Title

Spatiotemporal variation of Diptera changes how we evaluate High Nature Value (HNV) wet grasslands

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Abstract

Proposed strategies to protect biodiversity within agricultural systems are often based on botanical criteria with plant species richness generally considered the prime indicator of conservation potential. While wet grasslands dominated by rushes (*Juncus* spp.) are commonly considered to be of lesser ecological value than those which are more botanically diverse (e.g. *Carex* dominated grasslands), their value for invertebrates such as Diptera has not yet been fully explored. Data from two Diptera families (Sciomyzidae and Syrphidae) were examined at spatial, temporal and spatiotemporal scales to determine the contribution of two different (*Carex*/Grass and *Juncus*/Grass dominated) wet grassland habitats towards the maintenance of Diptera diversity. The two habitats were significantly different in terms of community structure for both families and temporal turnover was a significant component of dipteran diversity. Spatiotemporal analysis showed that species turnover between habitats at different times made the most significant contribution to overall Diptera diversity. Temporal variation of both families suggests that the relative importance of each habitat type to overall diversity fluctuates depending on sampling period, with both habitats supporting diversity at different times. Our results indicate that lowland wet grasslands characterised by *Juncus* cover needs to be recognised as ecologically important for the maintenance of dipteran diversity. We discuss the possible implications for the diversity of Diptera in wet grasslands if these commonly perceived marginal areas (both agriculturally and ecologically) are ignored in conservation strategies. The necessity of recognising spatiotemporal variation when evaluating habitats using invertebrates as indicators is also discussed.

Introduction

The loss of habitat heterogeneity in agricultural systems is considered a major factor in the overall decrease of farmland biodiversity. Simplification of agricultural land through the removal of less productive areas such as field boundaries and sward species with low grazing value contributes significantly towards the reduction in habitat diversity and overall spatial heterogeneity (Fahrig et al. 2011; Henle et al. 2008; Sullivan et al. 2013). This reduction in habitat variability can have impacts at temporal scales by limiting the availability of alternative habitats where resources become available at different times (Benton et al. 2003). The resulting habitat loss may be even more pronounced for insects, many of which rely on variability at spatial and temporal scales generally not considered in conservation strategies (Haslett 2001).

Approaches to maintaining spatial heterogeneity within agricultural areas include the identification and preservation of areas of High Nature Value (HNV) farmland which is typically characterised by mosaics of semi-natural habitat (Andersen et al. 2004; Paracchini et al. 2008; European Environment Agency 2009). In the west of Ireland, much of this HNV farmland is contained in areas of wet grassland (Sullivan et al. 2010) which are typified by extensive grazing regimes and periodic or seasonal flooding. Wet grassland in Ireland is classified as having >50% cover of grass, sedge or rush species with a significant proportion of drier grassland plants but not dominated by broadleaf herbs or reeds (Fossitt 2000). This criterion is broad enough to include many types of wet grassland with markedly different dominant vegetation, which has lead to the ecological quality of wet grasslands usually being determined by their plant species richness (Sullivan et al. 2010).

While botanical (and ornithological) interests are the principal drivers of wet grassland conservation, wet grasslands can also contain a high diversity of insect species including many scarce or threatened species (Drake 1998). Features of wet grasslands such as damp hollows (Kirby 1992), temporary pools (Nicolet et al. 2004) and drainage ditches (Verdonschot et al. 2011) have all proven to be important to invertebrate conservation in these agricultural landscapes. Though often the focus of conservation strategies in grasslands, increased plant species richness is not always a reliable indicator of invertebrate diversity (Vessby et al. 2002; Billeter et al. 2008; Maher et al. 2014). Features such as vegetation structure have been shown to be more important factors contributing towards the diversity of insects in grasslands (Kruess and Tscharntke, 2002a, 2002b). In wet grasslands in particular, certain dipteran species have been shown to respond more positively to characteristics such as the length of vegetation but not necessarily the plant species richness (Ryder et al. 2005; Williams et al. 2009a; Maher et al. 2014).

Patches of wet grassland frequently become dominated by rush species such as *Juncus effusus* (L.) and *Juncus conglomeratus* (L.) lowering the grazing potential of the sward and potentially reducing the overall plant species richness. In general, plant ecologists and farmers often place little value on fields with extensive *Juncus* cover but for different reasons. The former regard extensive *Juncus* cover as being of poor ecological value and the latter an indication of poor agricultural productivity. The control and removal of rushes from farmland using mechanical and chemical methods is actively encouraged in Ireland, even by agri-environmental schemes. A dense cover of rushes within any particular field can have financial consequences for farm subsidy schemes and is currently seen as a breach of Good Agricultural and Environmental Condition (GAEC) (Department of Agriculture Food and the Marine, 2015a, 2015b). While extensive rush cover offers limited grazing potential when compared to more intensively managed grass pastures, its environmental role is poorly understood, particularly in terms of its contribution to insect diversity.

Wet grasslands have previously been noted for their invertebrate species richness (Hayes et al., 2015; Joyce and Wade, 1998) and the temporal variations associated with wet grasslands, particularly inundation, are likely to have significant effects on invertebrate diversity (Maher et al. 2014). Organisms such as insects generally require combinations of spatial and temporal variation to complete their lifecycles. An adult insect, for example, may need to move to a different habitat patch to obtain resources if those resources are not available within its larval habitat (spatial variation). Alternatively an insect may be able to complete its lifecycle within a single habitat patch if that patch undergoes seasonal changes thereby providing the required resources on a temporal basis (temporal variation). Some species of Diptera which are considerably mobile such as Syrphidae (Hoverflies), can move more freely between habitats in search of resources (Sommaggio 1999; Burgio and Sommaggio 2007). Other dipteran families are less vagile in nature and may be more reliant on temporal variation within habitats to complete their lifecycles. Many species of Sciomyzidae (Marshflies) for example, require periodic inundation for larvae to feed on stranded aquatic snails but equally require dry periods where vegetation is accessible for adults to forage for food and reproduce (Knutson and Vala 2011).

By utilizing these two well-known families of Diptera which have contrasting mobility and life strategies, we examined the role that two different wet grassland vegetation types play in maintaining dipteran diversity in lowland wet grasslands. Both families are considered potentially good bioindicators of wetland habitats (Speight 1986) and meet the criteria for suitable bioindicators outlined in McGeoch et al. (2002) and Lindenmayer et al. (2000) in that they are easily captured and identified; are well understood biologically; and are taxonomically stable and ubiquitous within the habitat of investigation. There is a paucity of information regarding the insect diversity of wet grasslands within Europe, particularly Diptera, and this study, for the first time, examines the role that different wet grassland habitat types play in maintaining these communities.

Through an intensive and continuous sampling regime using Malaise traps we investigate:

1) The role that two different wet grassland vegetation types contribute towards maintaining dipteran diversity

2) The contribution and significance of temporal turnover to the species richness of our two target Diptera families within wet grasslands

3) The importance of considering spatiotemporal variation when making decisions regarding the protection of sites for biodiversity

To achieve these goals, our objectives were to compare Sciomyzidae and Syrphidae diversity at different scales through partitioning diversity and to examine the role each habitat plays in harbouring specific species.

Materials and Methods

Study area

Given that the west of Ireland is considered one of the most likely places in Ireland to contain HNV farmland (European Environment Agency 2009), we selected ten independent grassland sites (classified as wet grassland according to Fossitt [2000]) located in north Galway and south Mayo within a 100km^2 area east of Lough Corrib (the largest lake in the Republic of Ireland). Sites were selected using ortho-corrected aerial photographs and ground-truthed to ensure they conformed to the criteria outlined in Fossitt (2000). Plant species cover and vegetation length were recorded using five 50cm x 50cm quadrats randomly placed at each trap location in order to differentiate areas based on dominant vegetation type. Sites were subsequently classed as either *Juncus*/Grass or *Carex*/Grass habitats based on which vegetation type contributed most to overall percentage cover. Five each of the *Juncus*/Grass or *Carex*/Grass habitats were selected. All 10 of the sampling sites were grazed by livestock and none was subject to extensive cutting or fertilizer application. Within each wet grassland site, two black nylon Malaise traps of Townes design (Townes 1972) were placed 20m apart with the collection head facing in a southerly direction (Speight et al. 2000). A 70% ethanol solution was used in the Malaise Trap collecting bottles to kill and preserve the specimens. Traps were positioned a minimum of five metres away from any obvious flight line features such as wet flushes, hedgerows, ditches and obvious ecotones such as marked differences in vegetation types to facilitate invertebrate collection within each vegetation type. This method was employed to maximise the collection of insect species within the site rather than those utilizing the area as a corridor between habitats (Speight et al. 2000).

Sample collection and determination

A 5 x 5 metre area around each trap was excluded from livestock using a portable electric fence to protect the traps from damage. Malaise traps were activated on 1st May (2014) with samples subsequently collected from the traps every 14 days until 4th September (2014), creating a total of nine successive sampling periods, hereafter referred to as "periods". All 20 sampling traps had equal sampling intensity and all samples were collected on the same day. Each sample was moved to the laboratory where the two dipteran families (Sciomyzidae and Syrphidae) were determined to species level using Rozkošný (1987) and Vala (1989) for sciomyzids and Ball and Morris (2013) and Stubbs & Falk (2002) for syrphids. It should be noted that seven of the Syrphid 'species' were identified to group level only owing to difficulties associated with the determination of females e.g. *Sphaerophoria* species (Stubbs and Falk 2002).

Data analysis

Statistical analyses were carried out using PAST for univariate analysis (Hammer et al. 2001) and PC-Ord version 6.0 for multivariate analysis (McCune and Mefford 2011). Species accumulation curves, constructed using PC-Ord version 6.0, were used to assess the adequacy of sampling. Accumulation curves were made using each trapping event as a sample (n=180).

Non-metric multi-dimensional scaling ordinations (NMS) of untransformed trap data in species-space were performed using PC-Ord version 6. The ordination used the Sørensen distance measure and 250 real data runs. NMS ordinations do not assume linear relationships and allow the use of distance measures suited to data distributions considered non-normal (McCune and Mefford 2011). NMS was used to investigate patterns and differentiation in assemblage composition between habitats based on spatial and temporal configurations. A second NMS ordination of pooled samples from habitats based on period of capture ordinated in species-space was also performed e.g. all samples from *Carex*/Grass from period one were pooled and referred to as C1. This was considered a spatiotemporal ordination as both temporal variation and spatial variation (in the form of habitat type) were examined. Sequential vectors were utilized to illustrate the relationship between spatiotemporal samples. A non-parametric multivariate analysis of variance (PerMANOVA) was used to test the significance of differentiation between habitats using both untransformed and $\log_{10}(x+1)$ transformed data. An examination of $\log_{10}(x+1)$ transformed data was used to down-weight dominant species.

Additive and multiplicative partitioning of species richness along with Shannon’s and Simpsons diversity was performed using PARTITION 3.0 (Veech and Crist 2009). By performing the procedure outlined by Lande (1996) we were able to examine the contribution of each of the alpha and beta diversity components to overall (gamma) diversity (Veech et al. 2002). This methodology has previously been shown to be effective for analysing the role of spatial scale in species diversity. For spatial partitioning, data from each site was pooled across the sampling periods (n=10); for temporal partitioning, trap data were pooled together based on sampling period and habitat type (n=18); for spatiotemporal partitioning data from each site at each time period were considered a replicate (n=90). Comparisons were made between the observed diversities and 10000 individual based randomisations to account for any possible autocorrelation. Spatial diversity was partitioned into α (within sites), β_1 (among sites), and β_2 (between habitats). Temporal diversity was partitioned into α (within periods based on habitat type), β_1 (among periods based on habitat type) and β_2 (between habitats). Spatiotemporal diversity was partitioned into α (within samples), β_1 (among samples) and β_2 (among samples from different habitats at different periods).

Indicators species analysis (ISA) based on Dufrene and Legendre (1997) was carried out on the spatiotemporal dataset (n=90) with groups defined as habitat types and period as a blocking variable (McCune and Mefford 2011). This methodology is suited to an experiential set-up where blocks can be considered as temporal analogues to a traditional randomised complete block design where they would be spatial (McCune and Mefford 2011). The blocked ISA assesses group indicators based on the relative frequency and abundance within each group by examining relativized data from within each block (period). Monte Carlo permutation tests based on 4999 permutations give an estimated *P*-value for the percentage of perfect indication, or indicator value (IV). In this instance it was used to identify species with fidelity to particular habitat types.

Results

A total of 180 samples were collected from 20 Malaise traps over an 18 week period, with this sampling effort yielding 34 sciomyzid species (2,589 individuals) and 72 syrphid species (9,567 individuals). Species accumulation curves for both families approach an asymptote based on first order jackknife estimates (Figures 1a and 1b). Rare species (singleton and doubletons) accounted for 24% of Sciomyzidae and 31% of Syrphidae.

Spatial and Temporal differentiation

The ordination of traps in species-space resulted in two-dimensional solutions for both dipteran families explaining 69.2% of the variance for Sciomyzidae (Stress 12.73) and 89.5% of the variance for Syrphidae (Stress 9.16) (Figures 2a and 2b). Stress values of <10 are considered reliable for interpretation of ecological data (McCune and Mefford 2011). Habitats were significantly different for both families based on a PerMANOVA of traps in species space using both untransformed and transformed data (Table 1). In the Sciomyzidae data, *Juncus*/Grass habitats showed more marked variance among traps with an average Sørensen distance measure of 0.71 compared to *Carex*/Grass traps with an average distance measure of 0.58. Syrphidae data showed that traps from *Juncus*/Grass were less varied having an average distance measure of 0.40 compared with *Carex*/Grass which had an average distance measure of 0.53. Ordinations of samples from habitats pooled according to period of capture (Spatiotemporal analysis) resulted in a three dimensional solution for Sciomyzidae (stress 4.80) explaining 86.7% of the variance (Figure 2c). The same ordination for Syrphidae resulted in a two dimensional solution explaining 86.3% of the variance with a stress of 5.22 (Figure 2d). Sequential vectors for both families showed different temporal trajectories with Sciomyzidae having a linear pattern and Syrphidae showing a more cyclical pattern whereby early and late temporal samples were similar. Habitats were significantly different for Sciomyzidae in the spatiotemporal ordination but not significantly different for Syrphidae (Table 1).

Partitioning of Diversity

In terms of spatial scale, within and among site diversity contributed the most to overall diversity for both families (Table 2) although they are not significantly higher or lower than expected. A similar pattern is seen in temporal partitioning with within period and among period contributing the most to overall diversity (Table 2). In both of these scales, the contribution of habitat type was ≤20% of the total diversity, though in both scales the contribution of habitat (β_2) type is significantly higher than expected across all diversity measures (with the exception of Simpsons diversity in spatial scale and multiplicative diversity in temporal scale for Syrphidae). When diversity was partitioned using spatiotemporal replicates, which compare sites and habitats at different times, the contribution of habitat type markedly increases for both families and is significantly higher than expected by chance (Figure 3).

Indicator species analysis

Blocked indicator species analysis (Table 3) highlighted a total of seven species indicative of *Carex*/Grass habitats and 12 for *Juncus*/Grass habitats. Both habitats have similar numbers of sciomyzid indicators, however *Juncus*/Grass habitats had six Syrphidae indicators in comparison to two in the *Carex*/Grass habitats.

Discussion

Our results show that both types of wet grassland contribute towards the maintenance of Diptera diversity. An overall trend within the data indicates that diversity is spatially structured among sites and habitats with temporal turnover also an important factor. The resulting spatiotemporal variation between wet grassland habitats with different vegetation types is a significant contributor to species diversity in these areas. The results indicate that areas of wet grassland dominated by *Juncus* vegetation which are normally associated with low ecological and agricultural value play an important role in maintaining the diversity of Sciomyzidae and

Syrphidae. Further to this, our analysis shows that the role each habitat contributes to dipteran diversity is dependent on temporal considerations, with each habitat harbouring important levels of species at different times. It is only through the comprehensive spatiotemporal analysis of these sites that the ecological importance of *Juncus* dominated wet grasslands can be considered in terms of the diversity of these two Diptera families.

Dominant vegetation type significantly differentiated the Sciomyzidae and Syrphidae communities; a pattern previously noted in investigations of Diptera from different habitat types (Hughes et al. 2008; Savage et al. 2011). Spatial NMS analysis in this study suggests that this differentiation is a combination of the relative abundance of certain species within each habitat type and the preference of particular species for certain habitats as seen in the ISA. The species indicators of *Carex*/Grass habitats all have relatively similar ecological preferences whereas the species indicative of *Juncus*/Grass habitats are more multifarious in their larval and adult habitat preferences.

The sciomyzid species most significantly associated with *Carex/*Grass habitats are all predators of aquatic or semi-aquatic snails which become stranded or exposed during fluctuations in water levels (*Pherbellia ventralis* [Fallén, 1820], *Ilione albiseta* [Scopoli, 1763], *Sciomyza testacea* [Maquart, 1835], *Tetanocera fuscinervis* [Zetterstedt, 1838], *Colobaea bifasciella* [Fallén, 1820]) (Knutson and Vala 2011; Speight and Knutson 2012). This is consistent with the hydrology of the *Carex*/Grass sites examined in this study which are prone to winter flooding but are largely dry during the summer months which would facilitate the feeding strategy of the larvae of these indicator species. The two Syrphidae indicator species of these habitat types are largely associated with the combination of grassland and lush marsh vegetation typical of wet grasslands, as well as having larvae that can tolerate the inundation that is typical within the *Carex*/Grass habitats (*Platycheirus clypeatus* [Meigin, 1822] and *Platycheirus fulviventris* [Macquart, 1829] (Speight et al. 2000). *Platycheirus clypteatus*, in particular, is known to prefer unshaded, open grassy areas that are not subject to very heavy grazing (Stubbs and Falk 2002); both characteristic features of the *Carex*/Grass habitats in this study.

The sciomyzids associated with *Juncus*/Grass habitats range in trophic strategy between predators of aquatic snails (*Tetanocera robusta* [Loew, 1847], *Tetanocera ferruginea* [Fallén, 1820]), generalised predators (*Pherbellia argyra* [Verbeke,1967]), specialist predators of pea mussels (*Renocera pallida* [Fallén, 1820]) and terrestrial predators (*Tetanocera arrogans* [Meigen, 1830] and *Tetanocera elata* [Fabricius, 1781]) (Knutson and Vala 2011; Speight and Knutson 2012). This broad range of trophic guilds is also evident in the spatial NMS ordination which shows high variability between *Juncus*/Grass areas and illustrates that these sites may have assemblage types which are very variable and site-specific. This idiosyncratic mixture of species is also evident in the range of Syrphidae indicators of the habitat. Some of the *Juncus*/Grass syrphid indicator species such as *Platycheirus granditarsus* (Forster, 1771), *Platycheirus rosarum* (Fabricius, 1787) and *Neoascia tenur* (Harris, 1780) are typically associated with wet grassland habitat features such as marshy vegetation and standing water (Speight et al. 2000; Stubbs and Falk 2002). The remaining indicator species such as *Melanostoma scalare* (Fabricius, 1794) and *Chrysotoxum bincinctum* L., 1758 are associated with more sheltered grasslands, whereas *Volucella pellucens* L., 1758 is typically found in woodland and copses (Stubbs and Falk 2002). The long robust vegetation that typifies the *Juncus*/Grass habitats may well act as a refuge for certain syrphid species in the absence of significant shelter belts such as woodland or hedgerow features within these grasslands (Sarthou et al. 2005). In this respect, the dominance of *Juncus* in these areas appears to be beneficial to Hoverflies.

The spatiotemporal NMS results illustrate a cyclical successional pattern of Syrphidae and temporal differentiation between the habitat types. Syrphidae are exceptionally mobile and may move freely between habitat types in response to perturbations or resource requirements (Sommaggio 1999; Stubbs and Falk 2002). Several of our sampling sites were in close enough proximity to one another and had no significant barriers to hoverfly movement (Wratten et al. 2003). It is not unreasonable to suggest that this would have allowed species to move between habitat types in response to temporal changes in environmental condition e.g. seeking out newly available floral resources, shelter from predators or poor weather, or lekking sites (Sommaggio 1999; Sutherland et al. 2001; Haenke et al. 2014). This dynamic shifting of species between habitat types at different times is evident in the large contribution of beta diversity between habitats at different times to the overall diversity of Syrphidae. This somewhat suggests that Syrphidae may utilize certain *Juncus*/Grass sites at particular times and possibly relocate to *Carex*/Grass habitats in response to resource availability, disturbance in the form of grazing or a combination of both. A reduction in the availability of *Juncus* dominated wet grasslands could therefore have a negative effect on the diversity of Syrphidae at a landscape level.

In contrast to the vagile nature of Syrphidae, Sciomyzidae are relatively sedentary, having a marked habitat fidelity (Williams et al. 2010) and have previously shown very high site-specificity (Maher et al. 2014). The contribution of spatiotemporal partitioning to overall Sciomyzidae diversity is not solely an artefact of differences between habitats at different times but also the diversity among sites at different times as seen in figure 3. Sciomyzidae are unlikely to move between habitat types so changes in community composition are possibly a result of phenological shifts in community structure at site level whereby species with different over-wintering and reproductive strategies dominate sites at different times. Berg and Knutson (1978) remark that seasonal mortality or a hiatus in reproduction may limit the population of multivoltine Sciomyzidae in ephemeral wetlands such as wet grasslands. This interruption enables univoltine species to compete with multivoltine species on more even terms in these habitats, rather than in habitats that remain suitably wet throughout the summer. The univoltine species *I. albiseta* was a strong and significant indicator of *Carex*/Grass habitats which typically follow a predictable pattern of winter flooding followed by dry summer as proposed by Berg and Knutson (1978). Based on the wide range of species indicative of the *Juncus*/Grass habitats, it would appear that these habitats have a broader scale of hydrological variability which accounts for their support of sciomyzids that range from fully aquatic larvae e.g. *T. robusta*, to fully terrestrial larvae e.g. *T. elata.* The singular nature of each of the *Juncus*/Grass sites in terms of sciomyzid composition, therefore, contributes significantly to the overall species diversity, at a landscape scale, within these wet grasslands.

Patterns of differentiation between *Carex* and *Juncus* dominated grasslands have previously been reported for Sciomyzidae with *Juncus* dominated wet grasslands often supporting a wider range of species (Carey et al. 2015). It is also interesting to note that spatiotemporal habitat differentiation decreased in the Sciomyzidae samples at the later stages of the collection (Period 9). Flood depth and duration are known to benefit sciomyzid species richness (Maher et al. 2014) as well as molluscs (Ilg et al. 2009). It is possible that as sites started to become inundated towards the end of the collection period (Period 9), mollusc prey became more readily available and competition between species was reduced allowing for a more diverse fauna to co-exist within sites.

Several environmental factors including hydrological regime, vegetation structure and composition have all been shown to influence community structure and species richness of Sciomyzidae and Syrphidae (Carey, LeRoy et al. 2015; González-Megías et al. 2011; Maher et al. 2014; Ryder et al. 2005; Williams et al. 2009b). Various permutations of each of these variables, which themselves are subject to changes across temporal scales, may exist within each sample site and by reason within each habitat. Vegetation composition and structure, for example, continuously alters throughout the growing season and wet grasslands generally begin to inundate in the Autumn/Winter. It is likely that the contribution of temporal turnover to species diversity is related to a combination of these perturbations, the availability of resources associated with them and the phenology of the species within each of the families. In our study, spatial variability appears to act as a safeguard for Syrphidae allowing them to exploit different habitats at different times, whereas Sciomyzidae communities within wet grasslands are especially site specific and rely on temporal variation within sites to complete their life cycles.

The maintenance of habitat heterogeneity is largely considered an elixir for the conservation of biodiversity within agricultural areas (Benton et al. 2003; Tews et al. 2004; Fahrig et al. 2011), and the broad scale beta diversity associated with increased habitat heterogeneity is known to significantly increase the diversity of insects at spatial (Gering et al. 2003), temporal (Zamora et al. 2007; González-megías et al. 2011) and spatiotemporal scales (Sobek et al., 2009a; Sobek et al., 2009b; Tylianakis et al., 2005). It should also be noted that previous studies in regions with more extreme seasonality such as the Mediterranean have determined that temporal changes have a major influence of insect diversity (Zamora et al. 2007; González-megías et al. 2011). Our results suggest that even in a temperate climate such as the west of Ireland, these processes have similar influences on the γ-diversity and should be considered an integral component of wet grassland Diptera diversity.

Conclusions

Where conservation objectives continuously focus on one particular outcome such as maintaining or increasing plant species richness in wet grasslands, a consensus can (inadvertently) be formed that such aims are a suitable panacea for biodiversity protection in general. Few studies have examined the contribution of *Juncus* dominated wet grassland to biodiversity owing to its general lack of botanical diversity. However, when invertebrate groups such as Diptera are considered in evaluations, it is apparent that *Juncus* dominated wet grasslands play a vital role in maintaining the diversity of these groups. Our study demonstrates that both spatial and temporal turnover is a significant factor in dipteran diversity, and needs to be considered in the evaluation of habitats for conservation potential. The spatiotemporal variation between habitat types in lowland wet grasslands was a significant contributor to Sciomyzidae and Syrphidae in our study. While the work presented in this investigation is particular to the location of the study, similar spatiotemporal evaluations of habitats, normally not considered as ecologically important, may yield significant insights into the roles that such areas play in maintaining the diversity of overlooked groups such as Diptera. We suggest that in lowland wet grassland habitats, areas of dominant *Juncus* cover maintain highly varied communities of Sciomyzidae and provide resources on a wider scale for Syrphidae; therefore they should be regarded as ecological focus areas. The loss of *Juncus* dominated areas of lowland wet grasslands could have serious implications for the conservation of Sciomyzidae and Syrphidae in wet grassland ecosystems.

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Figure Captions

Table 1: Results of PerMANOVA based on Bray-Curtis dissimilarities of Diptera assemblages between two habitat types. Spatial groups are based on samples from sites; Spatiotemporal groups are based on samples collected from the same habitat at the same time period.

Table 2: Partitioning of additive, multiplicative species richness and Shannon's and Simpsons diversity between / among grouping variables. Figures followed by no asterisk were not significantly different from a random distribution based on 10000 individual-based iterations. $^*P < 0.05$ (higher than expected by chance). Null values in parentheses.

Table 3: Significant (P <0.05) Sciomyzidae and Syrphidae indicator species for wet grassland habitat type based on dominant vegetation cover (*Carex*/Grass or *Juncus*/Grass).

Fig 1: Sciomyzidae **a)** and Syrphidae **b)** species accumulation curve and distance (dissimilarity) decay curve for all samples. Dotted lines represent ± 2 SDs. First Order Jackknife estimates of total species richness were 38.97 (Sciomyzidae) and 87.91 (Syrphidae).

Fig. 2: Non-metric multi-dimensional (NMS) scaling of traps in **a)** Sciomyzidae species-space and **b)** Syrphidae species-space. Habitat type is denoted by grey circles (*Carex*/Grass) and black triangles (*Juncus*/Grass). Letters associated with traps refer to pair-wise counterparts from the same sites e.g. C1A and C1B are from the same sites. NMS ordination of pooled spatiotemporal samples in **c)** Sciomyzidae species-space and **d)** Syrphidae species-space. Numbers associated with habitats refer to the sampling period e.g. C1 are the pooled samples from *Carex*/Grass habitats from period one. Grey and black lines linking habitat-period samples are successional vectors.

Fig. 3: Percentage of total species richness (additive partitioning) explained by alpha and beta components of diversity. Beta diversity is partitioned among/between three spatial scales: sites (β_1) and habitats (β_2). Temporal beta diversity is partitioned among 18 samples based on habitat type and time (β_1) and between habitat type (β_2). Spatiotemporal beta diversity is partitioned into among samples from sites at different times (β_1) and among habitats at different times (β_2).

Table 2:

	Untransformed data			Transformed data		
	Df	Pseudo F value	*P*	Df	Pseudo F value	*P*
Spatial						
Sciomyzidae	1	3.738	0.0017**	1	3.468	0.001**
Syrphidae	1	5.957	0.0001**	1	2.065	0.028*
Spatiotemporal						
Sciomyzidae	1	3.6704	0.005**	1	3.6704	0.005**
Syrphidae	1	1.0943	0.332	1	0.8349	0.0480

Table 2:

	Additive species richness			Multiplicative species richness (q = 0)			Shannon's diversity (exp H) (q = 1)			Simpsons diversity (1/D) (q = 2)		
	α	β_1	β_2	α	β_1	β_2	α	β_1	β_2	α	β_1	β_2
Spatial (n=10)												
Sciomyzidae	15.30	12.20	**6.50*** **(4.05)**	15.30	1.80	**1.24*** **(1.14)**	7.70	1.47	**1.11*** **(1.01)**	4.91	1.44	**1.12*** **(1.00)**
Syrphidae	34.10	25.40	**12.50*** **(9.44)**	34.10	1.74	**1.21*** **(1.15)**	7.03	1.12	**1.03*** **(1.00)**	3.46	1.07	1.00
Temporal (n=18)												
Sciomyzidae	13.20	14.22	**6.50*** **(3.42)**	13.28	2.07	**1.24*** **(1.11)**	5.45	1.77	**1.25*** **(1.01)**	2.99	1.79	**1.41*** **(1.00)**
Syrphidae	24.78	35.72	**11.50*** **(9.92)**	24.78	2.44	1.19	7.76	1.14	**1.08*** **(1.00)**	4.34	0.93	**1.08*** **(1.00)**
Spatiotemporal												
Sciomyzidae	5.74	14.76	**13.50*** **(2.19)**	5.74	3.57	**1.66*** **(1.07)**	3.12	3.58	**2.85*** **(1.15)**	2.26	3.35	**3.92*** **(1.20)**
Syrphidae	10.87	13.80	**47.33*** **(42.75)**	10.87	2.27	**2.92*** **(2.46)**	4.47	1.67	**1.81*** **(1.14)**	2.85	1.46	**1.69*** **(1.03)**

Table 3:

	***Carex*/Grass**	
Sciomyzidae	IV (% perfect indication)	*P*-value
Pherbellia ventralis (Fallén, 1820)	49.8	0.0006
Ilione albiseta (Scopoli, 1763)	46.9	0.0058
Sciomyza testacea (Maquart, 1835)	24.4	0.0008
Tetanocera fuscinervis (Zetterstedt, 1838)	23.9	0.0070
Colobaea bifasciella (Fallén, 1820)	18.2	0.0254
Syrphidae		
Platycheirus clypeatus (Meigin, 1822)	64.9	0.0040
Platycheirus fulviventris (Macquart, 1829)	14.0	0.0410

	***Juncus*/Grass**	
Sciomyzidae	IV (% perfect indication)	*P*-value
Tetanocera ferruginea (Fallén, 1820)	36.7	0.0084
Renocera pallida (Fallén, 1820)	35.1	0.0122
Tetanocera arrogans (Meigen, 1830)	34.3	0.0224
Tetanocera robusta (Loew, 1847)	30.3	0.0016
Pherbellia argyra (Verbeke,1967)	17.8	0.0048
Tetanocera elata (Fabricius, 1781)	16.5	0.0174
Syrphidae		
Platycheirus granditarsus (Forster, 1771)	55.9	0.0080
Melanostoma scalare (Fabricius, 1794)	39.9	0.0280
Platycheirus rosarum (Fabricius, 1787)	36.2	0.0302
Neoascia tenur (Harris, 1780)	27.7	0.0314
Chrysotoxum bincinctum (L., 1758)	23.9	0.0260
Volucella pellucens (L., 1758)	10.4	0.0350

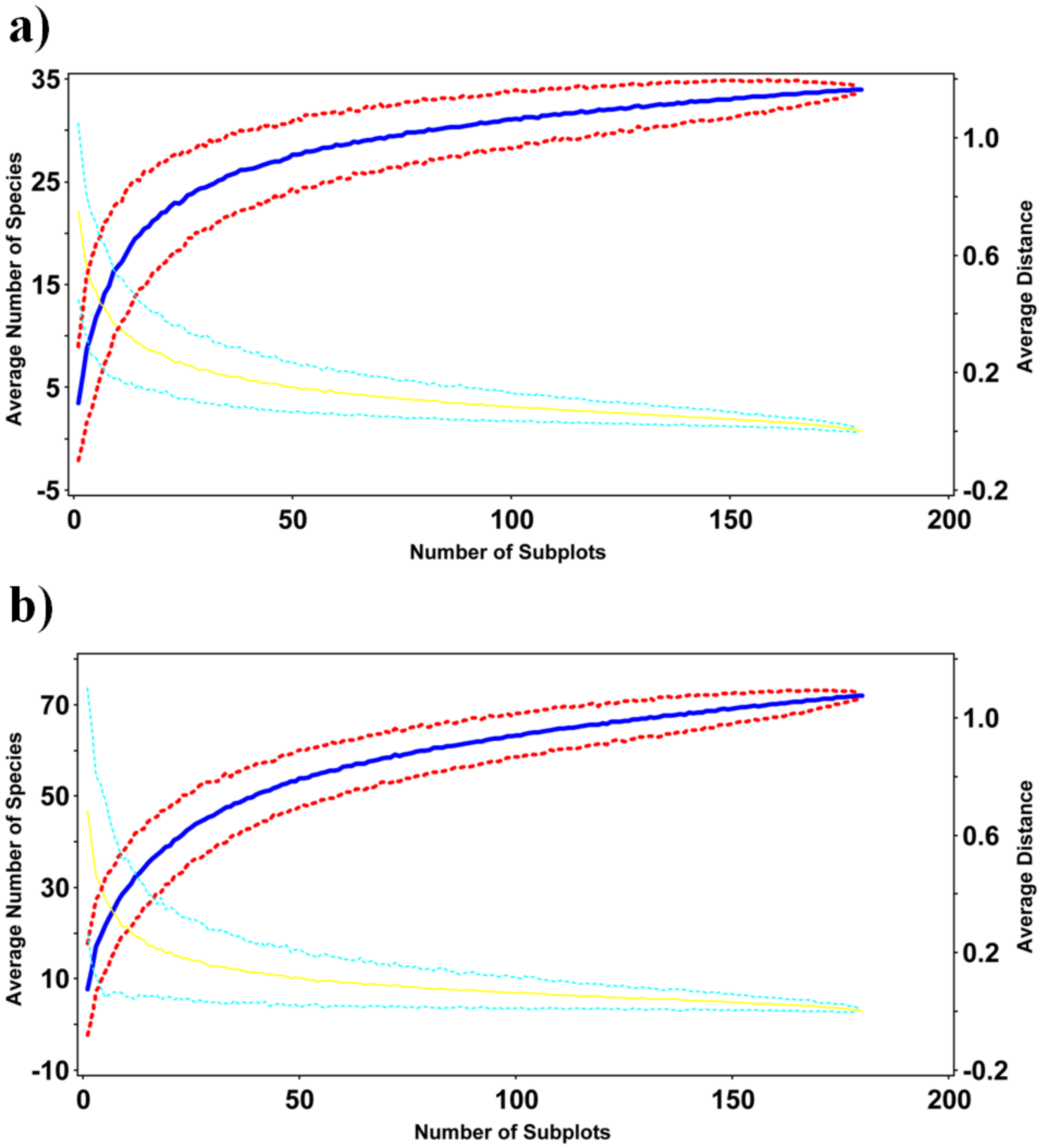

a)
35
25
15
5
-5
Average Number of Species
1.0
0.6
0.2
-0.2
Average Distance
0
50
100
150
200
Number of Subplots
b)
70
50
30
10
-10
Average Number of Species
1.0
0.6
0.2
-0.2
Average Distance
0
50
100
150
200
Number of Subplots

Fig 1:

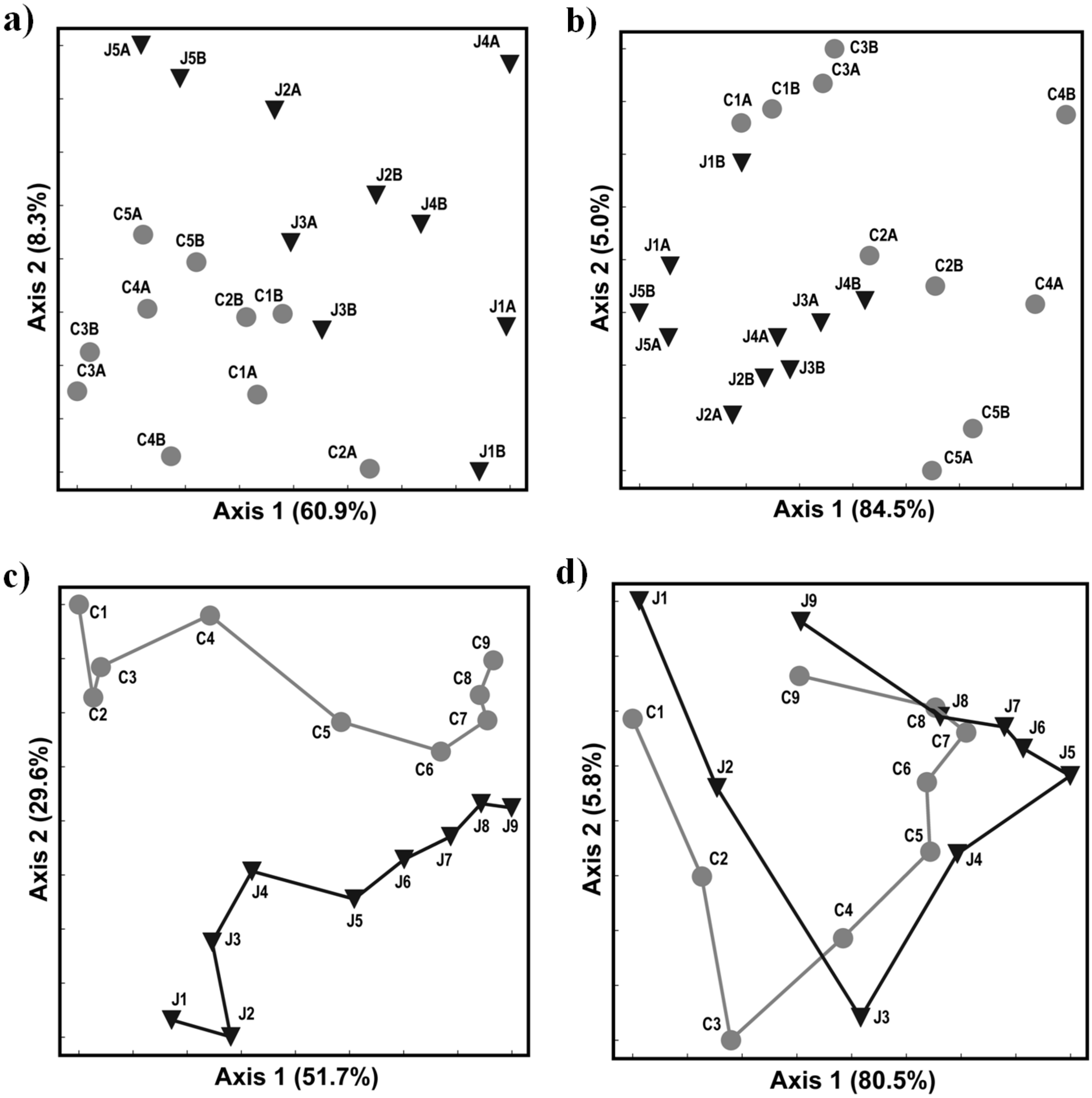
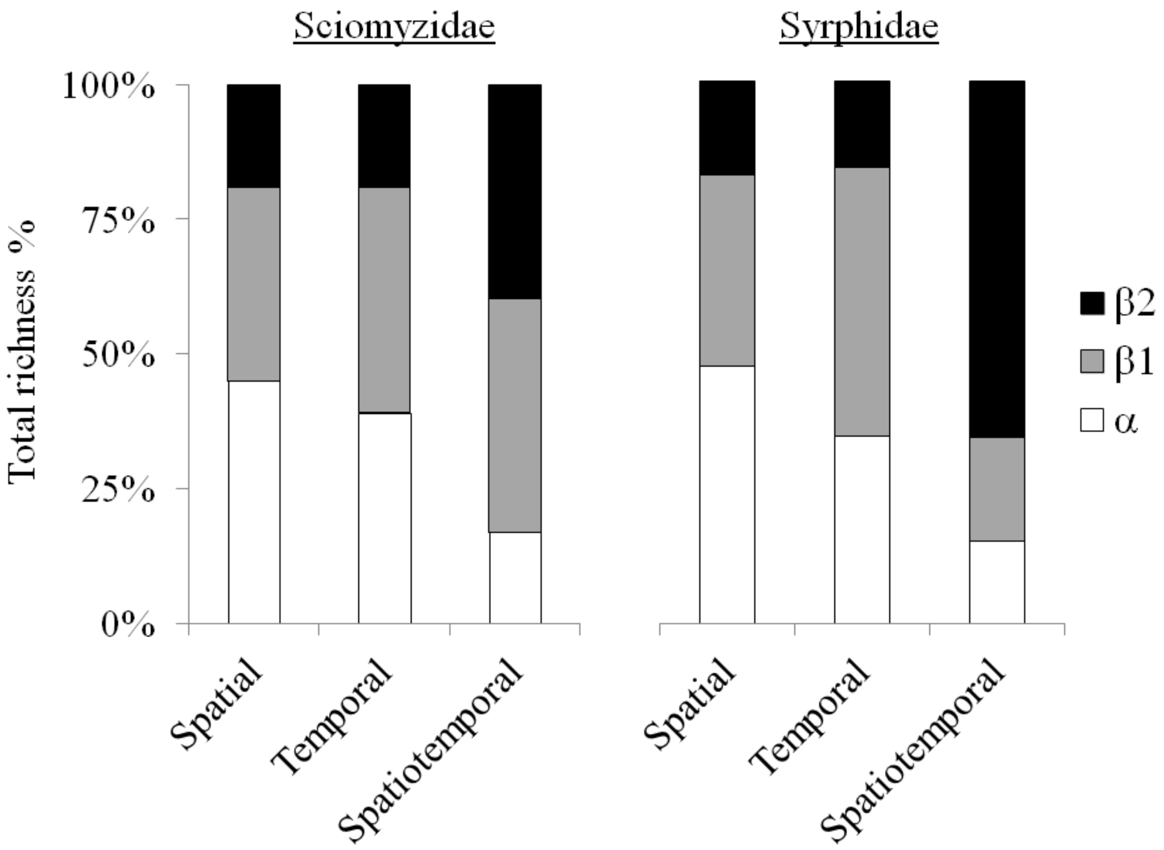

a)
J5A
J5B
J4A
J2A
J2B
J4B
C5A
J3A
C5B
C4A
C2B
C1B
J3B
J1A
C3B
C3A
C1A
C4B
C2A
J1B
Axis 2 (8.3%)
Axis 1 (60.9%)
b)
C3B
C3A
C1B
C1A
C4B
J1B
C2A
J1A
C2B
C4A
J4B
J5B
J3A
J4A
J5A
J3B
J2B
J2A
C5B
C5A
Axis 2 (5.0%)
Axis 1 (84.5%)
c)
C1
C4
C3
C2
C9
C8
C7
C5
C6
J8
J9
J7
J6
J4
J5
J3
J1
J2
Axis 2 (29.6%)
Axis 1 (51.7%)
d)
J1
J9
C9
J8
J7
C8
C1
J6
C7
J5
C6
J2
C5
J4
C2
C4
J3
C3
Axis 2 (5.8%)
Axis 1 (80.5%)

Fig. 2:



Sciomyzidae
Syrphidae
Total richness %
100%
75%
50%
25%
0%
Spatial
Temporal
Spatiotemporal
Spatial
Temporal
Spatiotemporal
β2
β1
α

Fig. 3: