Local biodiversity and multi-habitat use in empidoid flies (Insecta: Diptera, Empidoidea)

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The empidid fauna of four small adjacent biotopes bordering a pond was investigated for 2 consecutive years in Brittany (France). Adult activity was studied using yellow water traps, whereas suitable larval habitats were determined using emergence traps. While 24 species emerged from the soils, 45 flew above the four sites. The number of species emerging from each site was nearly identical. However, the highest number of individuals emerged from the heathland and numbers rapidly declined towards the pond banks. On the contrary, the greatest aerial activity occurred in the woodlot and near the pond banks. Fourteen times less flying activity was found above the dry heathland. The latter appeared to be a site of larval growth but mating and feeding of the adults took place in the woodlot. Reproduction sites and space used by the adults differed among the dominant species. The species assemblage could not be fully explained within the spatial limits of the four sites. Considering the species' behaviour, it is suggested that immigration of species and individuals from other sites should explain these differences. The study, which is supported by four other research works, emphasizes the role of key resource played by ecotonal zones between aquatic and terrestrial ecosystems in the persistence of species over a larger set of habitats. Considering the complementarity of habitats is essential to explain diversity patterns in species which need different space units to complete their life-cycle.

Keywords: biodiversity; habitat use; dispersal; spatial heterogeneity; key resource; Empididae; Diptera.

Introduction

An increasing number of studies are devoted to invertebrate taxa to evaluate natural areas or cropping systems for nature conservation. Besides carabid beetles and spiders for which an extensive knowledge of ecological requirements is available, other taxa must be considered to provide further evaluations of biodiversity. As suggested by Pollet (1992), Empidoidea, which includes the families Empididae, Dolichopodidae and Hybotidae, appears to be suitable for such purposes because, despite a relatively low number of ecological studies, a solid basis to define their ecological requirements has, however, accumulated (Tréhen, 1968, 1969; Bährmann, 1984, 1994; Stark and Wetzel, 1987; Meyer and Heydemann, 1990; Pollet and Grootaert, 1996).

The Empidoidea are among the most diverse and abundant flies in temperate zones. Species display contrasted life history traits and many of them need different habitats to

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complete their whole life cycle. Their predatory larvae are widely distributed from damp to dry soils and some of them, such as *Empis* (*Coptophlebia*) *vitripennis* Mg. and *Crossopalpus nigritell*a Zett., are primary colonizers in the Diptera succession on crushed household refuse (Duviard and Blanchet, 1983).

In Empidinae, exchanges are necessary between a large set of edaphic larval habitats and strictly defined locations for feeding, swarming and mating (Tréhen, 1972). Their colonizing abilities have been correlated with their flying behaviour (Tréhen, op. cit.; Tréhen *et al.*, 1977; Hövemeyer, 1987; Morvan, 1996). On the contrary, no swarms occur in the Tachydromiinae and their colonizing capabilities seem to be lower.

Such contrasted patterns of dispersal imply a different use of space by the adults and, conversely, a different impact of space heterogeneity on population dynamics. By studying both the emergence and the aerial activity of the adults in four adjacent habitats, we will try to demonstrate that some particular areas provide different resources to species and, thus, play an important role in species persistence and community structure.

Study sites, material and methods

Research area

This study was performed in the surroundings of the Paimpont Biological Station in central Brittany (France) where numerous small ecosystems overlap (Fig. 1a). Four habitats were studied near an acidic oligotrophic pond (Fig. 1b): (1) the wet pond banks covered with moss and rush and bearing some sparse trees, (2) a narrow wooded strip bordering the pond and afforested with hardwood (mainly oak, beech and birch trees) and an open shrub understory, (3) a small ascending mown grassland, and (4) a dry heathland located on a nearby crest of schistose rocks (average slope: 12%). Soils consist in humic brown soils in the first three sites and in brown eroded soil (ranker) at the heathland site. All of them are saturated with water in winter but a deep drought usually occurs in the heathland soil in summer. All these different habitats are closely related: the maximum distance from the pond to the most remote habitat (the heathland) does not exceed 50 metres. The whole area can be considered as a gradient (an ecotone) between aquatic and terrestrial ecological systems.

Light intensity, air temperature and relative humidity were measured at the same time on 5 days at the four sites (Fig. 2) using Bioblock™ LX-101 digital lux-meter and No-vasina™ MIK 3000 combined temperature-aerial humidity digital meter. Seasonal changes in microclimate and trees phenology interact to increase climatic heterogeneity: the light intensity was almost identical on the four sites on March 8. In May, when the trees were in full leaf, the light intensity in the wood and on the pond banks shaded by the trees was much lower than on the fully exposed grassland and heathland. Generally, the temperature was higher in the latter than in the woodlot and on the pond banks. A reversed situation was recorded for the air relative humidity.

Sampling

The species diversity and abundance of Empidoidea (families Empididae and Hybotidae) were determined with emergence traps and yellow pan traps. The emergence traps give a reliable estimate of the larvae which live in the soils whereas the yellow traps inform about the flying activity of the adult stage. A detailed study of the yellow traps efficiency is given by Bailliot and Tréhen (1974): empidids are not caught in such traps while swarming but
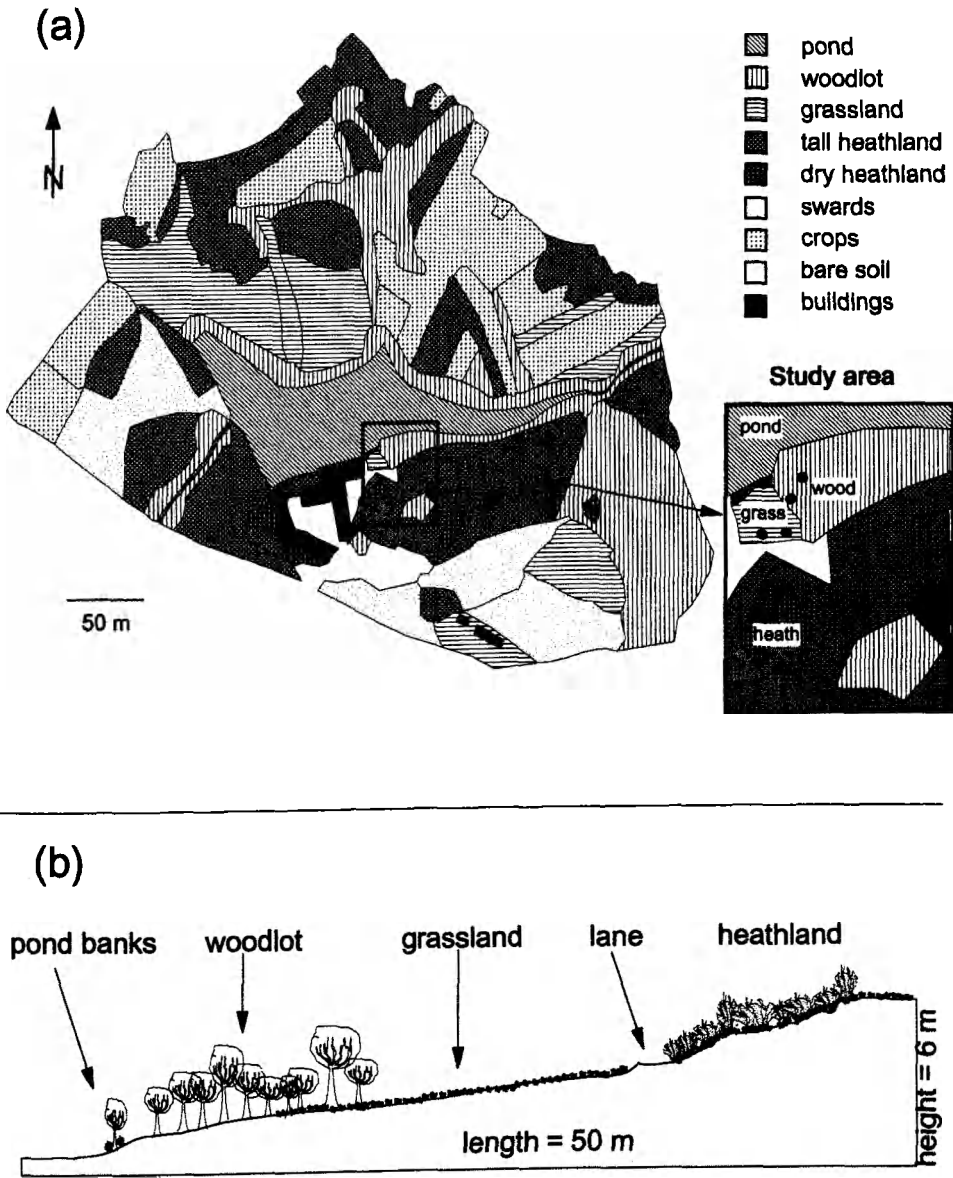
Figure 1. Map of the landscape (upper part) in which is included the study area (insert on the right). Yellow pan traps are indicated by black dots (emergence traps, not shown, are located on the same plots). Schematic transect over the four habitats (lower part).

only when they search for food or disperse. Furthermore, Pollet and Grootaert (1994) found that some nectar feeders were not correctly caught at the ground level by water traps but that catches increased with the height of the trap, with a maximum at 40 cm above the soil level. Krizelj (1971) proposed an optimal number of three traps per site but suggested that two traps usually provide a reliable estimate of the species assemblage if trapping occurs over a long period. Three emergence traps (0.25 m^2 each) were used per station. Trapping was continuous and samples were taken every week. Two yellow water
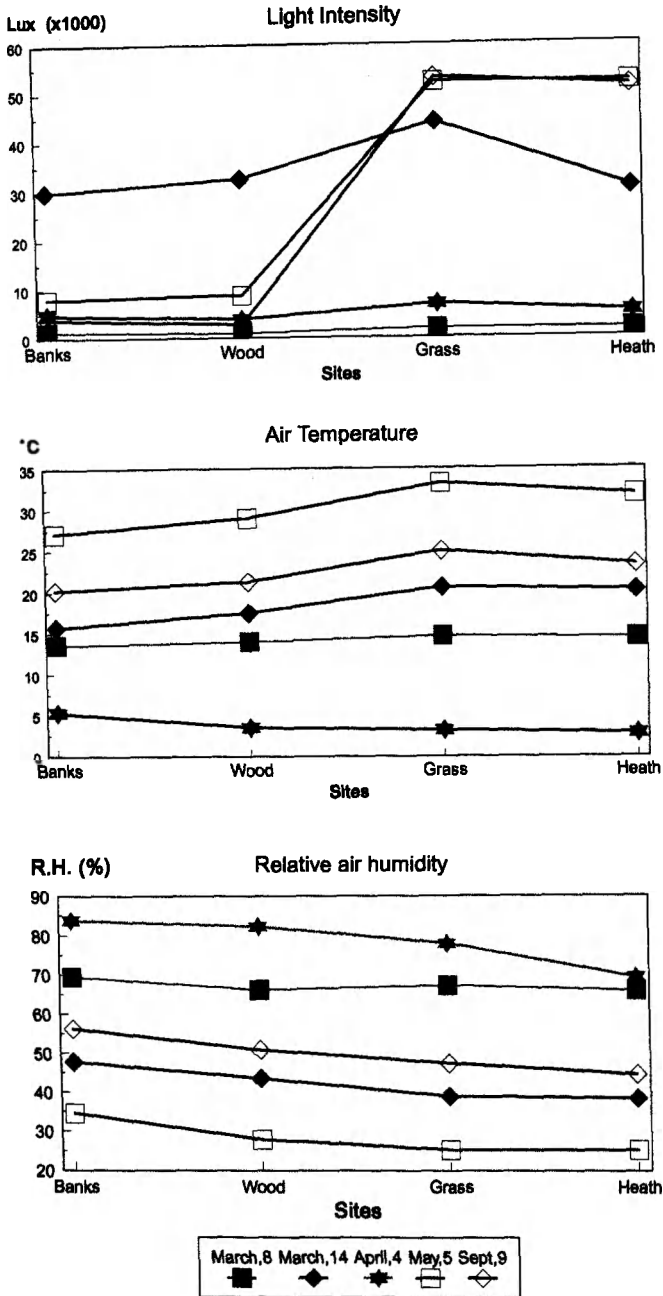
Figure 2. Light intensity (lux.10^3), air temperature (°C) and relative air humidity (%) in the four sites at five selected dates.

traps (0.10 m^2 each, filled with water and a small amount of detergent) were placed on the soil surface of each site and used only 1 day a week to avoid unnecessary overcollecting and possible population depletion. The study was carried out from May 1988 until April 1990.

Data analyses

At first, abundance data from emergence traps (matrix D1 = four columns on the left part of Table 1) and yellow pan traps (matrix D2 = four columns on the right part of Table 1) were analysed separately using two distinct Correspondence Analysis ('CA', Benzecri, 1973) and dissimilarity index (Chi-square distance and UPGMA clustering algorithm, NTSYS-PC software, Rohlf, 1990). In a second step, the possible effect of local emergence on aerial activity was tested as follows: total abundance data of flying individuals at each site (matrix D2, four variables to be explained) and presence-absence of species in emergence traps (all emergence traps pooled, resulting in a single nominal explanatory variable = column 'Total 1' in Table 1, encoded 0/1) were submitted to Canonical Correspondence Analysis ('CCA', Ter Braak, 1987; Lebreton *et al.*, 1991). Significance was tested using Monte Carlo permutations (Ter Braak, op. cit.).

Results

Community structure

Fifty-one species (listed in Table 1) were trapped: 37 during the first year and 14 additional ones during the second year. Six of the new species were found in the emergence traps and eight more in the yellow traps. The latter eight were all *Platypalpus* species. Only 16 species accounted for more than 10% of total catches and were numerically dominant during both years.

Comparing emergence data and yellow trap catches induces the following remarks: while only 24 species emerged from the soils in the four habitats, up to 45 species were found flying above the same sites. Eighteen species were recorded in both trapping systems. Six species emerging from the soil were not caught in yellow traps but five of them were rare species (see Table 1). These observations already suggest that many flying individuals do not originate in the four sites.

Considering the emergence process (Fig. 3a), the number of specimens (males and females) was the highest on the heathland (168 individuals m^{-2}) and decreased towards the pond banks (23 individuals m^{-2}). No clear trend in species number could be observed from the pond banks towards the heathland. The dominant taxa differed on the four sites: *Platypalpus notatus* (Mg.) was the main species emerging from the pond banks while *Phyllodromia melanocephala* (Fabr.) and *Rhamphomyia erythrophtalma* Mg. were more numerous in the woodlot (*Ph. melanocephala* was considered a typical species of forest rough humus by Tréhen, 1972). Emerging flies belonged mainly to *Empis (E.) praevia* Collin and *Platypalpus clarandus* (Collin) in the grassland while *E. (E.) aestiva* Loew. and *E. (E.) praevia* dominated in emergence traps on the dry heathland. From the Correspondence Analysis based on the abundance of the 24 emerging species (matrix D1), the grassland and the heathland sites exhibited closely related profiles while the pond banks and the woodlot were clearly different (Fig. 4). Chi-square distance and UPGMA clustering provided a similar result.

The activity of flying adults estimated by yellow pan traps contrasts with the previous results (Fig. 3b): the number of individuals found in yellow traps was the lowest on the heathland and increased gradually towards the pond banks where a very high flying activity occurred. Furthermore, the number of flying species followed the same trend. *P. clarandus* was the most active species, followed by *E. (E.) aestiva*, *Hilara manicata* Mg. and *P. pallidiventris* Mg. In the woodland, *Ph. melanocephala* was the dominant species in

Table 1. Total catches of Empidoidea per biotope in emergence traps and yellow pan traps over two years. Dominant species (more than 10% of total catches) are marked with an asterisk (*)

SPECIES	Code	Emergence Traps					Yellow Traps				
		Pond	Wood	Grass	Heath	Total 1	Pond	Wood	Grass	Heath	Total 2
Bicellaria sp.	Bisp					0	0	0	4	0	4
Bicellaria sulcata (Zetterstedt)	Bsul					0	0	0	3	0	3
Chelipoda vocatoria (Fallén)	Cvoc					0	2	0	0	0	2
Dolichocephala guttata (Haliday)	Dgut					0	2	0	0	0	2
Drapetis (Drapetis) exilis Meigen	Dexi	0	0	0	1	1	2	3	1	0	6
Drapetis (Elaphropeza) ephippiata Fallén*	Deph					0	16	14	0	0	30
Empis (Coptophlebia) albinervis (Meigen)	Ealb					0	0	1	0	0	1
Empis (Coptophlebia) vitripennis Meigen*	Evit	0	0	9	36	45					0
Empis (Empis) aestiva Loew*	Eaes	0	3	6	119	128	70	6	8	2	86
Empis (Empis) praevia Collin*	Epra	0	0	108	84	192	4	3	13	8	28
Empis sp.	Emsp	0	0	0	2	2	1	1	0	0	2
Hilara anglodanica Lundbeck	Hang					0	5	3	0	0	8
Hilara chorica Fallén	Hcho	2	0	0	0	2	5	0	1	0	6
Hilara cornicula Loew	Hcor					0	3	0	0	1	4
Hilara flavipes Meigen	Hfla					0	1	1	0	0	2
Hilara fulvibarba Strobl	Hful	1	0	0	0	1					0
Hilara fuscipes Fabricius	Hfus	1	0	0	0	1					0
Hilara interstincta (Fallén)	Hint					0	6	0	0	1	7
Hilara litorea (Fallén)	Hlit	0	0	2	0	2					0
Hilara manicata Meigen*	Hman					0	57	5	0	4	66
Hilara monedula Collin	Hmon					0	7	0	0	0	7
Hilara nigrina (Fallén)	Hnig	3	0	0	0	3	2	0	0	0	2
Hilara pilosa Zetterstedt	Hpil					0	1	0	0	1	2
Hilara primula Collin	Hpri					0	2	0	0	0	2
Hilara sp.	Hisp	0	0	2	0	2	1	2	0	0	3
Hybos culiciformis (Fabricius)*	Hcul	0	2	8	2	12	0	1	1	0	2
Hybos femoratus (Muller)	Hfem					0	3	1	0	0	4
Leptopeza flavipes (Meigen)	Lfla					0	0	3	0	0	3
Phyllodromia melanocephala (Fabricius)*	Pmel	3	44	0	1	48	44	71	7	0	122

Table 1 (*Continued*)

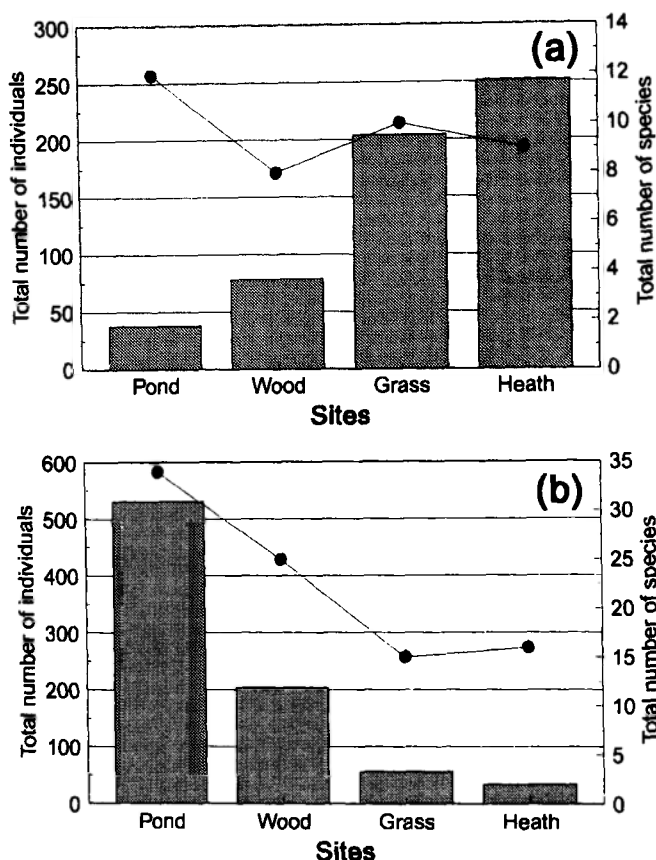| SPECIES	Code	Emergence Traps					Yellow Traps				
		Pond	Wood	Grass	Heath	Total 1	Pond	Wood	Grass	Heath	Total 2
Platypalpus agilis (Meigen)	Pagi					0	1	0	0	0	1
Platypalpus albiseta (Panzer)	Palb					0	0	0	0	1	1
Platypalpus annulipes (Meigen)*	Pann					0	10	3	1	2	16
Platypalpus aristatus (Collin)*	Pari					0	0	9	0	1	10
Platypalpus australominutus Grootaert*	Paus					0	27	0	0	0	27
Platypalpus calceatus (Meigen)	Pcal	1	0	0	0	1	1	0	0	0	1
Platypalpus ciliaris (Fallen)*	Pcil	0	1	0	0	1	0	29	1	0	30
Platypalpus clarandus (Collin)*	Pcla	2	0	37	2	41	181	34	6	3	224
Platypalpus cursitans (Fabricius)	Pcur	0	1	0	0	1					0
Platypalpus longiseta Zetterstedt*	Plon					0	5	3	0	2	10
Platypalpus minutus (Meigen)	Pmin					0	1	0	1	1	3
Platypalpus nigritarsis (Fallén)	Pnig					0	2	0	0	2	4
Platypalpus notatus (Meigen)*	Pnot	11	0	2	0	13	4	1	0	1	6
Platypalpus pallidiventris Meigen*	Ppal	1	0	0	0	1	57	1	3	0	61
Platypalpus pectoralis (Fallén)	Ppec					0	0	4	1	0	5
Platypalpus sp.	Plsp	0	1	1	0	2	1	0	0	0	1
Platypalpus verralli (Collin)	Pver					0	2	1	0	0	3
Rhamphomyia (A.) erythrophthalma Meigen*	Rery	0	25	29	0	54	1	0	6	3	10
Rhamphomyia sp.	Rhsp	2	0	0	0	2	0	0	0	1	1
Tachypeza nubila (Meigen)	Tnub	4	1	0	4	9					0
Trichina clavipes Meigen	Tcla	3	0	0	0	3	3	1	0	0	4
Trichinomyia flavipes Meigen	Tfla					0	0	3	0	0	3
SUM		34	78	204	251	567	530	204	57	34	825

Figure 3. Total number of species (line) and individuals (histogram) in the four habitats over 2 years. (a) emergence, (b) aerial activity.

the yellow traps. Above the grassland and the heathland, very few adults on wings were recorded despite the high rate of emergence. Again, a Correspondence Analysis performed on the abundance of the 45 flying species (matrix D2) provided the same result as the preceding one, but for different reasons (Fig. 5): the flying activity was more similar above the pondbanks and the woodlot, but highly different at the two other sites.

Use of space

Three sets of species could be distinguished by their spatial pattern. In the first one, species emerged in high number in one or several habitats but adults on wings were mainly recorded above the pond banks and in the woodlot (Fig. 6a). *P. clarandus* was the dominant emerging species when considering the four biotopes, with a peak of 25 individuals per square meter in the grassland. The flying activity of adults was very low in the heathland, increased slightly in the grassland and the woodlot and reached a maximum near the pond. The same situation occurred for *Ph. melanocephala* which could emerge from three different habitats although its larvae were more numerous in the woodlot. Adults on wings were mainly active in the woodlot and, in a lesser extent, near the pond. Adults of these two species are predators of about the same size. They hunt on the surface of the leaves of grasses, scrubs and trees. Thus, the adults concentrate in afforested areas
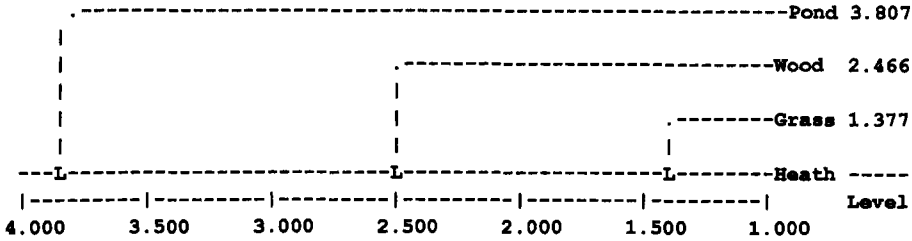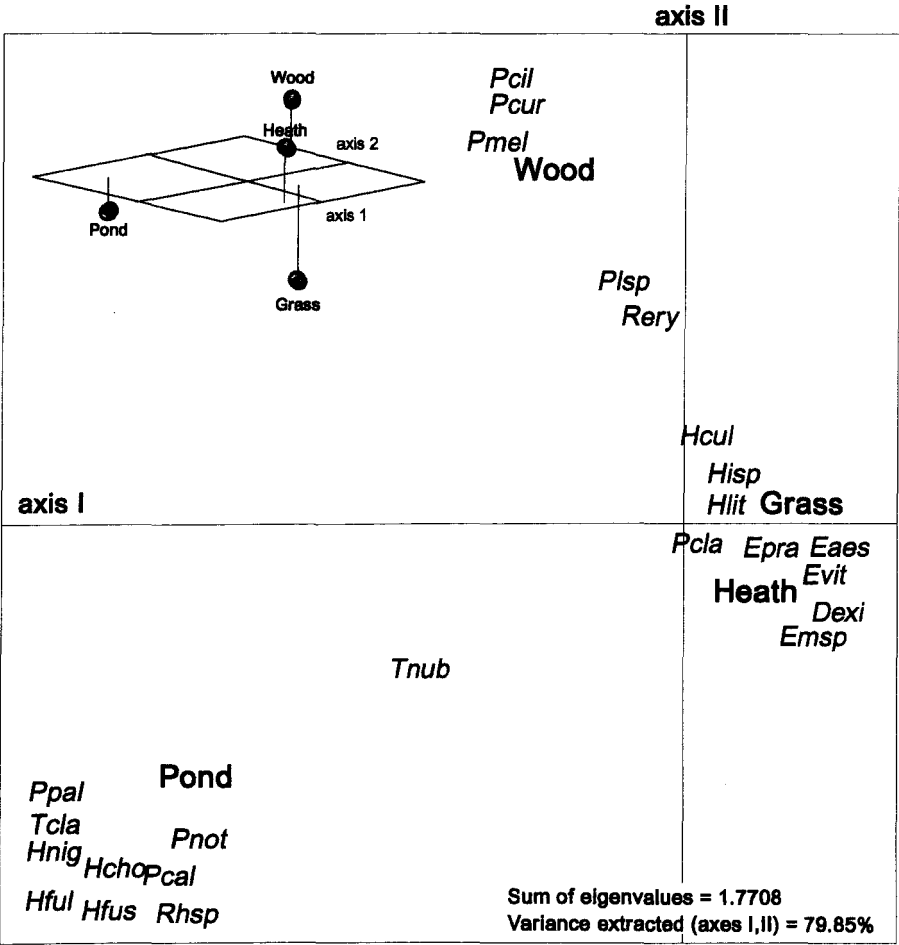
CA ordination diagram

Figure 4. Correspondence analysis ordination diagrams (two first axis plane and tri-dimensional diagram) on the total abundance of the 18 emerging species over 2 years (upper part). Species codes are given in Table 1. Chi-square distance and UPGMA clustering dendrogram (lower part).

but females can disperse from these hunting grounds to oviposit in other, more suitable, biotopes if necessary (e.g. the grassland for *P. clarandus*). *E. aestiva*, a nectar feeder, displays the same distribution: the larvae live in the dry heathland soil while the adults are found mainly near the pond.
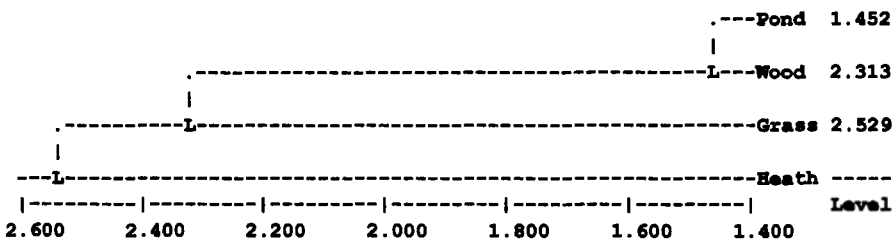
CA ordination diagram

axis II

Tfla Empi Tari
Tcii
Lfla **Wood**
Pmel   Tnot   Epra
              Grass
                            Aery

Bsul
Bice
Hcul

Heath Hpii
Hila   Rham   **axis I**
Hang Text   Hcor
              Eaes
              Tmin

Tcla

              Tnig

Pond

Eeph

      Hint
Hpri
Tach
Hnig Hfla

Heath
Wood
axis 2
Pond
axis 1
Grass

Sum of eigenvalues = 1.2096
Variance extracted (axes I,II) = 80.11%

```
                                        .---Pond  1.452
                                        |
       .--------------------------------L---Wood  2.313
       |
   .-------L--------------------------------Grass 2.529
   |
---L----------------------------------------Heath -----
|--------|--------|--------|--------|--------|--------| Level
2.600   2.400   2.200   2.000   1.800   1.600   1.400
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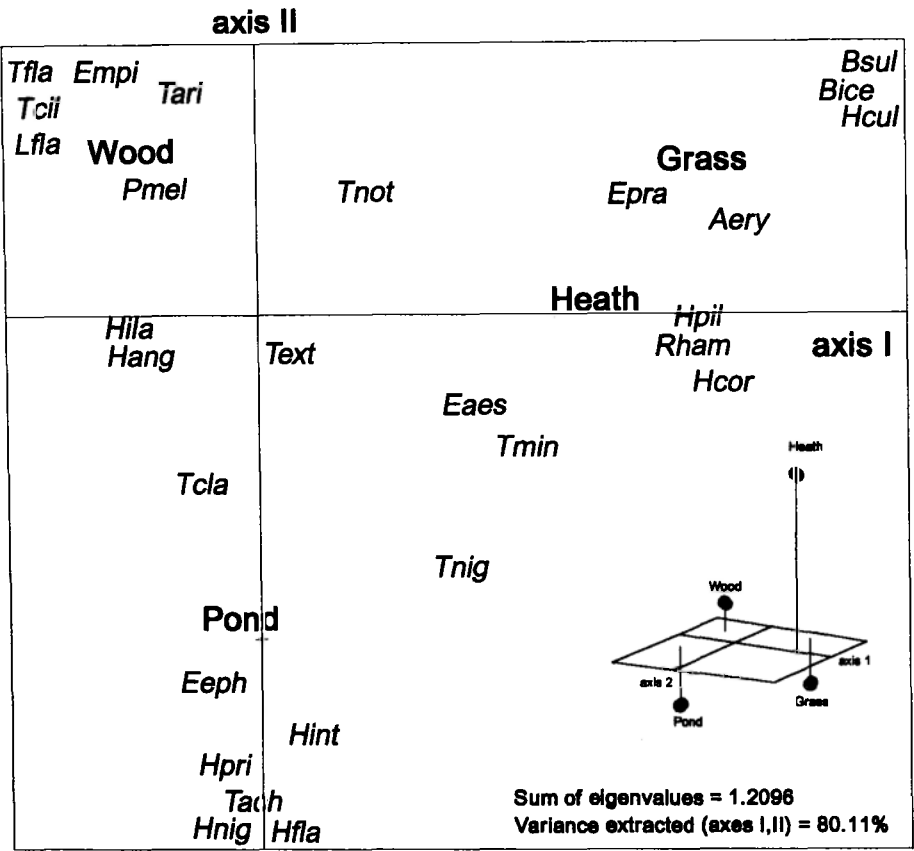
Figure 5. Correspondence analysis ordination diagrams (two first axis plane and tri-dimensional diagram) on the total abundance of the 45 flying species over 2 years (upper part). Species codes are given in Table 1. Chi-square distance and UPGMA clustering dendrogram (lower part).

To the second group belong *E. praevia*, *Rhamphomyia* (*A.*) *erythrophthalma* and *E.* (*C.*) *vitripennis* Mg. for which very few adults were caught in the yellow traps, whatever the habitat in which they breed (Fig. 6b). This fact could, at first, be explained by a bias in sampling due to the location of traps on the soil surface (see Methods). However, when considering the presence or absence of these species in the two types of traps, only one (*E.* (*C.*) *vitripennis*) was absent from yellow traps. Owing to the fact that the study area
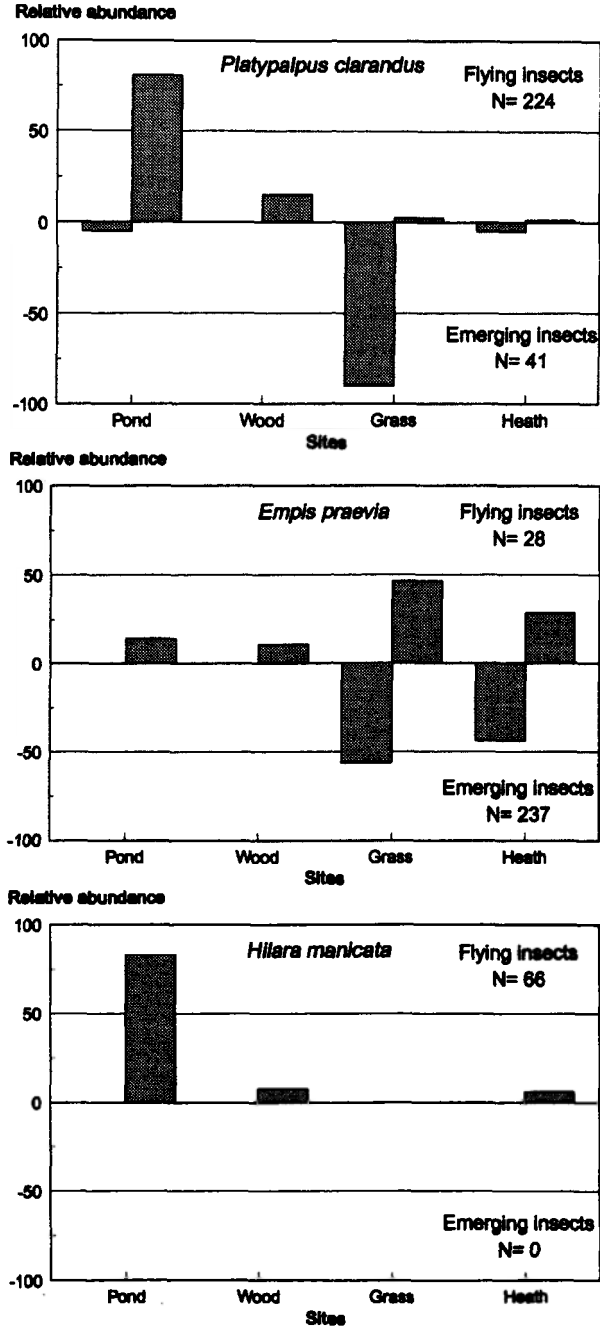
Figure 6. Relative abundance of *P. clarandus*, *E. praevia* and *H. manicata* in yellow pan traps (upper part of each graph) and emergence traps (lower part). Percentages of the total number collected per species over all traps, computed separately for the two trapping systems.

was quite poor in flowering plants, an alternative hypothesis is that these nectar feeders move away towards other sites (not sampled during this study) to find their food. Further studies will be needed to define more accurately their feeding requirements and to choose between these two possibilities.

At last, the third group (Fig. 6c) gathers a great number of species which do not emerge from the four investigated habitats but appears in the yellow traps, suggesting a wide dispersal from other habitats mainly towards the pond banks and the woodlot (e.g. *Hilara manicata*, *Platypalpus pallidiventris* or *Drapetis* (*E.*) *ephippiata* Fallén).

The possible impact of emergence on flying activity was studied using two Canonical Correspondence Analysis (see methods). When the whole set of 45 flying species was considered (matrix D2), only 1.43% of the variance in the flying activity (ratio: total CCA inertia/total CA inertia) was explained by the occurrence of species in emergence traps (column 'Total 1' in Table 1, encoded 0/1; Monte Carlo overall test: F-ratio = 0.60, p value = 0.59, not significant). On the other hand, if only the 18 species caught in both trapping systems were considered, no more than 13.14% of the variance in flying activity (subset of matrix D2) was explained by emergence scores (subset of column 'Total 1', encoded 0/1; Monte Carlo overall test: F-ratio = 2.42, p value = 0.10, ns). These two concordant results show that the observed aerial activity cannot be explained by local emergence and, again, suggest that many adult insects emerging from more or less distant (uninvestigated) habitats fly towards the pond banks and the woodlot.

Phenology

Four of the main species are typically summer species: *E. praevia* emerges in April–May while *P. clarandus*, *Ph. melanocephala* and *E. aestiva* emerge from May to July. On the contrary, *R.* (*A.*) *erythrophthalma* and *E. vitripennis*, emerge in autumn (from August to September and from September to November, respectively). The same timing is recorded for both years, although the number of adults could be different.

Comparing the emergence timing and the aerial activity provides some complementary insights on adult dispersal (Fig. 7). For instance, if the emergence pattern and the occurrence of flying individuals overlap in 1988 for *E. aestiva* and *Ph. melanocephala*, the duration of the aerial activity largely exceeds the emergence period in 1989 for the two species. This result suggests that immigration from other habitats was more extensive in the second, unusually dry, year and that the development rate of larvae was probably slower in distant areas, leading to a time lag in the emergence process and dispersal.

Conclusions

At first, our results reveal the importance of distant species on the composition of the local community. Only 24 of the 51 species emerged from the soils of the four studied sites. Other species were caught only in yellow pan traps. As an example, if we consider the genus *Hilara* (which has been more extensively studied in the literature than other genera) only four of the 13 species were found in emergence traps. This fact is not related to sampling since our study reveals the occurrence of 13 *Hilara* species while the full set of available studies in the same area (including brooks and several ponds over several years) leads to an overall number of 20 species, which suggests a good reliability of the current study in estimating species richness (Tréhen, 1971; Duviard, 1983; Grootaert, 1989 un-
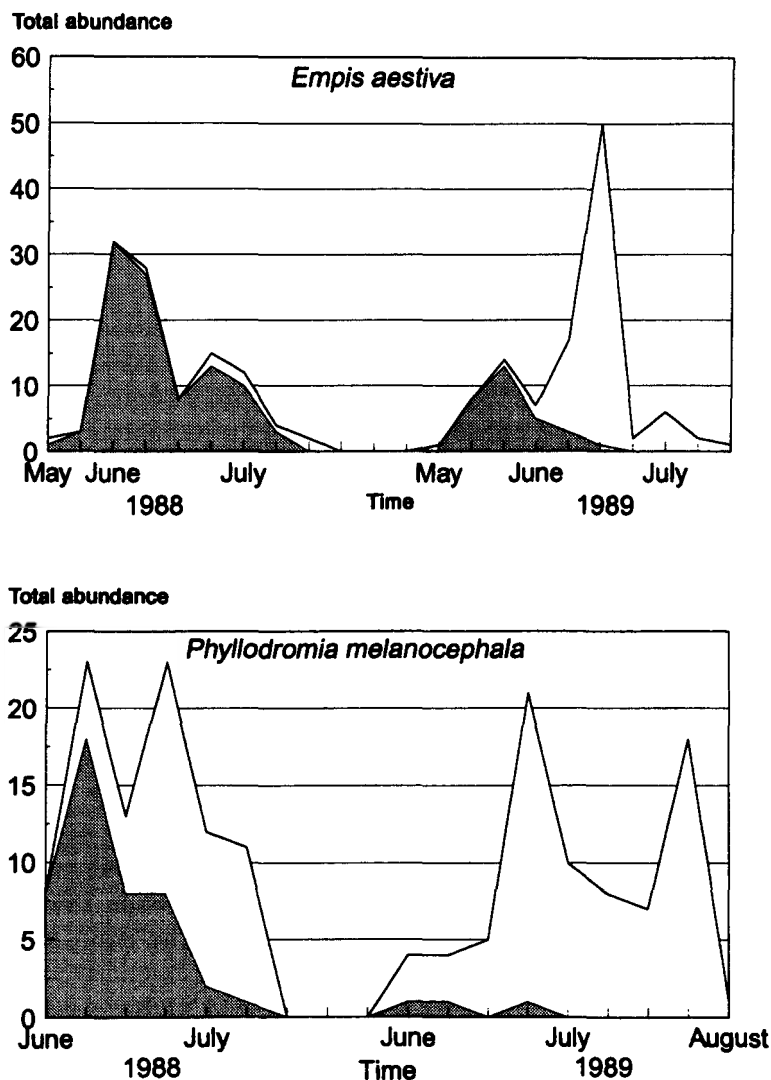
Figure 7. Emergence and aerial activity phenologies of *Empis* (*E.*) aestiva and *Phyllodromia melanocephala* (total numbers) in 1988 and 1989.

published data; Grootaert, 1994). Rather, this result means that species richness at a particular site depends on the heterogeneity of the surrounding habitats.

This is due to the fact that *Hilara* species need three different space units to allow the completion of their life cycle, as demonstrated by Tréhen (1972) and Delettre *et al.* (1992): a wide spectrum of habitats for larval development, a restricted set of patches for swarming and a third space for feeding. These different habitats must be considered as parts of the same functional spatial unit which is required to allow the completion of the full life cycle in *Hilara* species.

Furthermore, in the first study devoted to Empidoidea at the same locality, Tréhen (1971) caught only four *Hilara* species in emergence traps but four additional species in swarms or in aquatic drift. Re-interpreting his data from five distinct sites leads to the

same conclusion as above. In her detailed study on Empidoidea in three agricultural landscapes with hedgerow network, N. Morvan (Morvan *et al.*, 1994; Morvan, 1996) mentioned that two species of the genus *Hilara*, which were very numerous in swarms above brooks (*H. maura* and *H. quadrivittata*), were totally absent from emergence traps located on the soils of three different transects on each side of brooks. Furthermore, several other *Hilara* species, which were also abundant in swarms, were found only at low larval densities in the soils of the 29 locations investigated. These two observations suggest, in the same way, that adults originating in different terrestrial ecosystems concentrate in particular sites above brooks to swarm and find a mate.

All these results are in accordance with many studies investigating the ecological consequences of landscape heterogeneity on species persistence and community structure (for instance, see Turner, 1989 or Naeem and Colwell, 1991). Moreover, many empidoid species are good flyers and habitat heterogeneity increases the number of patches potentially suitable for their larval development, even though increased dispersal could lower their reproductive success (Roff, 1977). However, such a decrease can be avoided through larval migration of some dipteran species when the soil water content fluctuates, leading to a more successful pupation and emergence (Blanchart *et al.*, 1987). Such capabilities provide another way to escape unsuitable mesologic conditions and partly lower the impact of the oviposition choice made by the females.

In a dune landscape, Pollet and Grootaert (1996) demonstrated that the presence of canopy provided by scrubs and trees appeared to be important for the occurrence of many empidid species: their diversity and abundance increased from open to canopied sites. Furthermore canopied sites appeared to be a refuge from which typical dune species colonised more sun-exposed areas.

A very similar effect is observed here for several species, which reinforces the observations mentioned above, although they were conducted in a different set of habitats: fluctuations and asynchrony of the mesologic conditions between sites provide an extended set of microclimates which can benefit species. On the pond banks and in the woodlot, the vegetation induces shaded areas with increased humidity and buffered temperatures. These canopied sites not only provide suitable habitats for larval development in some species but also act as shelters for adults emerging in the neighbourhood (i.e. the grassland, the heathland and other uninvestigated areas). The unusual dryness in the summer of 1989 may have accounted for the increased arrival of adult empidids on the pond banks and in the woodlot. Such habitats probably act as refugia which prevent the extinction of species at a landscape level (Den Boer, 1982). Ecotonal zones are likely to play frequently this role and Dale (1988) suggested that species' boundaries often overlap in these transition areas.

This conclusion is supported by the present study which shows that other empidoid species belonging to different families, sub-families or genera also do need different space units. However, the use of several habitats differs according to species. For *P. clarandus* (Hybotidae, Tachydromiinae), it is obvious that adults emerging from the heathland are not active above this site, but near the pond banks. The same situation occurs in *Ph. melanocephala* (Empididae, Hemerodromiinae) but flying individuals of that species are most numerous on the site from which they emerge, leading to a more restricted use of space. This fact suggests that different species perceive and respond to environmental heterogeneity in different ways and, thus, can be sensitive to different spatial scales (Morvan, 1996).

Similar results were found by Delettre (1992) for Chironomidae (Diptera) on the same sites: some species were found in the four habitats while habitat fragmentation resulted in population isolation for other species. A third set of species switched between different habitats depending on mesologic conditions (Delettre, 1986).

Finally, four conclusions arise from this study, which are also supported by four other works (Tréhen, 1971; Grootaert, 1994; Morvan, 1996; Pollet and Grootaert, 1996). (1) It is quite clear that studies must be conducted at the specific level (or, at least, with genera displaying the same adult behaviour and larval capabilities) to assess the impact of habitat heterogeneity on population dynamics and community structure. (2) The study of a single biotope cannot explain the population dynamics of all its constitutive species and decisions in nature conservation must take the complementarity and spatial distribution of several habitats into account, at least for species needing different space units (Den Boer 1982, 1990; Taylor, 1990). Temporal heterogeneity must be examined as well. (3) Empidoid flies appear to be interesting markers of landscape heterogeneity and the diversity of their life history traits allows to investigate different patterns and processes. (4) Some particular habitats (e.g. the ecotonal zone between aquatic and terrestrial systems) play an important role in population dynamics and community structure. These landscape units must be considered as key resources for a large set of species and their disappearance (or disturbance) may threathen the persistence of many species over a large set of different habitats. Such areas are of primary importance in a conservation perspective.

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