

Space heterogeneity, space use and short-range dispersal in Diptera: A case study

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Abstract

This study investigates the impact of landscape heterogeneity on community structure and population dynamics in two families of Diptera (Empididae and Chironomidae). Adult emergence is compared with aerial flow by means of emergence traps and yellow traps on a transect across four habitats (pond banks, woodland, grassland and heathland) in close proximity to each other. Empids use different space units according to their larval development, sexual behaviour and food requirements. This creates an intermingling of species and individuals originating from different habitats in the lowest part of the transect. Adult chironomids of aquatic species exhibit a preferential use of open habitats while adults with terrestrial larvae disperse largely above the four sites. Habitat fragmentation and heterogeneity lead to opposite patterns in chironomid distribution: some species disperse over the whole set of macrohabitats but others are confined to a single patch, resulting in population isolation. The impact of spatial and temporal landscape patterning is discussed with a view to community structure, life-history tactics and population dynamics.

1. Introduction

The impact of landscape pattern on insect community structure and population dynamics depends on many intricate factors, including both space heterogeneity (Fahrig and Merriam 1985; Hastings 1989; Crespi and Taylor 1990) and species strategies (Roff 1977; Harrison 1980; Ward 1987). In Diptera, it is well known that adults of many taxa (*e.g.* Syrphidae, Empididae) are able to fly far away from their larval habitats while others (*e.g.* Sciariidae, Sphaeroceridae) are restricted to particular sites. Dolichopodidae and Chironomidae display intermediate capabilities. Long-range dispersal has been extensively studied in several taxa, most of which are agricultural pests. Conversely, short-range dispersal of natural populations in hetero-

geneous habitats has, to some extent, been understudied. This is why we planned a two-year study of aerial dispersal in the six previously mentioned families. These species display various flight capabilities associated with different aspects of behaviour (swarming, mating, feeding, colonization). This paper deals with the results of studies on Empididae and Chironomidae, as examples of different functions and impacts of habitat heterogeneity.¹

2. Study sites and methods

The area selected for study is typical of Central Brittany (France), where numerous small ecosys-

¹Results for other families will be published by Deleporte and Vernon (Paimpont Biological Station) and Brunel and Cadou (INRA, Rennes) respectively.

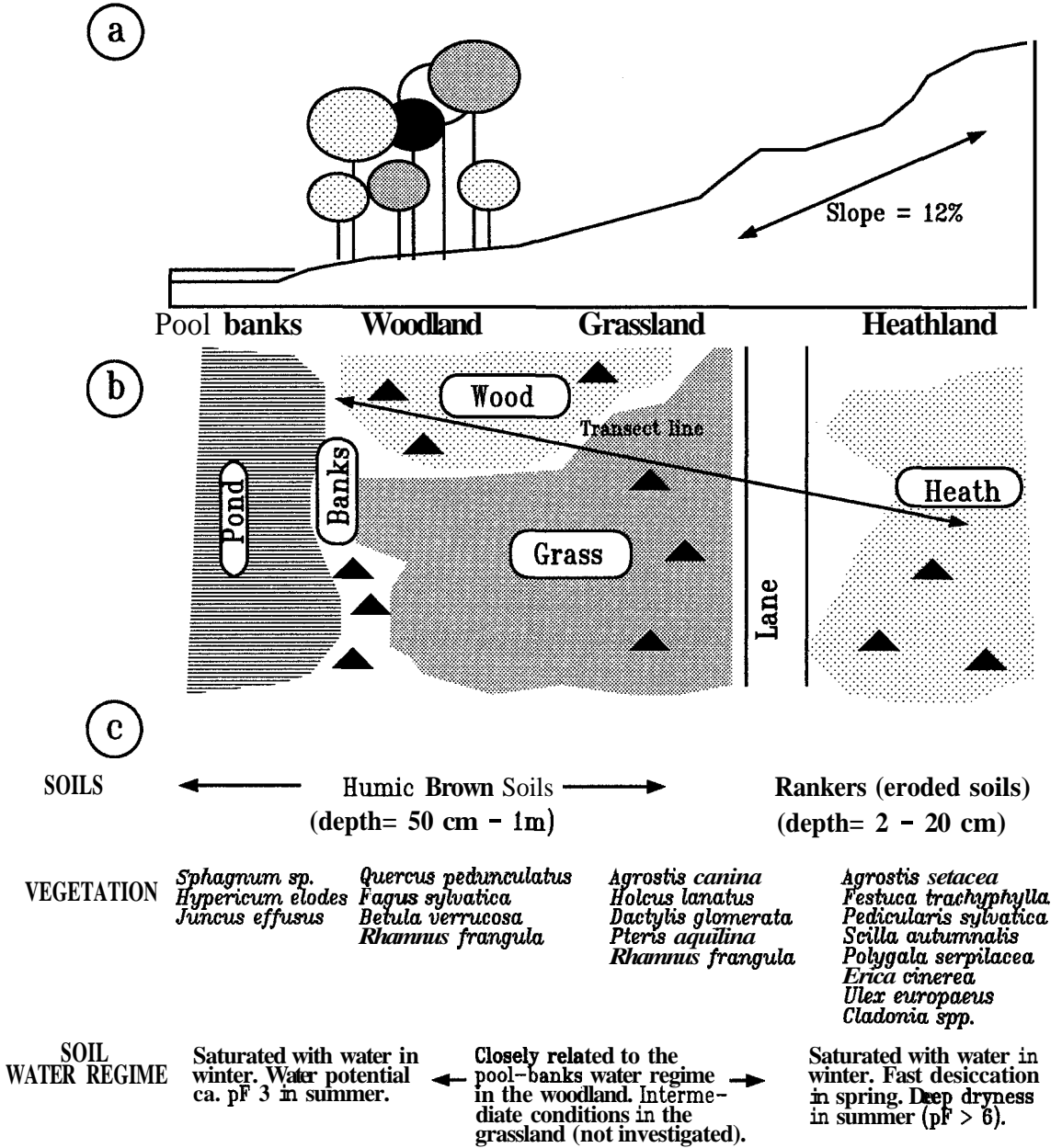


Fig. 1. Diagrammatic description of study site: a) Transect, b) map, c) soil, vegetation and soil water regime. Water potential is expressed in pF units: range 0 (flooded soil) to 7 (full dryness). Black triangles show trapping areas.

systems overlap. It consists of four habitats in close proximity to each other, which border an acidic, oligotrophic pond: the pond banks, a woodland, a small grassland and a dry heathland. These habitats are all part of a single landscape unit which is a transition area between the aquatic and terrestrial ecosystems. The main characteristics of the four

sub-units are summarized in Fig. 1.

Two types of traps were used (emergence traps and yellow water traps). Emergence traps have a steel frame (0.25m^2) sunken in the soil and bearing a pyramid of a black nylon sieve with a plexiglas collector on top. They catch adults emerging from the soil and give reliable estimate of species depen-

dence on a specific habitat. Yellow water traps consist of a yellow² painted plastic tray (0.1 m²) filled with water and a small amount of detergent. They are located on the soil surface and attract adults in passive or active flight.

Bailliot and Tréhen (1974) have defined the meaning of catches in yellow traps for the two families considered here. Empididae are caught only when they search for food or disperse. No capture occurs when adults are swarming. Chironomidae, however, are always caught in yellow traps while flying, irrespective of their behaviour. The comparison between catches in the two sets of traps provides meaningful information on community structure, aerial flow and cross-exchanges between populations in Diptera (Duviard and Blanchet 1983). Three emergence traps were placed in each habitat. Collectors were changed weekly. Two yellow traps were used one day a week at each site throughout the year. Catches were identified to species using Chvala (1975), Collin (1961), and Pinder (1978) keys.

Results

3.1. Diptera Empididae

The results from the present study can be grouped into three main categories which are species richness, adults numbers and sex-ratio. Six to eight species were caught in emergence traps while up to 25 species were recorded in yellow traps during the first year of sampling. The number of adults emerging from soils was greatest in the grassland and the dry heathland (Fig. 2). In contrast, flying adults were more numerous in the woodland and near the pond than in other habitats. While the sex-ratio was nearly balanced in newly hatched adults (55% females), flying females were dominant (70%) in the woodland. The results can be interpreted for each species in relation to its behaviour.

The dispersal of *Rhamphomyia spp.* is related to predation and its spatial distribution depends on the location of its prey (mainly Chironomidae). The

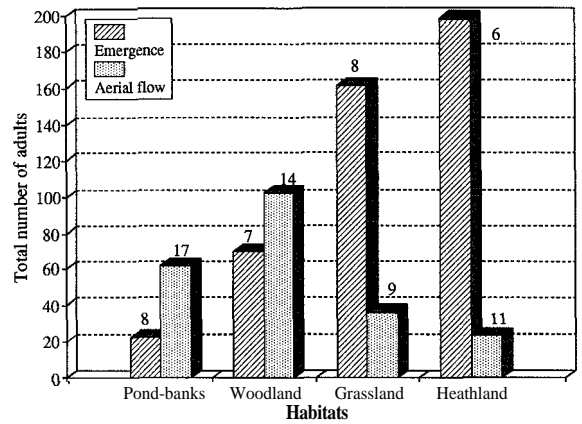


Fig. 2. Emergence and aerial flow of adult Empididae: total number of individuals (histogram) and total number of species (figures).

aerial flow of species belonging to the genus *Empis* is related to the distribution of flowers on which they feed.

The location of *Hilara* species depends mainly on their sexual behaviour. Spatial heterogeneity of habitat and mesoclimate are the two main factors which explain their distribution. Behaviour of *Hilara spp.* is dependant on a heterogeneous set of habitats (Tréhen 1969) as follows:

1. Open water surfaces (*i.e.* ponds, brooks) where males catch little insects which are offered to the female prior to mating.
2. An enclosed space of high vegetation and associated pockets of light and shade where female swarms are found and mating occurs.
3. A large space for dispersal, oviposition and larval development.

The species composition changed considerably during the season. Although the site in the present study belongs to the atlantic zoogeographic province which is quite poor in species, 17 *Hifara* species were found between April and July. *Hifara primula* Collin appeared during early spring and the swarms were found only above small brooks (Fig. 3). *H. maura* (Fabr.) swarmed in May. Swarming and mating depended on air temperature and time of day. In the morning, no swarms were found and the females searched for hunting males above water surfaces (Fig. 3,a). Mating was infre-

²Wavelength 5,800 Å

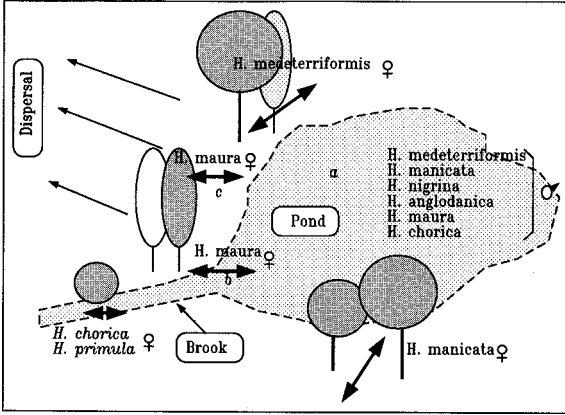


Fig. 3. Location of several species of the genus *Hilara*: males are hunting prey above the pond (dotted area) while females form directional swarms (double arrows). Letters a, b, c refer to the location of *H. maura* female swarms, which depends on climatic parameters: a) above open water, b) above banks and c) near tree tops (rounded and ellipsoidal shapes).

quent. When the temperature rose, females formed oriented swarms above brooks or near other markers (Fig. 3, b). At still higher temperatures, female swarms could be found near tree tops, far away from water surfaces (terrestrial swarms, Fig. 3, c). Other species also exhibited swarming behaviour at specific locations. All species tended to disperse over the four habitats after mating.

3.2. Dipteru Chironomidu

During the first year of sampling, more than 17,000 adults were trapped, belonging to 67 different species including only 12 terrestrial ones.

The 55 chironomid species with aquatic larvae will be considered briefly, since only 15 species were abundant (*i.e.* more than 10 adults per species). It is clear that adults were not restricted to the pond banks (Fig. 4) and flew above the four sites. The numbers were higher on the pond banks, grassland and heathland (260, 460 and 125 individuals, respectively) than in the woodland (56 ind.). This shows a preferential use of open habitats for dispersal and the avoidance of shady sites with high dense vegetation. The fact that the heathland is less visited than the grassland could be related to the longer distance between the former site and the pond, sug-

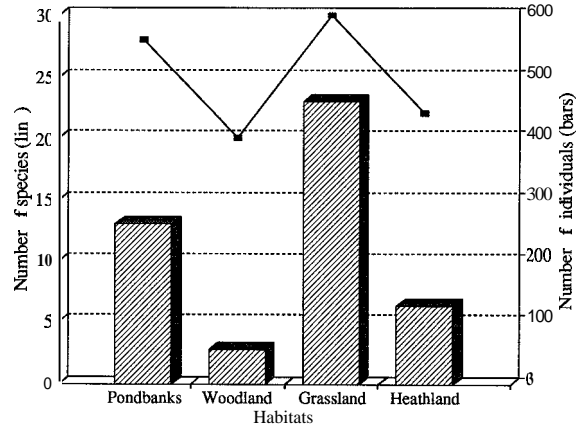


Fig. 4. Aerial flow of adult Chironomidae (aquatic species): total number of species (line) and total number of individuals (histogram).

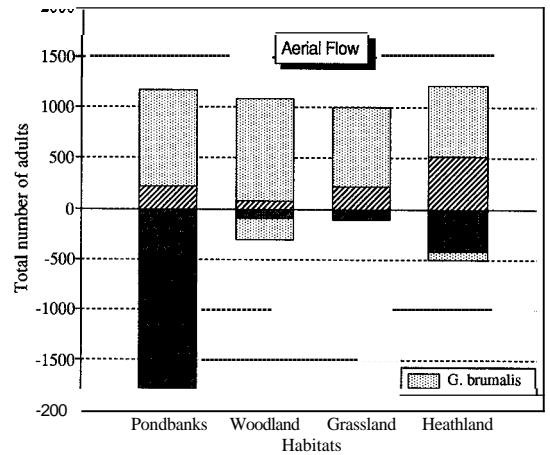


Fig. 5. Aerial flow (upper part) and emergence (lower part) of adult Chironomidae (terrestrial species only): total number of individuals. The most abundant species (*G. brumalis*) has been shown separately (some individuals which emerge from the pondbanks and from the grassland are not visible due to the scale).

gesting that many aquatic species do not move far from open water.

The distribution of the 12 terrestrial species was very different (Fig. 5). While the greatest number of emerging adults occurred near the pond (1784 ind.), the aerial flow appeared to be very important above the four habitats (998 to 1219 ind.), which demonstrated a large dispersal of individuals over all the sites. However, this was in fact mainly due to the

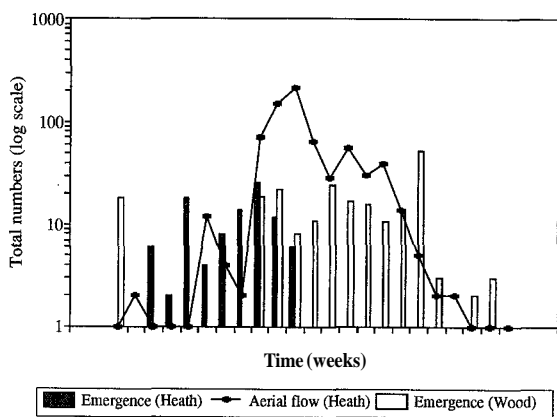


Fig. 6. Emergence (histogram) of *G. brumalis* from the dry heathland (black bars) and from the woodland (open bars). Aerial flow above the heathland (line). Total number of adults (log scale).

very abundant species: *Gymnometriocnemus (Rhabidocladius) brumalis* (Edw.).

Three groups could be distinguished among the terrestrial species:

- Species which emerged from the soils of the four habitats and dispersed widely: *G. brumalis*, *Limnophyes minimus* (Mg.).
- Species which flew above the four sites but only emerged from restricted areas, e.g. *Pseudosmittia curtica* (Edw.), *Limnophyes natalensis* (K.) and *Smittia pratorum* (G.)
- Species which were restricted to a single habitat, both as larvae and as adults, e.g. *Pseudosmittia angusta* (Edw.) on the pond banks and *Smittia sp.* on the dry heathland.

On the other hand, examination of emergence and flight phenologies clearly demonstrated exchanges between macrohabitats for some species. For instance, the aerial flow of *G. brumalis* lasted longer than the emergence period on the dry heathland (Fig. 6). This extended aerial flow occurred while the species was emerging from the woodland. The comparison between emergence and yellow trapping allowed the detection of immigrants of that species on the heathland. The same process occurred for *L. minimus*. A previous study (Delettre 1986) has shown that two generations of *L. minimus* occur each year on the pond banks but only one is success-

ful in spring on the heathland where the summer larval population is completely destroyed by the excessive soil dryness. Adults migrating from surrounding habitats re-establish the heathland population each autumn.

4. Discussion

Several conclusions may be drawn from the study of 34 different species of Empididae:

Species use different space units, according to their larval development, sexual behaviour and food requirements.

The clumping of species is often related to sexual behaviour in Empidinae. Exchanges among landscapes units are correlated both with predation and oviposition in suitable habitats.

Within the genus *Hilara*, the species assemblage depends on three independent sets of parameters: i) the spatial organization, which is a constant during the adult life-span, ii) the season, which triggers the emergence timing and iii) mesoclimatic heterogeneity which modifies the width of space used.

On the contrary, a single habitat is sufficient for some species, which display their complete behaviour pattern in the same restricted location.

Behavioural requirements of Empidinae, patch size, patch duration and heterogeneity interact during the adult whole life-span and induce, in precisely defined patches, a strong intermingling of species and individuals originating from different locations.

Species boundaries overlap in the environmental gradient produced by the four habitats, leading to an enriched aerial flow mainly on the pond banks and in the woodland. The same result, i.e. the clumping of species boundaries in the lowest part of a transect, was pointed out by Dale (1988) for seaweed species in the transition area from the littoral zone to the upper subtidal. Thus, the existence of particular patches in heterogeneous environments could be of critical value for species richness, life-cycle completion and gene flow at the whole landscape level.

As stated by Van Dorp and Opdam (1987), the interaction between dispersal flow, population

characteristics and landscape pattern strongly influences the spatial and temporal population dynamics. In Chironomidae, the impact of habitat fragmentation and heterogeneity appears to be different, even the opposite, for several species. Some benefit is derived from habitat diversity: regular exchanges between macrohabitats lower the risk of extinction at the landscape level, although local populations could become extinct in given patches. Patch connectivity and specific colonizing abilities are both involved in populations survival (Fahrig and Merriam, *op. cit.*). Conversely, habitat fragmentation results in isolation of some populations. In this case, extinction can be avoided through different processes, *e.g.* larval resistance to summer drought in *Smittia sp.* (Delettre 1984) or permanent use of a single, continuously suitable and predictable habitat (*e.g.*, for *P. angusta*, the pond banks which remain wet all summer (Blanchart *et al.* 1987)).

Variability in chironomid dispersal could arise from different flight abilities. However, Delettre (1988) showed that several species with the same wing morphology and body size exhibited opposite flight behaviour: some avoided downwind transport while others used active or passive flight. Such different behaviour has been correlated with the permanent or ephemeral suitability of patches (Southwood 1977, 1988) and temporal patterning was included in the concept of neighbourhood expanded by Addicott *et al.* (1987).

But species can perceive and respond in different ways to heterogeneity (Kotliar and Wiens 1990). In the present study, the four macrohabitats are likely to be perceived as different by Empididae and some Chironomidae whereas populations of other species are restricted only to a single patch, which implies hierarchical levels of heterogeneity. Several of the above authors have focused their studies on this problem. Morris (1987) tested how population density responded to different scales of heterogeneity while Turner (1989) emphasized the importance of the scale of observation of landscape functions. Investigations at higher levels of heterogeneity (a whole landscape, a region) frequently use high taxonomic levels (orders, families). These could benefit from more detailed studies at lower levels:

habitats and patches on one hand, species (or groups of species with the same use of resources) on the other.

Our study clearly shows that a population-centered view of boundaries and patches must be adopted to assess the impact of habitat diversity on species composition and population dynamics. Three conclusions can be drawn from this: i) studies should be conducted at the specific level since dispersal ability and behaviour change from one species to another, ii) different scales of observation (which depend on species and life-history tactics) should be used to expand the actual field of investigations (Kotliar and Wiens *op. cit.*), and iii) consequences of heterogeneity at a given scale on upper and lower hierarchical levels should be investigated to avoid inappropriate generalization and to provide more realistic conclusions.

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