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Assembly Rules in Muscid Fly Assemblages in the Grasslands Biome of Southern Brazil

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ABSTRACT - The distribution of muscid species (Diptera) in grasslands fragments of southern Brazil was assessed using null models according to three assembly rules: (a) negatively-associated distributions; (b) guild proportionality; and (c) constant body-size ratios. We built presence/absence matrices and calculated the C-score index to test negatively-associated distributions and guild proportionality based on the following algorithms: total number of fixed lines (F_L), total number of fixed columns (F_C), and the effect of the average size of the populations along lines (W) for 5000 randomizations. We used null models to generate random communities that were not structured by competition and evaluated the patterns generated using three models: general, trophic guilds, and taxonomic guilds. All three assembly rules were tested in each model. The null hypothesis was corroborated in all F_L X F_C co-occurrence analyses. In addition, 11 analyses of the models using the W algorithm showed the same pattern observed previously. Three analyses using the W algorithm indicated that species co-occurred more frequently than expected by chance. According to analyses of co-occurrence and guild proportionality, the coexistence of muscid species is not regulated by constant body size ratios. In flies of the grasslands, no rule was identified. Yet, a consensus did emerge from our analyses: species co-occur more frequently than expected by chance, indicating that aggregation is a recurring phenomenon among flies with saprophagous adults and predatory larvae. Therefore, competition does not seem to play an important role in the determination of muscid assemblages in the grasslands in Southern Brazil.

KEY WORDS: Community, competition, Diptera, Muscidae, niche theory, null model

The distribution of species in a given area is governed by deterministic assembly rules due to the importance of interspecific interactions (Diamond 1975). They are based on the assumptions that: (i) species with strong overlap in resource use or other niche dimensions cannot coexist (Gause 1934, Hardin 1960, Simberloff & Connor 1981) and (ii) species that do coexist differ in body size or functional morphology which allows their exploitation of different resources (Brown & Wilson 1956, Hutchinson 1959, Simberloff & Boecklen 1981). These two assumptions have been incorporated into the ecological niche theory that describes the existence of rules for the structuring and coexistence of species within communities.

Several rules have been described based on these assumptions, including body-size ratios, favorable states, guild proportionality, nestedness, environmental characteristics, forbidden species combinations, incidence functions, and checkerboard distributions (Diamond 1975, Patterson & Atmar 1986, Fox 1987, Wilson 1989, Fox & Brown 1993, Dayan & Simberloff 1994, Weiher & Keddy 1999). In most rules, the process is inferred, but not tested. This approach has often raised considerable criticism on the validity of these rules for niche theory (Weiher & Keddy 1999).

The process inferred as the underlying cause of the observed patterns is interspecific competition within a guild, functional group or taxonomic group more than among species of different groups (Root 1967, Simberloff & Dayan 1991, Blondell 2003). These groups would be structured through the principle of competitive exclusion due to the strong repulsion between pairs of species, thus generating negatively-associated distributions in a pattern known as "checkerboarding" (Diamond 1975). In this case, the number of species within a guild would be limited by competition, and the choice of the groups to be analyzed suggests that ecological guilds are the most appropriate units to reveal patterns caused by competitive interactions.

Assembly rules based on guilds posit that the proportion of species within guilds is not completely homogeneous among communities, such that each guild, functional or taxonomic group is not equally represented with respect to the number of species (Fox 1987, Pimm 1991, Simberloff & Dayan 1991, Wilson *et al* 1995). In these models, the null hypothesis, which is usually implicit, is that the relative frequency of guilds in the assembly represents a random sample from the regional set of species. When deviations are exceedingly large, certain guilds are over- or underrepresented in local assemblies. On the other hand, if co-occurrence or guild structure patterns are not different from the null hypothesis in either ecological or taxonomic groups, one can expect that the mechanisms leading to coexistence should be related to constant size ratios (Hutchinson 1959). The differences found among adjacent species would then result from character displacement in the recent past.

Simberloff & Dayan (1991), in a comprehensive review of the concept of guild and of the structure of communities, defined a taxonomic guild as a group of closely-related species using the same class of resources. This definition stems from the assumption that taxonomically close species have similar morphology, physiology and behavior, exploring their environments in a similar way. Also stems from the Darwinian assumption that congeners show high levels of competition because of taxonomic similarity, and therefore are similar in their niche use. This way of interpreting competition is inserted within the definition of the Hutchinsonian niche, according to the principle of competitive exclusion that leads to biological diversification, niche theory, and character displacement (Gause 1934, Brown & Wilson 1956, Hutchinson 1957, 1959, MacArthur & Levins 1967).

These assembly rules are very general with respect to the tested groups. In an analysis of 96 presence/absence matrices, Gotelli & McCabe (2002) found significant differences among taxonomic groups in the tested null models, with differences in the patterns of species distributions. According to the authors, most matrices were non-random among homeotherms when compared to poikilotherms. Among the latter, plant and ant matrices were more structured than those of fish and reptiles. Two possible causes have been raised for this pattern: i) plants and ants are groups that disperse less than other groups, and ii) there could have been a dilution effect among the random matrices. The dilution effect has been proposed by Gilpin & Diamond (1982) as a criticism to the tests carried out by Connor & Simberloff (1979). This effect refers to the analysis of taxonomic groups or entire faunas using presence/absence matrices, without considering the existing guilds in these groups.

The designation of a guild is not a simple task, and its delimitation can influence tests using null models (Gotelli & Graves 1996). The central idea of the dilution effect is that species of different guilds will do not overlap in the used resources, and therefore the analysis using a matrix that represents interactions among species would dilute the effects of competition (Gilpin & Diamond 1982). Another interpretation of this effect is that a presence/absence matrix of all species could have apparent structure due to historical processes rather than competitive interactions among the species (Gotelli 2000).

Given the importance of guilds and the tested habitats, Rodriguez-Fernández *et al* (2006) assessed the structure of muscid assemblages in eight locations in the State of Paraná, southern Brazil. They build models based on all analyzed species with respect to the feeding habits of adults and found significant segregation among species according to the ecological guild and the tested scale. Because of the geographical scale of the study, such structure could have resulted from historical effects, habitat heterogeneity and competitive interactions.

Muscidae is one of the most diverse dipteran families, with nearly 4,500 described species distributed among 180 genera throughout all biogeographical regions. The Neotropical region harbors 846 species and 84 genera, although these figures are probably underestimated (Carvalho & Couri 2002, Carvalho *et al* 2005). This underestimate is due to the wide range of habitats used by muscids. Adults and larvae have feeding strategies that allow for the occupation of several niches, including vertebrate carcasses and faeces, nests of mammals, birds, and many insects, decomposing tree trunks, roots, and leaves, as well as fungi; water columns in tree hollows, bromeliads, river and lake margins, flooded areas and mud; and live animal tissues, where they can cause obligatory or facultative myiasis. Adults can feed on the substrates where their larvae develop, as well as visiting flowers to obtain nectar, thus playing a role in pollination (Skidmore 1985, Ferrar 1987).

In addition to adult habits, larvae also possess characteristics that can be investigated in inferences on assembly structure from null models and assembly rules. Data on resource use of immature insects, particularly dipterans, have been used to test the limits to coexistence in ephemeral systems, such as carcasses, macroscopic fungi, and fruits (Sevenster & van Alphen 1996).

In this study, we assess patterns in muscid assemblies in the grasslands biome in southern Brazil using null models from assumptions based on deterministic rules for verification of dilution effect. Such null models exclude the biological effects on species distributions in different locations. If the observed patterns are different from those expected based on the null model, we would conclude that competition or aggregation play a role as a biological mechanism that could structure muscid assemblies, or else the observed structures will be interpreted as having been randomly formed.

The null hypothesis to be tested is that the presence of a given muscid species does not influence the occurrence of other species, and therefore there would be no evidence that competition is the structuring force in muscid communities in the grasslands biome. If the co-occurrence index estimated from the original matrix is within the 95% confidence interval of the randomized matrices, the null hypothesis is accepted and the existence of a biological mechanism to determine species distributions is not corroborated. On the other hand, if the co-occurrence index of the original matrix is above the 95% confidence interval of the randomized matrices, the null hypothesis should be rejected and the role of competition in structuring the studied competitions is confirmed. Finally, if the observed C-score is smaller than that estimated in the null model, the observed occurrence patterns are most consistent with aggregation that with segregation (Stone & Roberts 1990).

In guild proportionality analyses, the constitution of the guilds becomes the *a priori* hypothesis. Despite the extensive review of the habits of muscid species by Skidmore (1985) and Ferrar (1987), knowledge of resource use by larvae and adults is still incipient in the Neotropical region. Therefore, we followed the classification of Muscidae for taxonomic guilds (Carvalho *et al* 2005) and the considerations of Skidmore (1985) for ecological guilds. These analyses provide the significance of the co-occurrence patterns among different guilds (ecological and taxonomic). Should the variance be larger than estimated, we would conclude that guilds differ much from one another in their pattern of co-occurrence. On the other hand, if the variance is smaller than estimated, this would indicate that the patterns of co-occurrence of the guilds are similar, suggesting strong aggregation among species with respect to their distribution patterns within guilds. This test was carried out to assess the distribution of species among different groupings, given that the C-score values obtained from the co-occurrence analyses can be different from those obtained in guild proportionality analyses (Gotelli & Entsminger 2001b).

In the analysis of co-occurrence and guild proportionality, we are exploiting the body-size ratios. In this case, a community structured by competition should present species with differences in size with a minimal niche overlap. It is therefore expected a relatively small variance in the body-size ratios when compared to the null model. Two distinct processes can explain non-random results from these analyses: (i) a biological mechanism is an important process that leads to a constant body-size ratio, thus reducing its variance; and (ii) the variance is so large that groups either show very small or large body sizes when compared to each other in each location depending on the model. The null hypothesis is that there is no difference in the observed and estimated variances, where we expect that structuring in morphological traits should be more likely than spatial structuring.

Material and Methods

Sampling. The material for the present study was obtained from collections carried out in four locations within the Grasslands biome in the southernmost region of the state of Rio Grande do Sul, Brazil, in the following municipalities: Arroio Grande (32°13’22”S, 53°11’57”W), Capão do Leão (31°48’16”S, 52°24’13”W), Morro Redondo (31°40’22”S, 52°35’30”W), and Pelotas (31°44’39”S, 52°13’22”W).

A Malaise trap was installed in rural fragments of secondary forest with less than 2 ha in each municipality. Traps were installed near trees with constant shadow, and set up weekly between June 29, 2002 and June 27, 2003, for a total of 52 samples in each locality. Specimens were identified based on Carvalho & Couri (2002), Couri & Carvalho (2002), Nihei (2004, 2005), Costacurta & Carvalho (2005), and Costacurta *et al* (2005).

Ecological guilds in Muscidae. Skidmore (1985) defined muscid taxonomic groups based on the morphology of immature stages, especially larvae. In particular, the author listed eight anatomical characteristics that indicate the habit of the species, mainly involving the morphology of the cephalo-pharyngeal skeleton and the anal spiracles (Skidmore 1985: 14). From these results, two basic morphological types of cephalo-pharyngeal skeleton morphology could be distinguished. One type includes saprophagic larvae with anal spiracles and well-developed suction mechanisms and lacking accessory oral sclerites, thus characterizing trimorphic larvae. Another basic type includes predatory larvae with developed oral hooks and sclerites, with or without a suction mechanism. Predatory species with some suction mechanism are facultative carnivores in their third-instars, whereas those without suction mechanisms are obligatory carnivores.

With respect to adults, three types of habits could be identified. One type includes hematophagous with mouth apparatus adapted to penetration and suction; lickers in the case of saprophagous species and predators, as among species of Coenosiinae. For additional details on the morphology, substrates used by immatures, and species biology, see Skidmore (1973, 1985) and Ferrar (1987).

An ecological guild is defined as a group of species that exploit the same class of resources in a similar manner (Root 1967). Therefore, we defined three ecological guilds or functional groups (Blondel 2003): species with saprophagous larvae and adults; species with predatory larvae and saprophagous adults; and species with predatory larvae and adults (Fig 1).

Taxonomic guilds in Muscidae. A taxonomic guild is defined as a group of closely-related species that exploit the same class of resources in a similar manner (Simberloff & Dayan 1991). Therefore, we defined six taxonomic guilds based on subfamilies of Muscidae (Carvalho *et al* 2005) (Fig 1).

Co-occurrence analyses. A presence/absence matrix was obtained for each of the four sampled locations to build models according to the general model for all muscid species in all four samples locations. To test the ecological guilds model we only used the habits of larvae and adults of Muscidae with seven sub-models: (i) saprophagous larvae; (ii) predatory larvae; (iii) saprophagous adult; (iv) predatory adult; (v) both larvae and adults saprophagous; (vi) predatory larvae and saprophagous adult; and (vii) both larvae and adults predatory. This model was built to assess the influence of the habits of the species according to their developmental stage. Taxonomic guilds model was based on the classification hypothesis of subfamilies based on Carvalho *et al* (2005). This model included six subfamilies or submodels: Muscinae, Azeliinae, Cyrtoneurininae, Mydaeinae, Phaoniinae, and Coenosiinae (Fig 1).

Matrices were submitted to null model analyses using the software EcoSim 7.0 (Gotelli & Entsminger 2001a). The C-score was used as the community structure index based on species interactions (Stone & Roberts 1990). This index is the average of the “checkerboard units” calculated for all species pairs that occurred at least once in the same group. The number of checkerboard units (CU) for each species pair was calculated as $CU = (r_i\text{-}S)\ (r_j\text{-}S)$, where r_i and r_j are the number of locations where species i and j were collected, and S is the number of locations where both species were collected together. The C-score is an index that is negatively correlated with species co-occurrence; therefore, in a community that is structured by competition, the C-score should be significantly lower than expected by chance. Null communities for the C-score index were built using the following algorithms according to Gotelli (2000):

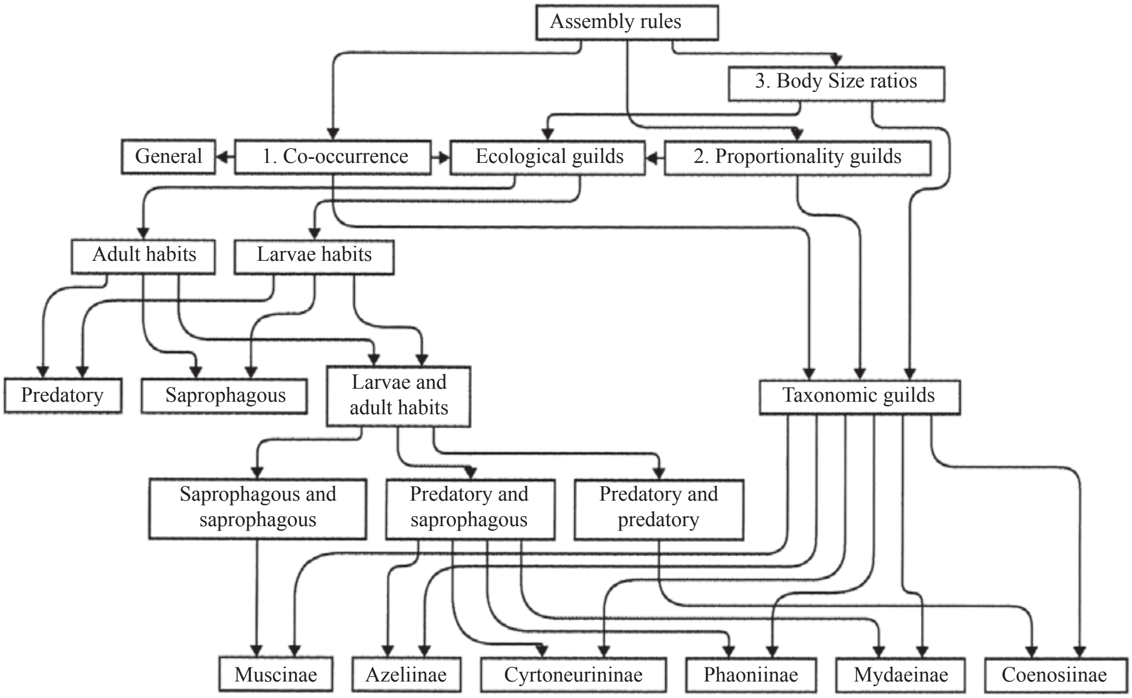

Fig 1 Scheme for the analysis of assemblage models of flies in the family Muscidae in the Grasslands biome.

Fixed lines (F_L) vs. fixed columns (F_C): in this simulation, the sum of the lines and columns of the original matrix are preserved. Each randomly generated community has the same number of species as the original community (the fixed column sum) and each species occurs at the same frequency as the original matrix (the fixed line sum; Connor & Simberloff 1979). This algorithm has good statistical properties (low frequency of both type-I and type-II errors) when used in random or structured matrices (Gotelli 2000), showing considerable power to detect patterns in noisy datasets using the C-score.

Weighted lines (W) vs. fixed columns (F_C): weighting (W) was used as a measure of the relative abundance of each species in each model. The used weighing scheme shows a proportional relationship with the size of the populations in the sampled regions.

The use of this algorithm (W) is due to two factors: i) it relates to the success of the species in a given environment, given that the size of its populations could be related to female reproductive success; and ii) some species occur more frequently than others and therefore some combinations are more common, leading to pairs of common species to be found more commonly than pairs of rare species (Harvey *et al* 1983).

All simulations were carried out using the "swap" algorithm, in which the original matrix is resample repeatedly, generating random submatrices (Stone & Roberts 1990, but see Gotelli 2000, Gotelli & Entsminger 2001b, 2003).

Guild proportionality analyses. A presence/absence matrix of all four localities was considered for the implemented models according to the following ecological and taxonomic guilds model, where species were combined according to the habits of their larvae, adults, or both larvae and adults, and based on the classification hypothesis proposed by Carvalho *et al* (2005).

The analysis procedure was similar to the co-occurrence analyses, also using the C-score index and the swap algorithm. Matrices were built according to the ecological or taxonomic classification of each species. In this analysis, a guild must possess at least two associated taxa, such that EcoSim calculates the significance pattern of the variance in the co-occurrence indices among guilds. A variance that is much larger than the estimated average indicates that guilds differ significantly from one another in their co-occurrence levels. On the other hand, a much reduced variance indicates that guilds are very similar to each other. A value within the 95% confidence interval indicates that the species are randomly added to the guilds.

Analysis of body size overlap. The hypothesis that body size ratios show regular spacing was tested based on the $\log_{10}$-transformation of this measure, followed by the calculation of the differences among species with adjacent sizes. Variances were obtained as an index of body-size ratio constancy (Poole & Rathcke 1979). The measure of the body size ratio was Weber's length, which is frequently used in ant studies as a simple measure of body size (i.e. the distance between the anterodorsal and the posterodorsal margins of the mesonotum) (Brown 1953). Weber's length was calculated for each species in each location, and the overall mean was used as a body size index. Our measure did not take into consideration variation within species (Losos 1990). The uniform null model was used to generate communities with random body sizes. In this model, the end-points of the distribution are fixed and the remaining species (n-2) are randomly chosen in a $\log_{10}$ distribution within those limits. This model assumes that over evolutionary time, everybody size combination is equally probable within the limits imposed by the smallest and largest species (Simberloff & Boecken 1981). This model was used both at the regional (general model) and local scale (locations). Analyses included the models described above (Fig 1).

Results

Community composition. A total of 5,594 specimens belonging to 87 species and 32 genera in six subfamilies of Muscidae (Diptera) were collected. The assemblages of Arroio Grande, Capão do Leão, Morro Redondo, and Pelotas had 53, 61, 65, and 64 species, respectively. *Bithoracochaeta calopus* (Bigot) and *B. plumata* Albuquerque were dominant in the Morro Redondo and Arroio Grande assemblages, whereas as *Phaonia* sp. 1 was the dominant species in the assemblages Pelotas and Capão do Leão. *Limnophora* was a highly abundant genus in all locations. Coenosiinae and Phaoniinae were the subfamilies with the highest richness levels, with 28 and 20 species, respectively (See *Online Supplementary Material* for more detailed list of species by assemblage).

Co-occurrence patterns. Two analysis deviated from the null model, which considered the taxonomic and ecological guilds that used the abundance of species. Based on these analyses, muscid assembly matrices were not structured by competition, nor did they show evidence of checkerboarding in any of the tested models. In the ecological guilds with predatory larvae and saprophagous adults, we observed an aggregation pattern. In another test the pattern of species distribution was random (Table 1).

Guild proportionality. Of the four tested models, three were similar to the null models. Only the species with saprophagic adults indicated a deviation from the null model, with pairs of species with a tendency to co-occur more than expected by chance (average C-score smaller than the observed). However, the co-occurrence patterns within the guilds behaved very differently (observe variance values larger than estimated) (Table 2).

Table 1 Analysis of co-occurrence patterns at the local scale.

Model	Submodel	Algorithm	I_{obs}	I_{sim}	P
General		WxF_C	0.310	0.496	<0.001
Ecological guilds					
	Predatory larvae	WxF_C	0.318	0.458	<0.001
	Saprophagous adult	WxF_C	0.389	0.546	0.006

I_{sim} = mean index of the simulated communities, I_{obs} = observed index, p = tail probability, F_L = line fixed, F_C = column fixed, W_L = line with weight.

Table 2 Analysis of guild proportionality patterns at the local scale.

Model	I_{Mobs}	I_{Msim}	p_M	I_{Vobs}	I_{Vsim}	p_V
Ecological guilds						
Adult	0.251	0.297	0.013	0.037	0.009	0.027

I_{sim} = mean index of the simulated communities, I_{obs} = observed index, p = tail probability, M = mean, V = variance. The algorithm was used F_L to F_C that are the line fixed and column fixed with c-score index.

Body-size overlap patterns. The coexistence of flies in the family Muscidae on Grasslands biome indicated in the co-occurrence and guild proportionality analyses is not regulated by constant body-size ratios. Conversely, the variance was larger than expected by chance in the ecological guild model with saprophagic adults and in the combined larvae and adult sets, indicating that such ecological groups consist of either very small or very large species on aggregated pattern (Table 3).

Discussion

The goal of the proposed models was to determine the effect of dilution on the tested matrices (Diamond & Gilpin 1982, Gilpin & Diamond 1982). Based on this effect, our models were built to take into account the historical relationship among subfamilies and the similarity in their niches due to their shared history (Skidmore 1985, Carvalho 1989, Couri & Carvalho 2003, Carvalho *et al* 2005, Nihei & Carvalho 2007).

The analysis scheme permitted an assessment of the effect of dilution in the general model for ecological guilds, and from this model to taxonomic and sub-family guilds as well (Fig 1). In these models negatively associated distributions between pairs of species were absent, as well as assemblages structured by proportionately-composed guilds, corroborating null hypotheses for the tested patterns from the hypothesized assembly rules. The high level of coexistence between pairs of species is possible based on niche theory if there is a constant ratio of body-size spacing. However, the results indicate that species show aggregation within groups with predatory larvae and saprophagous adults, in sizes either very small or very large, refusing the hypothesis that competition or any mechanism of segregation locally structured muscid assemblies.

On local scales, the negatively-associated distributions were not apparent in the species matrix structures. This has been observed for ants, flies, ectoparasites of small mammals, and coral reef fishes (Sale & Williams 1982, Gotelli & Ellison 2002, Rodriguez-Fernández *et al* 2006, Krasnov *et al* 2006). Moreover, Gotelli & McCabe (2002) observed that assembly rules cause matrix structuring according to the taxonomic group. Studies on larger scales usually do not agree with those obtained on smaller scales (Resetaris & Bernardo 1998), as observed for ant and fly assemblages (Gotelli & Ellison 2002, Rodriguez-Fernández *et al* 2006).

On a regional scale, matrices are highly structured, as

Table 3 Body size overlap patterns at local scale of analysis.

Models	Arroio Grande			Capão do Leão			Morro Redondo			Pelotas		
	I_{obs}	I_{sim}	P	I_{obs}	I_{sim}	P	I_{obs}	I_{sim}	P	I_{obs}	I_{sim}	P
General	0.00012	0.00011	0.680	0.00011	0.00009	0.832	0.00013	0.00008	0.025	0.00012	0.00008	0.050
Ecological guilds												
Larvae												
Pre	0.00013	0.00013	0.582	0.00012	0.00010	0.216	0.00017	0.00010	0.028	0.00013	0.00009	0.062
Adult												
Sap	0.00085	0.00026	0.002	0.00028	0.00015	0.031	0.00028	0.00010	0.000	0.00023	0.00009	0.002
Larvae-adult												
Pre-Sap	0.00095	0.00030	0.001	0.00034	0.00019	0.050	0.00050	0.00014	0.001	0.00026	0.00011	0.004

The I_{obs} and I_{sim} give the observed and simulated variance in segment length (s^2), a measure of the constancy of size ratios of adjacent species. For the habitats, the null model is one in which species body sizes are distributed randomly and uniformly (log scale) between the end points of the largest and smallest observed species in the assemblage. Communities structured by competition should exhibit unusually small variances and $I_{obs} < I_{sim}$, corresponding to relatively constant body size ratios and even spacing of species body sizes on a logarithmic scale. Communities structured by aggregation should exhibit unusually larger variances and $I_{obs} > I_{sim}$, corresponding to relatively constant body size ratios and even spacing of species body sizes on a logarithmic scale and $P < 0.05$. Sap = saprophagous, Pre = predator.

opposed to matrices on a local scale. Historical processes on those areas and habitat heterogeneity have often been suggested as hypotheses with the same explanatory power of these segregation patterns (Ricklefs & Schluter 1993, Ribas & Schoereder 2002). The use of exceedingly large areas leads to the issue of phylogenetic relationships among the species, which could potentially mask the relative importance of biological phenomena demonstrated by the patterns of negative association between pairs of species (Caddle & Greene 1993), as well as leading to another effect: spatial autocorrelation (Wilson 1999).

On a local scale, the filters that determine the composition of assemblies are most strongly linked to the abiotic conditions of the habitat and of the resources utilized by these groups than by competition (Grubb 1977, Southwood 1988, Keddy 1992). Filters associated with other factors such as predation and parasitism can impose stronger limits to the growth of populations than interspecific competition. As a consequence, the environmental carrying capacity is not reached, resulting in more aggregation than segregation (Connel 1975, Simberloff 1983, den Boer 1986, Keddy & Weiher 1999), as observed when line with weight (W) is utilized in the models with saprophagic adults and predatory larvae.

The frequency, intensity and temporal sequence of the manifestation of the abiotic conditions that work as filters could lead to an effect analogous to disturbance in local or regional habitats, depending on the type of condition. The spatial scale of the disturbance can determine the capacity of colonization of local habitats by potential colonizers, thus strongly influencing the structure and function of communities according to the historical trajectory of the disturbance (Welborn *et al* 1996, Trexler *et al* 2005). In the case of the Grasslands biome, seasonal variation in temperature, humidity, rainfall, photoperiod, and productivity regulate population sizes and decrease the pressure on resources. In addition to the stress caused by the climate variation on the fitness of those populations, the strong fragmentation of this biome can determine the rhythms of expansion and retraction of occupation areas and abundance of several taxa. In this case, temporal or spatial resource partitioning can occur (Tilman 1982, Paulson & Arke 1991, McCabe & Gotelli 2000, Campos & Schoereder 2001). In these environments, dispersal ability becomes an important persistence factor (Darlington 1957, Roff 1974a, b). If species of the same taxonomic group have the same dispersal ability and are good colonizers, as is the case in flies (Bishopp & Laake 1921, Oldroyd 1964), there should be a strong tendency for the composition of assemblies to converge to a high similarity in more homogeneous environments. In these environments, the difference of richness between localities is lower, and the composition of local assemblies is very similar to the regional pool.

When the difference on richness between localities is high, assembly composition in different locations is very distinct, considerably increasing the regional diversity because of resource partitioning or due to the existing environmental filters (Chase 2003, Kneitel & Chase 2004). In muscid assemblies, if there were an effect of habitat heterogeneity (in the sense of an association between heterogeneity and diversity), there should be apparent structuring by segregation in some of the tested models. This did not occur despite the argument by Wilson (1999) that even in heterogeneous environments a segregation pattern might not be present, as long as the variance in guild proportionality in different locations is high. In this case, habitat colonization would occur in a different way, with aggregation based on similar ecological need displayed by some groups (Wilson *et al* 1987).

Another factor that should be considered is the relative numerical dominance of some groups. Dominance has two aspects in the context of interspecific interactions: behavioral dominance (aggressiveness) or ecological dominance (high frequency of individuals) (Cerdá *et al* 1997, Ribas & Schoereder 2002). *Phaonia* sp. 1 and *Bithoracochaeta* were dominant groups in several environments. The former was most abundant in Pelotas and Capão do Leão, whereas species of *Bithoracochaeta* dominated the locations of Morro Redondo and Arroio Grande. Such dominance was evident in matrix structure when the W algorithm was used, generating aggregation patterns among the tested models. Such patterns were very distinct from those recorded for birds in the Amazon region and ants in bogs and forests of New England, USA (Graves & Gotelli 1993, Gotelli & Ellison 2002). A difficulty in considering the results from matrices that use weighting as an algorithm is the quantification of the statistical error associated with that procedure. Nevertheless, aggregation was evident in the guild proportionality analyses, indicating that this phenomenon is present in muscid assemblies as the feeding habits of adults.

Our results suggest that interspecific competition is not the main force underlying the structure of communities of flies in the family Muscidae in the Grasslands biome on Southern Brazil. Other factors might play a role in determining the composition of assemblies of this taxon. Among these factors, variation in abiotic conditions along a temporal axis may be the main rule to be tested as a necessary environmental characteristic for the formation of the composition of assemblies (*sensu* Weiher & Keddy 1999). Keddy & Weiher (1999) pointed out that few studies on community assembly are explicit in the states of their rules. In muscids of the Grasslands biome, no rule was identified, even though a consensus did emerge from our analyses: species are randomly distributed and co-occur in any guild more frequently than expected by chance, indicating aggregation. We hypothesize that an environmental characteristic that promotes the abundance of resources and allows for aggregation of species of the subfamilies Cyrtoneurininae, Mydaeinae and Phaoniinae is more important than biological interactions.

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Online Supplementary Material

Krüger R F, Carvalho C J B , Ribeiro P B (2010) Assembly rules in muscid fly assemblages in the grasslands biome of Southern Brazil. Neotrop Entomol 39(3): 345-353.

Species and morphospecies of Muscidae (Diptera) at four localities on Grasslands bioma, southern Brazil. Arroio Grande (AG), Capão do Leão (CL), Morro Redondo (MR), Pelotas (PEL). Classification in was based on Carvalho *et al* (2005).

Species	AG	CL	MR	PEL
Muscinae				
Biopyrellia bipuncta	1	1	1	1
Haematobia irritans	1	0	1	0
Morellia humeralis	0	0	0	1
Morellia paulistanensis	1	1	1	1
Musca domestica	0	0	1	0
Polietina orbitalis	1	1	1	1
Sarcopromusca pruna	1	1	1	1
Stomoxys calcitrans	0	1	1	1
Trichomorellia tricops	1	0	0	0
Trichomorellia sp.	0	0	1	0
Xenomorellia holti	0	0	1	0
Azeliinae				
Micropotamia cilitibia	1	0	0	0
Micropotamia minuscula	1	1	1	0
Ophyra aenescens	0	0	1	0
Philornis sp.	0	1	0	0
Psilochaeta chlorogaster	0	0	0	1
Cyrtoneurininae				
Cariocamyia maculosa	0	0	0	1
Cyrtoneurina costalis	1	1	1	1
Cyrtoneuropsis brunnea	1	1	1	1
Cyrtoneuropsis pararescita	1	1	1	1
Neomuscina inflexa	0	0	1	0
Neomuscina neossimilis	0	0	0	1
Neomuscina pictipennis	0	0	0	1
Neomuscina sanespra	0	0	1	1
Neomuscina zosteris	1	1	1	1
Neomuscina sp. 1	1	1	1	1
Neurotrixa felsina	1	1	1	0
Neurotrixa sulina	0	0	1	1
Phaoniinae				
Dolichophaonia plaumani	0	1	1	1
Dolichophaonia trigona	1	1	1	1
Dolichophaonia sp. 1	1	0	0	0
Dolichophaonia sp. 2	0	0	1	0
Helina angustipennis	1	0	1	1
Helina sp. 1	1	1	1	1
Helina sp. 2	0	1	0	1
Phaoniinae				
Helina sp. 3	1	1	1	1
Helina sp. 4	1	1	1	0
Phaonia advena	0	1	1	1
Phaonia annulata	0	1	1	1
Phaonia grajauensis	1	1	1	1
Phaonia nigriventris	1	1	1	1
Phaonia similata	0	1	1	1
Phaonia trispila	1	0	1	0
Phaonia sp. 1	0	1	1	1
Phaonia sp. 2	0	0	1	1
Phaonia sp. 3	0	1	0	1
Phaonia sp. 4	1	0	1	1
Phaonia sp. 5	1	1	1	0
Mydaeinae				
Brontaea delecta	0	1	0	1
Brontaea debilis	0	1	0	1
Brontaea quadristigma	1	1	1	1
Brontaea normata	0	0	1	1
Graphomyia analis	1	0	1	0
Graphomyia auriceps	0	1	0	0
Graphomyia maculate	0	1	0	0
Mydaea plaumani	1	1	1	1
Myospila meditabunda	0	1	1	1
Myospila obscura	1	1	1	1
Myospila pallidicornis	0	0	0	1
Coenosiinae				
Bithoracochaeta calopus	1	1	1	1
Bithoracochaeta equatoralis	1	1	1	1
Bithoracochaeta plumata	1	1	1	1
Coenosia sp. 1	1	1	1	1
Coenosia sp. 2	0	0	1	0
Limnophora aurifascies	1	1	1	1
Limnophora paranaensis	1	1	1	1
Limnophora sp. 1	1	1	1	1
Limnophora sp. 2	0	1	0	1
Lispe serotina	1	1	0	1
Neodexiopsis erecta	1	1	1	1
Neodexiopsis flavipalpis	1	1	1	1

Continue

Continuation

Species	AG	CL	MR	PEL
Coenosiinae				
Neodexiopsis legitima	1	1	1	1
Neodexiopsis neoaustralis	1	1	1	1
Neodexiopsis nigerrina	1	1	1	1
Neodexiopsis paranaensis	1	0	1	1
Neodexiopsis paulistensis	1	1	1	0
Neodexiopsis rara	1	1	0	0
Neodexiopsis rufitibia	1	1	1	1
Neodexiopsis rustica	1	1	1	1
Neodexiopsis setipuncta	1	1	0	0
Neodexiopsis similes	1	1	1	1
Neodexiopsis sp. 1	1	1	0	1
Neodexiopsis sp. 2	1	1	1	1
Neodexiopsis sp. 3	0	1	0	1
Neodexiopsis sp. 4	1	1	1	1
Neodexiopsis sp. 5	0	1	1	1
Stomopogon hirtitibia	1	1	1	1