous shrubs	0.011	0.003	3.709	<0.001***
Detritivorous Diptera Density				
Plant N:P ratio	−0.049	0.020	2.47	0.014*
Cover of ericaceous shrubs	0.014	0.004	3.321	<0.001***
Plant C:N ratio	−0.023	0.015	1.5	0.134
Herbivorous Carabidae species richness				
Plant N:P ratio	−0.042	0.015	2.826	0.005**
Cover of ericaceous shrubs	−0.008	0.003	2.504	0.012*
Plant C:N ratio	0.008	0.013	0.57	0.569
Carnivorous Carabidae species richness				
Plant C:N ratio	0.021	0.006	3.305	< 0.001***
Plant N:P ratio	−0.019	0.007	2.516	0.012*
Cover of ericaceous shrubs	−0.005	0.002	3.147	0.002**
Herb species richness	0.073	0.026	2.787	0.005**
Herbivorous Carabidae activity-density				
Plant N:P ratio	−0.059	0.025	2.361	0.018*
Cover of graminoids	0.020	0.006	3.627	< 0.001***
Plant C:N ratio	−0.020	0.019	1.062	0.288
Carnivorous Carabidae activity-density				
Plant N:P ratio	−0.023	0.013	1.775	0.076.
Herb species richness	0.114	0.071	1.603	0.109

Notes: Models included in parameter estimation are all models listed in Table 1, with Akaike weight > 0.10. Adjusted standard error (Adj. Std. Error: standard error estimation adjusted for small sample sizes; see par. 4.3 in Burnham and Anderson, 2002), z-values and significance scores were calculated using the conditional averaging method, which means that each predictor variable is only averaged over models in which it appears. For all analyses n = 57.
* p < 0.05
** p < 0.01
*** p < 0.001

Detritivorous Diptera density did not differ significantly over site clusters (F = 0.57) and was highly variable within clusters, indicating low predictive power of vegetation composition on this group. Species richness as well as activity-density of herbivorous Carabidae differed significantly between site clusters and were highest in clusters A–C. Carnivorous Carabidae species richness was highest in clusters A–B and H, the latter however showing high variation between sites. Activity-density of carnivorous Carabidae did not differ significantly between sites (F = 2.30), due to high within-cluster variation. Clusters A–C did however show highest mean activity density.

4. Discussion

Our results support our hypotheses that heathland vegetation N:P ratio in areas with high N deposition rates is mainly determined by soil acidity and P-availability (H6; H7), and that vegetation N:P ratio is an important factor in shaping invertebrate communities of heathland ecosystems, in conjunction with habitat structure and (herbaceous) plant species richness (H4F). Our results also suggest that soil acidity and P-availability were also the main causes for loss of habitat structure and plant species richness in these areas, further strengthening our main hypothesis that soil acidification negatively impacts heathland biodiversity of both plants and animals. In Fig. 3, we schematically present these findings as a novel pathway, existing in concert with the conventional pathway as discussed in the introduction.

4.1. Drivers of plant macronutrient stoichiometry

Apart from low plant available P, high vegetation N:P ratios were found in soils with high soil exchangeable Al concentrations, reflecting lower soil buffering status. Thus, soil acidification seems to increase P-limitation, either directly through stronger formation of Al- and Fe-bound PO_4 (Blume et al., 2016), or indirectly due to Al toxicity, possibly hampering P uptake by plant roots (De Graaf et al., 1997; Foy et al., 1978). One may argue that the vegetation N:P ratio measured in this study is a mere reflectance of vegetation composition, as vegetation N:P stoichiometry affects vegetation composition (Koerselman and Meuleman, 1996). However, our results suggest that the general increase in vegetation N:P ratio results from both interspecific differences

Table 7

Overview of site characteristics of the site clusters with respect to location and management. For a full overview, see Table C.1. Cluster (A–H) corresponds to the clusters in the vegetation based hierarchical tree (Fig. B.1).

Cluster	SB		DV		Sod-cutting		Grazing		No man > 30 yrs.		GC	ET	NG	Other
	n	Freq.	n	Freq.	n	Freq.	n	Freq.	n	Freq.	n	n	n	
A (n = 1)	0	0.00	1	1.00	0	0.00	0	0.00	0	0.00	1	0	0	Relic drift sand (1)
B (n = 9)	5	0.56	4	0.44	3	0.33	6	0.67	0	0.00	9	0	0	Limed after sod-cutting (1), Burning (2), Small-scaled sod-cutting (1)
C (n = 3)	0	0.00	3	1.00	0	0.00	1	0.33	0	0.00	2	0	1	Former agricultural activity (1), Formerly afforested (1), Burning (1)
D (n = 12)	8	0.67	4	0.33	0	0.00	3	0.25	8	0.67	12	0	0	Mowing (1)
E (n = 4)	4	1.00	0	0.00	2	0.50	1	0.25	1	0.25	3	1	0	
F (n = 4)	4	1.00	0	0.00	3	0.75	2	0.50	0	0.00	4	0	0	Relic drift sand (1)
G (n = 18)	1	0.06	17	0.94	12	0.67	12	0.67	1	0.06	9	9	0	Mowing (1), Burning (2)
H (n = 6)	6	1.00	0	0.00	6	1.00	4	0.67	0	0.00	2	4	0	

Notes: n = number of sites having this characteristic. Freq.: frequency of sites having this characteristic in a given cluster. SB = site located at Strabrechtse Heide, DV = site located at Dwingelderveld. Sod-cutting management, grazing management or no management for at least 30 years (No man > 30 yrs.) are indicated per site. GC; ET; NG: number of occurences of *Genisto-Callunetum*, *Ericion tetralicis* and *Nardo-Galion* communities in the clusters. In the column "Other", all other types of management and/or site characteristics are described, with in parentheses the number of sites in the cluster to which this other type of management/characteristic applies.

in plant N:P ratio (turnover of species) as well as intraspecific changes in plant N:P ratio (*C. vulgaris*).

While soil NO_3^- concentrations did relate to vegetation C:N ratios, its explanatory value for vegetation N:P ratio was only marginal, suggesting that increased N-availability due to increased N deposition has only minor effects on plant stoichiometry, something that is also exemplified by vegetation N:P ratio being correlated more strongly to plant P content than to plant N content. However, N deposition could indirectly affect plant nutritional quality as it is known to enhance soil acidification, through release of H^+ due to nitrification of NH_4^+ to NO_3^- (van Breemen et al., 1984). As the deposition of SO_x in Europe has decreased by 50–90% in the last decades, and further decreased by 50% between 2000 and 2006 and 2010 in the Netherlands (Velders et al., 2011), soil acidification is nowadays mainly driven by N deposition, which in this country is mostly in the form of NH_y. Although N deposition has also

decreased (by 40%), this decrease is much lower than that of S deposition, and still greatly exceeds the critical deposition levels (500–1000 mol·ha^{-1}·yr^{-1}; Bobbink and Roelofs, 1995) for the investigated heathlands by a factor of 1.7 (Velders et al., 2015). Thus, N deposition is likely to have pronounced indirect effects on plant stoichiometry via increased rates of soil acidification, rather than direct effects of increased N availability.

Secondly, intensive management will also alter soil P availability and buffer capacity. From our cluster analysis of heathland vegetation, it became clear that clusters dominated by sites with sod-cutting management typically showed a substantially higher N:P ratio compared to the clusters dominated by sites without sod-cutting. Although proven effective in restoring dominance by ericaceous shrubs, sod-cutting implies the removal of a large fraction of the humus layer, and with it large quantities of all nutrients are indiscriminately removed from the
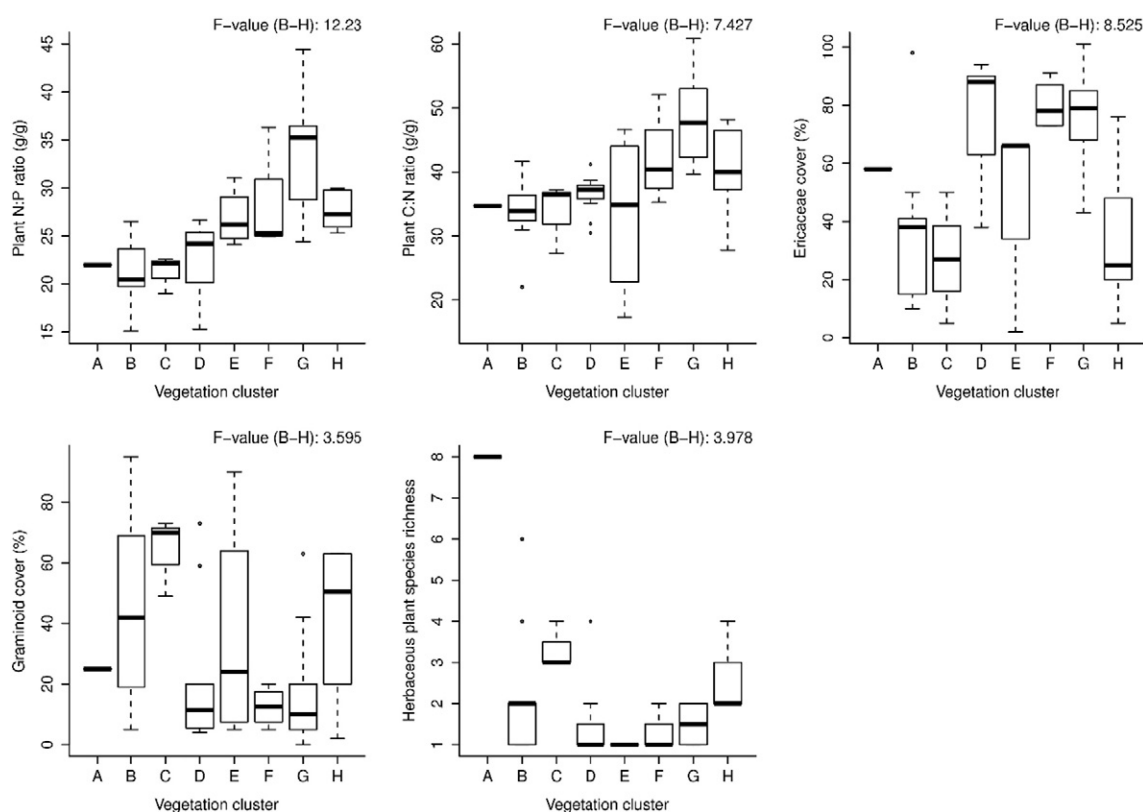

Fig. 1. Box- and whisker plots of all significant predictor variables explaining variance in invertebrate density models (see Tables 1 and 2), sorted by clusters from the vegetation composition based dendrogram (Fig. B.1). F-values of ANOVA models with the corresponding plotted variable with cluster (B–H) as predictors are given in each graph.

Fig. 2. Box- and whisker plots of all animal response variables tested, sorted by clusters from the vegetation composition based dendrogram (Fig. B.1). F-values of ANOVA models with the corresponding plotted variable with cluster (B–H) as predictors are given in each graph.
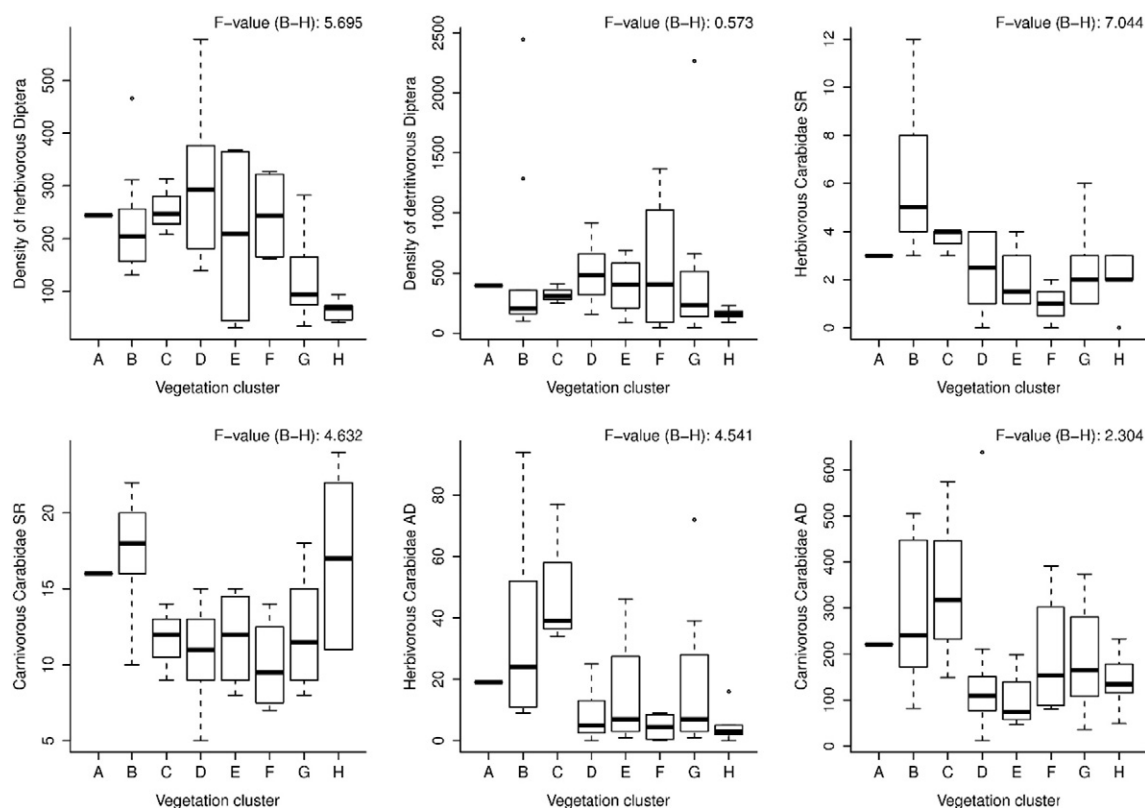
system. In doing so, N but also P and other elements are removed (Härdtle et al., 2009; Niemeyer et al., 2007). As annual deposition of P is very low, total soil P will recover very slowly. Thus, removal of organic matter by sod-cutting only exacerbates P-limitation. Sod-cutting has

also been linked to decreased soil buffer capacity, as soil organic material with associated base cations is largely responsible for the acid buffering and Al-immobilization capacity of these systems (van den Berg et al., 2003).
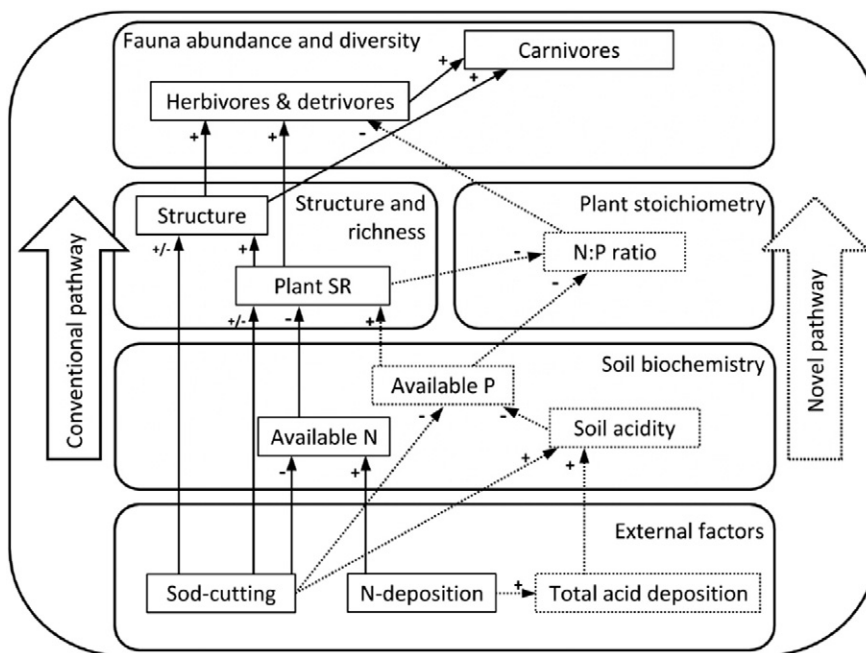

Fig. 3. Schematic overview of biochemical and ecological pathways, ultimately affecting fauna abundance and diversity of heathlands. Solid arrows and variables depict the conventional pathways as described in the introduction, dashed arrows and variables depict the additional pathway described in our results and discussion section. Plus and minus signs represent positive or negative relations between two variables, plus/minus signs represent either positive or negative influence between two variables, depending on local site conditions and/or time since sod-cutting management.

4.2. Vegetation stoichiometry and fauna communities

All trophic groups in the investigated taxa showed significant correlations with at least one vegetation macronutrient ratio, either in density, species richness, or activity-density. Vegetation N:P ratio was found to be the most consistent predictor in all top ranking models, being significantly and negatively correlated with all fauna-related parameters investigated except for carnivorous carabid beetles activity-density, for which all tested models performed poorly in predicting activity density. For predaceous animals, correlations with vegetation nutrient stoichiometry are expected to be less strong, as C:N and N:P ratios of insect prey are much more similar to the needs of the predators than is the case between plants and herbivores (Sterner and Elser, 2002). Lower densities of herbivorous and detritivorous invertebrates can ultimately also negatively impact predaceous species, through diminishment of prey. While C:N ratios are traditionally emphasized, in our examined heathlands, C:N ratio seems much less important, and correlations are found to be inconsistent, sometimes affecting heathland animals negatively and sometimes positively. Our results indicate that in the study areas, P is generally more limiting than N for the animal groups investigated.

4.3. Vegetation structure and fauna communities

Vegetation structure and plants species richness were also found to play a significant role in determining density and species richness of the investigated fauna groups, but the effects differed considerably for each group examined. For Diptera, cover of ericaceous shrubs was strongly positively correlated with densities of both trophic groups. A high continuous cover of shrubs ensures a thermally stable and humid environment, which possibly reduces desiccation risks of larvae. In contrast to the response observed for dipterans, carabid beetles were negatively impacted by increasing ericaceous shrub cover. A high cover of ericaceous shrubs, leading to relatively cold, humid conditions, has earlier been found to negatively affect the abundance and/or occurrence of xerophilic species (Buchholz et al., 2013; Schirmel and Buchholz, 2011), and 40% of the species in our data set were xerophilic species (see Table E.1). Activity density of herbivorous carabid beetle activity-density was positively correlated with graminoid cover. As most of these species are granivorous species (Thiele, 1977), this probably reflects their preference of grass seeds over those from *Calluna* as food items.

4.4. Management implications

With plant macronutrient stoichiometry as an important driver in shaping animal communities of heathlands, beneficial effects of management efforts that only target the improvement of structural heterogeneity (e.g. herded grazing) will be limited, as these efforts do not solve the problem of changed plant stoichiometry. Management efforts in maximizing removal of accumulated N will only further enlarge this problem and therefore are expected to prove detrimental for heathland fauna. Measures aimed at improving the soil buffer status will improve plant nutrient status (i.e. lower N:P ratios) and are therefore expected to yield great benefits for the fauna. This contrasts with past and current management practices in lowland heathland remnants in north western Europe, where many hectares of heathland area have been subject to intensive sod-cutting management, aimed at reducing N stocks in the soil and opening up the vegetation structure of formerly grass encroached sites. Our results suggest that managers should instead aim to combine their efforts in improving habitat structure with efforts aimed at reducing the effects of acidification, by restoring the acid neutralizing capacity of heathland soils. Restoration of soil buffer capacity by means of liming (De Graaf et al., 1998; Dorland et al., 2004) or adding mineral sources of base cations (Aarnio and Martikainen, 1996; Aarnio et al., 2003) are promising management options. While it remains of paramount importance to reduce the deposition rates of N below the critical loads for heathlands, restoring soil buffering status could mitigate some of the negative impacts of N deposition and thus prevent further loss of heathland animal species.

In conclusion, our study clearly shows that effects of increased N deposition on animals reach beyond mere deposition driven changes in plant composition and structure. Broadening the focus to also include the field of biogeochemistry and ecological stoichiometry has proven to be invaluable in unravelling the causal mechanisms responsible for the decline of characteristic animal species in these ecosystems, and ultimately, in designing sound management practices that are able to prevent a further loss of the animal biodiversity of the heathland landscape.

Acknowledgements

Appendix A. Detailed description of statistical analyses

A.1. Site exclusion criteria

Prior to all statistical analyses, all predictor and response variables were screened for extreme outliers. We considered sites with response and/or predictor values which were higher than 5*IQR of the total dataset as sites containing extreme outliers. Extreme outliers were found in three sites; two sites at the Strabrechtse Heide heathland reserve, and one site at the Dwingelderveld Heathland reserve, which could be related to the sites' land use histories.

The sites at Strabrechtse Heide were known to have a history of extensive small-scaled farming, and were at the time of sampling in a transitional development of a species-rich acidic grassland vegetation type (*Nardo-Galion* communities). This however also resulted in extreme outliers with respect to the cover of herbaceous plant species, which was higher than 25% at these sites (mean herb cover of all other sites was 4.03%). The Dwingelderveld site was influenced by a nearby ditch that transported excess water from a nearby intensive agricultural field. In periods with high precipitation, this ditch could flood the surrounding heathland, leading to extremely high soil concentrations of Ca, but also NH_4^+. As extreme outliers often have a strong influence of the outcome of regression analyses due to high potential leverage they obtain, and the cause of these outliers was well-known, we excluded these sites from all statistical analyses.

A.2. Collinearity

Prior to model formulation, all predictor variables in the models were screened for collinearity. Two variables were considered collinear when the absolute Pearson correlation coefficient was higher than 0.6. Variables with high collinearity were excluded from combined entry into regression model formulations. Within plant macro-chemical stoichiometry parameters, plant C:P ratio was highly collinear with plant N:P and C:N ratio, hence plant C:P ratio was excluded from use in the model formulations. Within vegetation structural variables, ericaceous shrub cover was highly collinear with graminoid cover and herb species richness was highly collinear with total vascular plant species richness. Plant macro-chemical stoichiometric parameters and vegetation structural parameters showed no collinearity ($|r| < 0.3$), and could thus be combined in the model formulations. Within soil chemical parameters, Ca^{2+} vs. NH_4^+; $NO_4:NO_3$ ratio vs NH_4^+ and Al:Ca-ratio vs. Ca^{2+} were highly collinear, and therefore excluded from combined entry into model formulations.

A.3. Types of models used

For all models that explored the relationship between soil chemical parameters and plant chemical ratio response variables, response data was continuous, and a normal error distribution was appropriate. For these analyses, Linear Mixed Effects models (LMM's) were used.

For the analyses that focus on the relationship between plant chemistry, vegetation composition and invertebrate response variables, generalized linear mixed effects models (GLMMs) were used, as the number of individuals and number of species trapped represent count data, which do not follow a normal error distribution. In all cases, initial models were analysed using a Poisson GLMM, and then checked for overdispersion. Invertebrate density based response variables were in all cases significantly overdispersed when using a Poisson GLMM (dispersion statistic significantly >1), thus these models were then fitted using negative binomial GLMMs. For species richness response variables, no significant overdispersion was found, so for these models, Poisson GLMMs were used.

A.4. Site clustering by vegetation relevé data

We used standard hierarchical clustering of sites (complete linkage method) based on calculated Bray-curtis dissimilarity indices on number transformed (on a scale of 1 to 10) Braun-Blanquet scores. The resulting tree was then restructured into an ordered community table using the order of the sites on the first axis of a Canonical Correspondence Analysis (following Oksanen et al., 2015). The ordered tree was subsequently cut into eight clusters, using a cutting limit of 0.725. The resulting clusters of sites were further explored in differences in management, and for differences between clusters of the parameters present in the best models identified in the model selection approach. The degree of difference between these clusters with respect to all measured variables were quantified using the F-statistic of an ANOVA model on the clusters that contained >1 site (effectively removing 1 single site cluster from the ANOVA models). As we were not particularly interested in the between-cluster significance of these parameters, and the clustering also resulted in an imbalanced replicate number per group (violating the assumption of balanced design in ANOVA post-hoc testing), no post-hoc testing was performed on these clusters.

A.5. Cited references

Oksanen, J., 2015. Multivariate analysis of ecological communities in R: Vegan Tutorial.

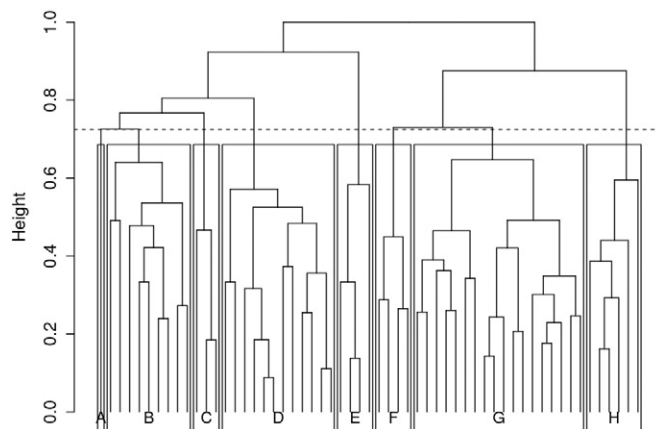### Appendix B. Hierarchial tree of sampling sites

Fig. B.1. Hierarchical tree of all sampling sites at Dwingelderveld and Strabrechtse Heide, based on calculated Bray-Curtis dissimilarity of 10 m × 10 m vegetation relevé data. Separate clusters were defined as clusters with height < 0.725 (dotted line), resulting in a total of 8 (A–H) site clusters.

Appendix C. Site characteristics

Table C.1
Complete overview of site characteristics, in chronological order with the dissimilarity-based cluster dendrogram (Fig. B.1).

Cluster	Location	Sod-cutting	Grazing	Not managed > 30 yrs.	Other
A	Dwingelderveld				Relic drift sand
B	Dwingelderveld	X			Limed after sod-cutting
	Dwingelderveld		X		
	Strabrechtse Heide		X		
	Strabrechtse Heide		X		Burning
	Strabrechtse Heide		X		Burning
	Strabrechtse Heide	X			Small scaled sod-cutting
	Strabrechtse Heide		X		
	Dwingelderveld	X			
	Dwingelderveld		X		
C	Dwingelderveld				Former agricultural activity
	Dwingelderveld				Formerly afforested
	Dwingelderveld		X		Burning
D	Strabrechtse Heide		X		
	Strabrechtse Heide		X		
	Dwingelderveld		X		
	Dwingelderveld			X	
	Dwingelderveld			X	
	Dwingelderveld			X	
	Strabrechtse Heide			X	
	Strabrechtse Heide			X	
	Strabrechtse Heide			X	
	Strabrechtse Heide			X	
	Strabrechtse Heide				Mowing
	Strabrechtse Heide			X	
E	Strabrechtse Heide		X		
	Strabrechtse Heide	X			
	Strabrechtse Heide	X			
	Strabrechtse Heide			X	
F	Strabrechtse Heide	X			Relic drift sand
	Strabrechtse Heide		X		
	Strabrechtse Heide	X	X		
	Strabrechtse Heide	X			
G	Dwingelderveld	X	X		
	Dwingelderveld		X		
	Dwingelderveld	X	X		
	Dwingelderveld				Mowing
	Dwingelderveld		X		Burning
	Dwingelderveld		X		
	Dwingelderveld			X	
	Dwingelderveld		X		
	Dwingelderveld	X	X		
	Dwingelderveld	X	X		
	Dwingelderveld	X	X		Burning
	Dwingelderveld	X	X		
	Strabrechtse Heide	X	X		
	Dwingelderveld	X			
	Dwingelderveld	X	X		
	Dwingelderveld	X			
	Dwingelderveld	X			
	Dwingelderveld	X			
H	Strabrechtse Heide	X	X		
	Strabrechtse Heide	X			
	Strabrechtse Heide	X	X		
	Strabrechtse Heide	X			
	Strabrechtse Heide	X	X		
	Strabrechtse Heide	X	X		

Appendix D. Overview of single predictor variables and invertebrate response
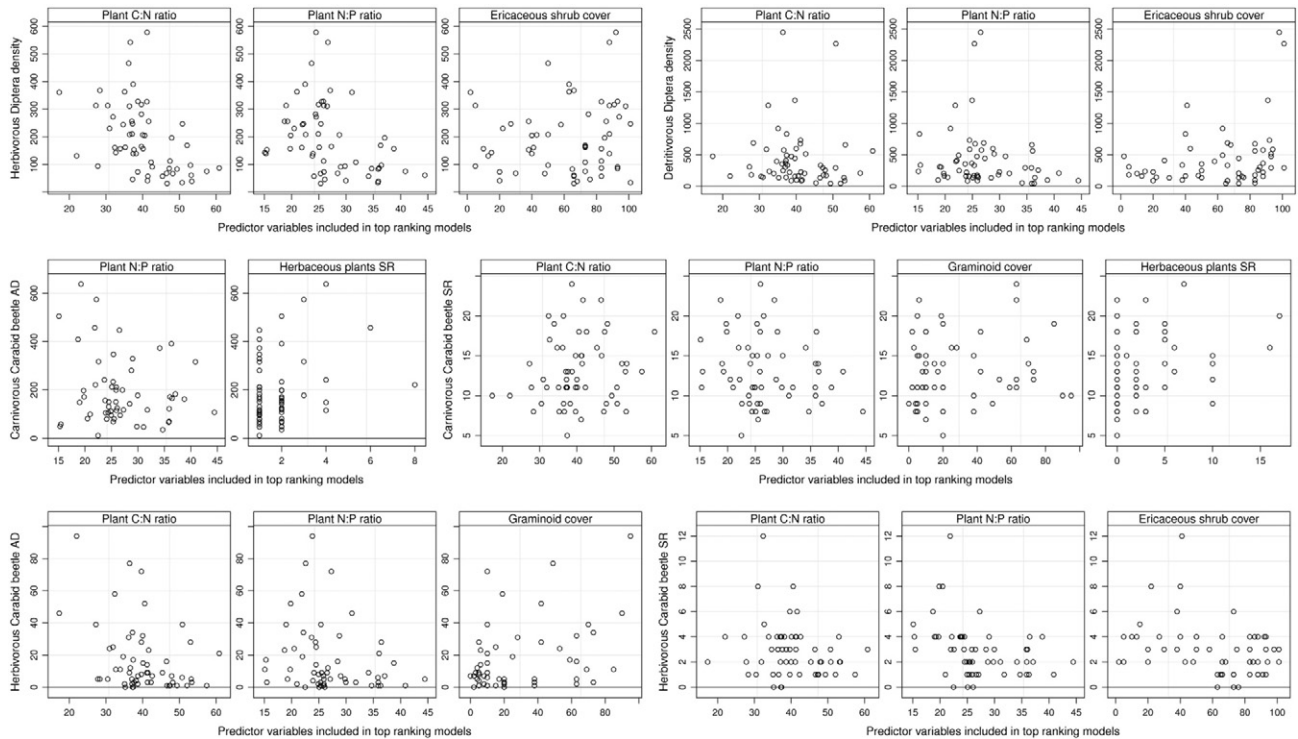

Fig. D.1. Scatter plots of herbivorous and detritivorous Diptera density and herbivorous and carnivorous Carabid beetle SR and AD versus all predictor variables retained in the respective top ranking invertebrate response models (Tables 5 and 6).

Appendix E. Autecological information of trapped invertebrates

Table E.1

Overview of all species of Carabid beetles sampled in this study. Mean activity-density and Std. Error (in parentheses) are given for each species for each corresponding vegetation relevé-based site cluster (Fig. B.1). Species richness (SR) and activity-density (AD) for each trophic group and for total carabid beetles are given at the end of this table. Troph. group: corresponding trophic group of the species: cv = carnivorous, hv = herbivorous, ov = omnivorous. Lindroth class: revised habitat specialization classification by Lindroth (1949), revised by Turin (2000): H1: highly hygrophilic; H2: moderately hygrophilic; HW: hygrophilic - sylvicol; N1:mesophilic and/or ruderal; NH: ruderal - hygrophilic; NW: ruderal - sylvicol; W1: highly sylvicol; W2: moderately sylvicol; WA: sylvicol-arboricol; X1: highly xerophilic; X2: moderately xerophilic. Eurytopy: scale of habitat specificity based on aggregated data of many Dutch carabid beetle sampling studies (Turin, 2000): 10 = highly eurytopic, 1 = highly stenotopic. 0 = insufficient data for classification.

Taxon				Site cluster							
	Troph. group	Lindroth class	Eurytopy	A (n = 1)	B (n = 9)	C (n = 3)	D (n = 12)	E (n = 4)	F (n = 4)	G (n = 18)	H (n = 6)
Acupalpus brunnipes (Sturm, 1825)	ov	H1	2					0.3 (0.3)	0.3 (0.3)		0.7 (0.5)
Acupalpus dubius Schilsky, 1888	ov	HW	3						0.3 (0.3)	0.2 (0.2)	0.2 (0.2)
Acupalpus parvulus (Sturm, 1825)	ov	H1	6							0.2 (0.2)	0.2 (0.2)
Agonum ericeti (Panzer, 1809)	cv	H1	5							0.1 (0.1)	
Agonum fuliginosum (Panzer, 1809)	cv	HW	8							0.1 (0.1)	
Agonum marginatum (Linnaeus, 1758)	cv	H1	7								0.2 (0.2)
Agonum muelleri (Herbst, 1784)	cv	H2	9								0.2 (0.2)
Agonum sexpunctatum (Linnaeus, 1758)	cv	H2	7				0.1 (0.1)			0.1 (0.1)	0.5 (0.3)
Amara aenea (Degeer, 1774)	hv	X1	9		1.2 (0.9)		0.2 (0.1)	0.3 (0.3)			
Amara apricaria (Paykull, 1790)	hv	N1	8				0.1 (0.1)				
Amara communis (Panzer, 1797)	hv	N1	10		1.3 (1.2)	3.7 (3.2)	0.1 (0.1)	0.3 (0.3)		0.4 (0.4)	
Amara convexior Stephens, 1828	hv	X2	8				0.1 (0.1)				
Amara equestris (Duftschmid, 1812)	hv	X2	4		0.9 (0.5)		0.1 (0.1)			0.1 (0.1)	
Amara famelica Zimmermann, 1832	hv	H2	8		1.0 (0.9)		0.2 (0.1)				0.2 (0.2)
Amara familiaris (Duftschmid, 1812)	hv	N1	9		0.1 (0.1)						
Amara fulva (Mueller, 1776)	hv	X2	7		1.2 (0.8)						
Amara infima (Duftschmid, 1812)	hv	X1	4	5.0 (NA)	0.1 (0.1)					0.1 (0.1)	
Amara lunicollis Schioedte, 1837	hv	N1	8	1.0 (NA)	14.8 (8.7)	4.7 (3.7)	2.5 (1.0)	14.0 (10.4)	4.0 (2.0)	6.6 (2.0)	2.7 (2.3)
Amara similata (Gyllenhal, 1810)	hv	N1	7				0.1 (0.1)				
Amara spreta Dejean, 1831	hv	X2	9		1.3 (1.1)					0.1 (0.1)	
Amara tibialis (Paykull, 1798)	hv	X2	6		0.6 (0.4)		1.1 (1.1)	0.5 (0.3)			
Anisodactylus binotatus (Fabricius,	ov	H2	7		0.2 (0.1)		0.1 (0.1)			0.8 (0.6)	2.0 (1.1)

(continued on next page)

Table E.1 (*continued*)

Taxon	Troph. group	Lindroth class	Eurytopy	A (n = 1)	B (n = 9)	C (n = 3)	D (n = 12)	E (n = 4)	F (n = 4)	G (n = 18)	H (n = 6)
1787)											
Anisodactylus nemorivagus (Duftschmid, 1812)	ov	X2	0							0.1 (0.1)	
Asaphidion flavipes (Linnaeus, 1761)	cv	H2	8		0.1 (0.1)						
Bembidion femoratum (Sturm, 1825)	cv	H2	6		0.1 (0.1)						
Bembidion humerale (Sturm, 1825)	cv	H2	0								0.2 (0.2)
Bembidion lampros (Herbst, 1784)	cv	N1	9	1.0 (NA)	0.8 (0.2)	0.3 (0.3)		0.8 (0.3)	1.8 (1.8)	1.2 (0.6)	0.5 (0.3)
Bembidion nigricorne Gyllenhal, 1827	cv	X2	4					1.8 (1.4)		0.3 (0.2)	0.7 (0.4)
Bembidion properans (Stephens, 1828)	cv	N1	8				0.1 (0.1)	0.5 (0.3)		0.1 (0.1)	0.3 (0.3)
Bembidion quadrimaculatum (Linnaeus, 1761)	cv	N1	7		0.3 (0.3)		0.1 (0.1)				
Bradycellus caucasicus (Chaudoir, 1846)	ov	N1	8		0.8 (0.8)		0.1 (0.1)				
Bradycellus harpalinus (Serville, 1821)	ov	X2	9	2.0 (NA)	3.0 (1.8)	0.7 (0.7)	0.9 (0.8)	2.3 (1.9)	1.8 (1.4)	0.1 (0.1)	2.8 (1.2)
Bradycellus ruficollis (Stephens, 1828)	ov	N1	7	2.0 (NA)	2.3 (1.4)		5.8 (1.5)	2.5 (1.3)	1.5 (0.9)	1.3 (0.3)	0.8 (0.7)
Bradycellus verbasci (Duftschmid, 1812)	ov	X2	7							0.1 (0.1)	
Broscus cephalotes (Linnaeus, 1758)	cv	X1	6	12.0 (NA)	0.9 (0.5)						
Calathus cinctus (Motschulsky, 1850)	cv	NX	4		0.3 (0.2)				0.3 (0.3)		
Calathus erratus (C.R. Sahlberg, 1827)	cv	X2	9	47.0 (NA)	24.0 (16.5)		0.7 (0.7)	1.5 (1.5)	23.3 (23.3)	4.7 (3.2)	8.3 (6.0)
Calathus fuscipes (Goeze, 1777)	cv	N1	9		10.1 (5.2)	3.3 (3.3)	5.7 (4.7)		0.5 (0.5)	0.4 (0.2)	0.3 (0.3)
Calathus melanocephalus (Linnaeus, 1758)	cv	N1	10		5.0 (1.6)	0.7 (0.7)	1.7 (0.6)	0.3 (0.3)	2.5 (1.6)	2.7 (0.9)	2.7 (2.1)
Calathus micropterus (Duftschmid, 1812)	cv	W2	5		0.1 (0.1)		0.2 (0.2)				
Calosoma inquisitor (Linnaeus, 1758)	cv	WA	1		0.1 (0.1)						
Carabus arcensis Herbst, 1784	cv	X2	6	2.0 (NA)	13.9 (5.5)	73.0 (23.8)	22.7 (18.3)	3.0 (2.3)	57.5 (43.9)	18.8 (6.2)	13.2 (7.2)
Carabus clatratus Linnaeus, 1761	cv	H1	0		3.2 (2.4)		1.1 (0.4)	9.0 (2.5)	4.5 (3.0)	1.3 (1.3)	35.2 (13.3)
Carabus granulatus Linnaeus, 1758	cv	H2	7				0.1 (0.1)				
Carabus nemoralis Müller, 1764	cv	N1	8		4.4 (1.9)	6.0 (5.5)	2.1 (0.7)	2.0 (1.4)	9.3 (9.3)	0.6 (0.4)	3.3 (1.5)
Carabus nitens Linnaeus, 1758	cv	H2	5		6.3 (3.7)	0.7 (0.7)	0.6 (0.4)	1.5 (0.9)		1.5 (0.6)	8.7 (3.5)
Carabus problematicus Herbst, 1786	cv	X1	7	8.0 (NA)	4.0 (1.4)	1.7 (1.7)	3.3 (1.3)	0.3 (0.3)	0.3 (0.3)	1.8 (0.7)	1.5 (0.8)
Cicindela campestris Linnaeus, 1758	cv	X2	5		3.3 (1.6)		1.3 (1.1)	4.3 (2.5)		0.6 (0.4)	6.0 (3.0)
Cicindela hybrida Linnaeus, 1758	cv	X1	5		1.9 (1.5)						0.2 (0.2)
Clivina fossor (Linnaeus, 1758)	cv	H2	9		0.4 (0.3)		0.3 (0.3)			0.4 (0.2)	
Cymindis humeralis (Geoffroy, 1785)	ov	X1	3					0.3 (0.3)			
Cymindis vaporariorum (Linnaeus, 1758)	ov	X2	4	1.0 (NA)							
Dyschirius aeneus (Dejean, 1825)	cv	H1	3								0.2 (0.2)
Dyschirius globosus (Herbst, 1784)	cv	NH	9	11.0 (NA)	13.2 (5.0)	13.0 (5.5)	14.5 (4.2)	27.5 (12.9)	37.3 (13.2)	18.7 (2.5)	7.8 (3.4)
Harpalus affinis (Schrank, 1781)	hv	X2	9		1.1 (0.9)	0.3 (0.3)				0.1 (0.1)	0.2 (0.2)
Harpalus anxius (Duftschmid, 1812)	hv	X1	5		0.3 (0.2)		0.3 (0.2)	0.3 (0.3)			0.2 (0.2)
Harpalus distinguendus (Duftschmid, 1812)	hv	X1	2		2.4 (2.2)						0.2 (0.2)
Harpalus latus (Linnaeus, 1758)	hv	N1	8	13.0 (NA)	5.2 (3.1)	29.3 (18.9)	3.1 (1.8)		0.5 (0.5)	5.9 (2.7)	0.7 (0.7)
Harpalus rubripes (Duftschmid, 1812)	hv	X2	5		0.1 (0.1)						0.3 (0.2)
Harpalus rufipalpis Sturm, 1818	hv	X1	6		0.9 (0.5)						0.3 (0.2)
Harpalus rufipes (Degeer, 1774)	hv	N1	10		1.1 (0.4)	12.0 (11.0)	0.2 (0.1)			0.5 (0.2)	
Harpalus smaragdinus (Duftschmid, 1812)	hv	X1	5		0.1 (0.1)						0.2 (0.2)
Harpalus solitaris Dejean, 1829	hv	X2	6		0.9 (0.4)					1.8 (1.3)	
Harpalus tardus (Panzer, 1797)	hv	X2	8				0.2 (0.1)				
Laemostenus terricola (Herbst, 1784)	cv	NW	5				0.2 (0.1)				
Leistus ferrugineus (Linnaeus, 1758)	cv	HW	8		0.9 (0.7)		0.3 (0.3)	0.3 (0.3)	0.3 (0.3)	0.1 (0.1)	2.2 (2.0)
Leistus spinibarbis (Fabricius, 1775)	cv	X1	4							0.1 (0.1)	0.3 (0.2)
Loricera pilicornis (Fabricius, 1775)	cv	NH	10						0.3 (0.3)	0.1 (0.1)	0.2 (0.2)
Masoreus wetterhalli (Gyllenhal, 1813)	ov	X1	6		0.1 (0.1)				0.5 (0.5)		
Nebria brevicollis (Fabricius, 1792)	cv	N1	10		3.6 (1.4)	7.7 (4.1)	0.6 (0.2)	0.3 (0.3)	0.3 (0.3)	1.1 (0.6)	0.7 (0.5)
Nebria salina Fairmaire & Laboulbene, 1854	cv	X2	5	38.0 (NA)	106.6 (41.9)	17.3 (15.4)	3.6 (1.8)	2.0 (1.2)	3.8 (3.8)	2.6 (1.4)	13.8 (5.7)
Notiophilus aquaticus (Linnaeus, 1758)	cv	NX	9	3.0 (NA)	3.1 (1.5)		0.4 (0.2)	1.0 (1.0)		0.6 (0.2)	2.5 (1.1)
Notiophilus germinyi Fauvel, 1863	cv	X2	6		0.1 (0.1)						0.2 (0.2)
Notiophilus palustris (Duftschmid, 1812)	cv	NH	8			0.7 (0.7)					
Notiophilus substriatus Waterhouse, 1833	cv	H2	7				0.1 (0.1)		0.3 (0.3)		
Olistophus rotundatus (Paykull, 1790)	cv	X2	5	1.0 (NA)	0.7 (0.4)			0.5 (0.5)		2.1 (1.0)	0.7 (0.3)
Oxypselaphus obscurus (Herbst, 1784)	cv	HW	8	7.0 (NA)	4.2 (2.2)	9.0 (4.0)	46.8 (12.7)	23.0 (21.7)	36.8 (28.3)	5.6 (2.5)	4.7 (2.3)
Paradromius linearis (Olivier, 1795)	ov	X1	7				0.2 (0.2)				
Philorhizus melanocephalus (Dejean, 1825)	ov	X2	8		0.1 (0.1)						
Poecilus cupreus (Linnaeus, 1758)	cv	NH	7		0.1 (0.1)						

Table E.1 (*continued*)

Taxon	Troph. group	Lindroth class	Eurytopy	A (n = 1)	B (n = 9)	C (n = 3)	D (n = 12)	E (n = 4)	F (n = 4)	G (n = 18)	H (n = 6)
				Site cluster							
Poecilus lepidus (Leske, 1785)	cv	X1	6	54.0 (NA)	28.9 (7.1)	0.7 (0.7)	6.3 (2.7)	11.5 (6.1)	3.8 (3.1)	32.4 (10.4)	16.2 (6.8)
Poecilus versicolor (Sturm, 1824)	cv	N1	9	13.0 (NA)	46.6 (27.0)	138.0 (89.3)	23.5 (15.0)	2.5 (1.6)	6.5 (4.2)	61.6 (14.1)	3.8 (1.0)
Pterostichus aterrimus (Herbst, 1784)	cv	H1	1		0.1 (0.1)						0.2 (0.2)
Pterostichus diligens (Sturm, 1824)	cv	H1	8	4.0 (NA)	5.1 (2.8)	14.0 (9.5)	6.1 (3.2)	5.3 (3.1)	5.3 (2.2)	8.4 (3.3)	4.3 (1.5)
Pterostichus melanarius (Illiger, 1798)	cv	N1	9		0.8 (0.5)	0.3 (0.3)	1.3 (0.7)		0.3 (0.3)	0.1 (0.1)	0.2 (0.2)
Pterostichus minor (Gyllenhal, 1827)	cv	H1	7								0.2 (0.2)
Pterostichus niger (Schaller, 1783)	cv	HW	9	18.0 (NA)	1.9 (0.9)	36.7 (18.2)	7.8 (5.0)			11.8 (3.8)	
Pterostichus nigrita (Paykull, 1790)	cv	H1	9							0.1 (0.1)	0.2 (0.2)
Pterostichus oblongopunctatus (Fabricius, 1787)	cv	W1	7		0.2 (0.2)						
Pterostichus rhaeticus Heer, 1837	cv	H2	0	1.0 (NA)			0.2 (0.1)	0.3 (0.3)		0.6 (0.3)	
Pterostichus vernalis (Panzer, 1796)	cv	NH	9	1.0 (NA)	0.8 (0.6)	0.3 (0.3)	0.1 (0.1)		0.8 (0.8)	1.2 (0.5)	0.8 (0.3)
Stomis pumicatus (Panzer, 1796)	cv	NH	6				0.1 (0.1)				
Syntomus foveatus (Geoffroy, 1785)	ov	X1	8	9.0 (NA)	2.8 (1.0)		1.1 (0.5)	0.5 (0.5)		0.2 (0.1)	1.2 (0.7)
Syntomus truncatellus (Linnaeus, 1761)	ov	X2	8		0.2 (0.2)		0.2 (0.1)				
Synuchus vivalis (Illiger, 1798)	cv	NH	8		0.1 (0.1)	0.7 (0.7)				0.1 (0.1)	
Trechus obtusus Erichson, 1837	cv	N1	8				22.7 (19.7)				
Trichocellus cognatus (Gyllenhal, 1827)	ov	X2	4							0.2 (0.1)	
	herbivore	SR		3.0 (NA)	6.0 (1.0)	3.7 (0.3)	2.4 (0.4)	2.0 (0.7)	1.0 (0.4)	2.4 (0.3)	2.0 (0.4)
	herbivore	AD		19.0 (NA)	34.8 (9.4)	50.0 (13.6)	8.0 (2.2)	15.3 (10.4)	4.5 (2.3)	15.5 (4.4)	4.8 (2.3)
	omnivore	SR		4.0 (0.0)	2.4 (0.5)	0.3 (0.3)	2.0 (0.2)	2.0 (0.8)	2.0 (0.7)	1.6 (0.3)	3.0 (0.5)
	omnivore	AD		14.0 (0.0)	9.6 (1.3)	0.7 (0.7)	8.3 (2.3)	5.8 (3.1)	4.3 (2.1)	3.1 (0.8)	7.8 (2.1)
	carnivore	SR		16.0 (0.0)	17.1 (1.3)	11.7 (1.5)	10.8 (0.8)	11.8 (1.7)	10.0 (1.6)	12.3 (0.8)	17.0 (2.3)
	carnivore	AD		221.0 (0.0)	296.3 (52.5)	346.7 (123.6)	151.5 (46.7)	98.8 (34.1)	195.0 (71.6)	181.9 (24.5)	140.8 (25.3)
	total	SR		23.0 (NA)	25.6 (2.0)	15.7 (2.0)	15.2 (1.1)	15.8 (2.6)	13.0 (2.1)	16.3 (1.0)	22.0 (3.0)
	total	AD		254.0 (NA)	340.7 (50.5)	397.3 (120.7)	167.8 (46.9)	119.8 (31.1)	203.8 (71.8)	200.6 (25.1)	153.5 (26.1)

Table E.2

Overview of all terrestrial Diptera families sampled in this study. Mean density (total number of individuals trapped) and Std. Error (in parentheses) are given for each family for each corresponding vegetation relevé-based site cluster (Fig. B.1). Total density for each trophic group and summed density for all groups are given at the end of this table. Troph. group: corresponding trophic group of the families: hv = herbivorous, dv = detritivorous, cv = carnivorous (not used in the analyses), mixed = family consists of species differing in trophic status (not used in the analyses).

Family	Troph. group	A (n = 1)	B (n = 9)	C (n = 3)	D (n = 12)	E (n = 4)	F (n = 4)	G (n = 18)	H (n = 6)
		Site cluster							
Agromyzidae	hv	0.0 (NA)	0.0 (0.0)	1.0 (1.0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Bibionidae	hv	2.0 (NA)	1.4 (0.6)	0.3 (0.3)	3.6 (2.4)	0.0 (0.0)	0.3 (0.3)	1.8 (0.9)	0.0 (0.0)
Opomyzidae	hv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
Anthomyiidae	hv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.4 (0.3)	1.8 (1.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Cecidomyiidae	hv	238.0 (NA)	225.7 (35.5)	254.7 (31.5)	302.4 (41.9)	202.3 (91.8)	243.3 (45.3)	118.9 (17.1)	64.0 (8.1)
Scathophagidae	hv	3.0 (NA)	0.2 (0.1)	0.0 (0.0)	0.4 (0.2)	0.0 (0.0)	0.3 (0.3)	0.2 (0.2)	0.0 (0.0)
Anisopodidae	dv	0.0 (NA)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)
Diastatidae	dv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)
Heleomyzidae	dv	0.0 (NA)	0.1 (0.1)	1.0 (0.6)	0.3 (0.2)	0.3 (0.3)	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)
Lauxaniidae	dv	0.0 (NA)	2.3 (2.0)	0.3 (0.3)	0.0 (0.0)	0.5 (0.3)	0.3 (0.3)	0.3 (0.1)	0.3 (0.3)
Milichiidae	dv	0.0 (NA)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Mycetophilidae	dv	0.0 (NA)	0.9 (0.6)	2.3 (1.5)	1.3 (0.5)	2.8 (2.4)	2.0 (0.9)	0.8 (0.2)	0.8 (0.5)
Psychodidae	dv	4.0 (NA)	1.8 (0.7)	9.7 (2.7)	2.9 (1.5)	0.8 (0.5)	1.3 (0.5)	3.1 (0.9)	0.8 (0.3)
Rhagionidae	dv	0.0 (NA)	0.0 (0.0)	1.7 (1.2)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Scatopsidae	dv	1.0 (NA)	3.1 (2.1)	1.0 (1.0)	0.6 (0.2)	2.3 (0.9)	0.8 (0.5)	0.8 (0.3)	0.0 (0.0)
Sciaridae	dv	384.0 (NA)	540.3 (265.0)	272.0 (37.5)	475.9 (68.0)	375.8 (125.6)	543.5 (303.3)	366.6 (119.5)	136.5 (18.5)
Sepsidae	dv	0.0 (NA)	1.0 (0.6)	1.0 (0.6)	1.0 (0.5)	0.0 (0.0)	0.3 (0.3)	0.6 (0.3)	0.2 (0.2)
Sphaeroceridae	dv	0.0 (NA)	3.0 (0.9)	14.3 (2.4)	5.8 (2.3)	4.8 (4.8)	2.5 (1.7)	2.4 (0.4)	2.2 (1.0)
Trichoceridae	dv	0.0 (NA)	0.0 (0.0)	0.3 (0.3)	1.0 (0.8)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
Drosophilidae	dv	0.0 (NA)	1.8 (0.7)	1.3 (1.3)	2.3 (0.6)	0.0 (0.0)	1.3 (0.8)	0.8 (0.3)	0.0 (0.0)
Ephydridae	dv	0.0 (NA)	1.7 (0.5)	2.0 (1.2)	3.6 (1.1)	2.5 (0.6)	2.5 (1.7)	2.0 (0.5)	1.3 (0.3)
Muscidae	dv	7.0 (NA)	10.3 (4.1)	15.7 (9.3)	5.0 (3.8)	6.8 (1.9)	1.8 (1.2)	14.9 (3.4)	15.8 (5.1)
Acroceridae	cv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.2)
Asilidae	cv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Calliphoridae	cv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Carnidae (Meoneura)	cv	0.0 (NA)	0.8 (0.5)	0.3 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)	0.2 (0.2)
Dolichopodidae	cv	1.0 (NA)	9.2 (3.0)	13.0 (6.9)	5.5 (1.1)	17.3 (7.8)	10.0 (3.1)	23.1 (6.2)	72.2 (29.3)
Empididae	cv	2.0 (NA)	27.2 (5.7)	16.7 (7.7)	16.9 (2.8)	29.3 (11.2)	45.0 (23.6)	6.3 (1.7)	13.2 (5.4)
Hybotidae	cv	0.0 (NA)	0.3 (0.3)	0.0 (0.0)	0.5 (0.2)	0.0 (0.0)	0.3 (0.3)	0.1 (0.1)	0.0 (0.0)
Odinniidae	cv	0.0 (NA)	0.1 (0.1)	0.3 (0.3)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)

Table E.2 (continued)

Family	Troph. group	Site cluster							
		A (n = 1)	B (n = 9)	C (n = 3)	D (n = 12)	E (n = 4)	F (n = 4)	G (n = 18)	H (n = 6)
Pipunculidae	cv	0.0 (NA)	0.2 (0.1)	0.7 (0.3)	0.3 (0.3)	0.8 (0.8)	0.5 (0.5)	0.3 (0.1)	0.0 (0.0)
Tabanidae	cv	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.2)
Tachinidae	cv	0.0 (NA)	0.3 (0.2)	0.3 (0.3)	0.4 (0.3)	0.5 (0.5)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)
Therevidae	cv	0.0 (NA)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Tipulidae	mixed	1.0 (NA)	1.6 (0.7)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.0 (0.0)	0.3 (0.2)	0.8 (0.4)
Keroplatidae (Keroplatinae)	mixed	0.0 (NA)	0.7 (0.7)	0.7 (0.3)	1.0 (0.5)	0.3 (0.3)	0.8 (0.5)	0.7 (0.3)	0.3 (0.2)
Keroplatidae (Macrocerinae)	mixed	0.0 (NA)	0.1 (0.1)	0.0 (0.0)	1.6 (0.8)	1.3 (0.9)	0.0 (0.0)	0.1 (0.1)	0.3 (0.3)
Chloropidae	mixed	2.0 (NA)	5.2 (1.6)	16.7 (5.7)	4.5 (2.8)	4.3 (3.6)	1.0 (1.0)	1.0 (0.3)	0.8 (0.5)
Culicidae	mixed	0.0 (NA)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.3)	0.2 (0.2)	0.0 (0.0)
Limoniidae	mixed	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.2 (0.1)	0.0 (0.0)	0.0 (0.0)	0.6 (0.5)	0.2 (0.2)
Phoridae	mixed	20.0 (NA)	106.4 (24.9)	89.0 (25.1)	139.8 (20.4)	90.8 (34.2)	108.8 (41.6)	72.2 (9.3)	36.7 (8.7)
Syrphidae	mixed	0.0 (NA)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	hv	243.0 (NA)	227.3 (35.6)	256.0 (30.6)	306.9 (42.0)	204.0 (92.8)	243.8 (45.2)	121.0 (17.0)	64.0 (8.1)
	dv	396.0 (NA)	566.7 (264.9)	322.7 (47.0)	499.8 (69.1)	396.8 (126.9)	556.3 (303.8)	392.8 (119.3)	158.0 (19.3)
	cv	3.0 (NA)	38.3 (7.6)	31.3 (3.7)	24.0 (3.0)	47.8 (12.6)	55.8 (22.6)	30.3 (6.3)	86.0 (28.4)
	mixed	23.0 (NA)	114.1 (25.4)	106.3 (25.2)	147.0 (20.6)	96.8 (34.3)	110.8 (43.0)	75.1 (9.3)	39.2 (8.5)
	total	665.0 (NA)	946.4 (267.1)	716.3 (38.8)	977.7 (92.1)	745.3 (243.7)	966.5 (364.7)	619.1 (129.1)	347.2 (37.5)

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