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# Small water colonization in pulse stable (várzea) and constant (terra firme) biotopes in the Neotropics*

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With 2 figures and 3 tables in the text

## Abstract

Short-term succession of macrobenthic fauna was studied in field-experiments near Manaus/Amazonas (Brazil). During three months the colonization of six experimental pools (with a capacity of 1000 l, each) was recorded, once in the terra firme and twice in the várzea. In all cases Chironomidae were the most important benthic colonizers in terms of their abundance, biomass, and species richness. In the várzean small waters detritophagous mayflies (Polymitarcidae) were also numerous. The benthic biomass in the terra firmean pools became dominated by predacious dragonflies (Libellulidae).

Colonizer communities of both biotopes show distinct successional patterns in respect to their trophic organization and their abundance dynamics. These differences express synecological adaptions to the constant biotope terra firme and to the pulse stable várzean floodplains, respectively.

Finally various community attributes are compared with those suggested by Odum (1969) to be diagnostic of early successional stages.

## Introduction

The present paper is part of a study carried out near Manaus in 1981/82, representing the first work on succession in aquatic communities of Central Amazonia. This is surprising as the Amazon floodplains are characterized by enormous annual rises of water. Consequently, colonization and short-term succession of both limnetic and terrestrial communities are fundamental ecological events in these pulse stable biotopes. Moreover the floodplains of whitewater rivers are of economic importance due to their comparatively fertile soils and richness in fish used for food (cf. Junk 1984). The várzea thus was chosen for investigations of succession, whilst for comparison small water colonization in the constant terra firmean rain forest was studied.

## Methods

In order to investigate basic successional patterns in neotropical small water communities, simplified limnetic microsites were studied. In three series of experiments,

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each of which lasted for three months, six water tanks were exposed close to the shore of natural waters and their colonization recorded. Each tank had a capacity of 1000 l and a surface of 1.4 m². Colonization was studied once in the terra firmean and twice in the várzean pools. A detailed description and discussion of the experiments are presented elsewhere (Nolte 1986), therefore only the main aspects are summarized in this paper.

In each series of experiments three tanks were filled with whitewater and three with blackwater, to study the colonization of both types of water in the same locality and at the same time. The water was filtered (150 μm gauze) to remove larger organisms and detritus. The tanks were varnished to prevent an ionic exchange between the walls and waters, which are extremely poor in electrolytes (e.g. Furch 1984). The bottom of each tank was stocked with four types of substratum. Three kinds of sands, distinct in grain size, were exposed in petri-dishes of 60 cm², acrylic tiles of 400 cm² served as hard bottom. Initially samples of substrata were taken every two or three days, since the rate of change is expected to be highest during early colonization. After one month samples were taken weekly and, from then on, every second week. 180 individual samples were available from each series of experiments for the analysis of benthic succession. Additionally samples of plankton, nekton and epineuston were taken and some basic abiotic factors were measured regularly (see Nolte 1986).

Succession was studied from June until September in the terra firme. The tanks stood within a clearing on the bank of the creek Barro Branco (direct radiation). In the várzea the tanks were colocated on a wooden float near the shore of Marchantaria Island. These experiments were carried out during the low water period of the Solimões (October until December) and during the rise of the water level (January until April) (localities are described by Franken 1979 and Worbes 1986).

Evaluation of such consecutive studies should also take seasonal differences into account. However, most of the colonizers were winged insects with aquatic larvae which are not subjected to a seasonal phenology in the tropics. Even though such field-experiments always include artefacts due to the lower system complexity, some basic patterns in colonization and successional processes in terra firme and várzea were revealed.

## Results and discussion

### Community composition (dominant taxa)

In all experimental pools Chironomidae were the most important colonizers. Over the three months period, at least nine genera with several species were found per tank [*Coelotanypus, Procladius, Ablabesmyia* (+ *A. annulata*-group), *Larsia, Labrundinia*, Tany. Gen 4-dnt. and Gen 2-dnt. (acc. to Nolte 1986), *Goeldichironomus, Parachironomus, Asheum, Polypedilum*, Chir. Gen A6 (acc. to Reiss 1976) plus Tanytarsini]. Their abundance peaks were as high as 5,600 (várzea) to 6,000 ind./m² (terra firme) with a mean density of about 1,000 to 2,000 ind./m² (Table 1). Chironomidae always contributed half of the benthic biomass, with a maximum of 90 % of the standing crop.

Ephemeroptera were also always present (Table 1). In the terra firmean pools three to four species of Baetidae and one of Caenidae occurred with highest densities of about 400 nymphs/m², but a mean of barely 100 ind./m². In the várzea, in contrast, even the average abundance of mayflies was about 3,200 nymphs/m², but only in the whitewater tanks (see below). Here the de-

Table 1. Insect colonization of the experimental pools. A comparison of number of taxa and mean abundance in terra firmean and várzean communities.

| | insect families | number of discernible taxa* | | mean abundance during 3 months | |
|---|---|---|---|---|---|
| | | terra firme | várzea | terra firme | várzea |
| bottom (no./m²) | Chironomidae | 9–12 | 9–10 | 2,000 | 1,000 |
| | Baëtidae | 3– 4 | – | 10–14 | – |
| | Caënidae | 1 | 2 | 20–85 | 7–14 |
| | Polymitarcidae | – | 1 | – | 3,200 |
| | Libellulidae | 1– 2 | – | 35 | – |
| water body (no./m³) | Culicidae | 1– 2 | – | 70–80** | – |
| | Chaoboridae | 1 | 1 | 8 | 28 |
| | Notonectidae | 1 | 1 | 70 | 8 |
| | Corixidae | 1– 2 | 1 | 10 | 7 |
| Total (max.) | | 25 | 16 | | |

* Diptera: genera; others: species. ** restricted to the first 20 days.

tritophagous Polymitarcidae *Campsurus notatus* was eudominant. Two species of Caenidae were found sporadically (Table 1).

Odonata colonized only the terra firmean pools. Libellulidae were important predators with a maximum abundance of 300 ind./m². In the várzea only a few Zygoptera were found in the small waters.

In the free water bodies the following insect taxa were recorded (Table 1): In the terra firme two genera of Culicidae occurred with 70 to 80 ind./m³, but only during 16 to 20 days after the experiment had started. From the third week on Notonectidae became numerous (avg. 70 ind./m³) and their offspring had reached the 3rd, 4th and 5th instar. These are known to be effective culicid-feeders (ELLIS & BORDON 1970), preventing mosquitoes from becoming established. In the open várzea, neither Culicidae occurred, nor did Notonectidae show a higher abundance (avg. 8 ind./m³). Some Chaoboridae, Ceratopogonidae, Dixidae and Corixidae were recorded in each series of experiments.

The observed composition of insect coenoses is characteristic of sparsely structured, astatic small waters in various climatic zones of the world, but it is noteworthy that Coleoptera did not take part in the colonization of the studied neotropical micro sites.

It is not possible to deduce a definite order of colonization within the insect taxa. Whilst chironomids were recorded earlier than mayflies, which in turn appeared earlier than dragonflies, this can be attributed to the different developmental times of their eggs rather than to successive oviposition. It should be mentioned that among the chironomid taxa a colonization order was observed to some extent in all three series of experiments (NOLTE 1986). In the várzea and terra firme, algal and detrital feeders became established first. Predators appeared in higher densities only during the third month when the benthos had become more complex, and sufficient prey was available.

### "r-selection"

As expected, most of the colonizers show features of r-strategists: All recorded Chironomidae take 11 to 16 days from egg to emergence, Culicidae only 4 to 7 days. High reproductivity of mayflies is realized in different ways: *Campsurus notatus* produces some thousand eggs per female, considerably more than other Polymitarcidae. *Brasilocaenis irmleri* takes only 14 days for development (Irmler 1981) and *Caenis cuniana*, the other colonizing Caenidae of the várzea, is parthenogenetic (Froehlich 1969). Flexibility in the feeding habits was observed in predacious Tanypodinae (*Larsia* spec., *Ablabesmyia annulata*-group), which switched to algal food when their prey ran short. The high dispersal power of all recorded insect taxa also favours r-selection.

Primary colonizers are mainly generalists. In the case of *C. notatus* a specialization to sediments with a mean grain-size of 0.1 mm was observed, and it does not tolerate blackwater conditions (see Nolte 1986). Therefore this várzean colonizer can not be called eurioecious.

### Abundance dynamics and standing crop

The insect coenoses from várzea and terra firme show differences in community attributes which can be seen in quantitative data (abundance, biomass). In Fig. 1 the abundance dynamics of Chironomidae on the four exposed types of substrata is given. Exemplary, their colonization of water appropriate to the biotope (blackwater/terra firme, whitewater/várzea) is compared. The densities of Tanytarsini and Chironomini, tribes comprising mostly primary consumers, and of the mainly predacious Tanypodinae, are plotted separately.

The abundance of midges from the terra firme fluctuated over three months, eventually reaching their maxima after 10 to 11 weeks. Várzean Chironomidae, on the other hand, attained one clear density peak of 4,500 to 5,000 ind./m$^2$ within the first four weeks. Two weeks later their abundance evened out to about 10% of the initial densities. Such continuous density fluctuations of colonizers from the terra firme, in contrast to early maxima with subsequently well-balanced abundances of insects from the várzea were also observed in Ephemeroptera. The várzean *C. notatus* attained highest densities within the first four weeks with enormous peaks of 16,700 to 16,900 nymphs/m$^2$ on silt (exposed Solimões sediment). Three weeks later these extremely high abundances decreased to about 1,300 ind./m$^2$, when older *C. notatus* had grown from barely 1 mm to about 8 mm in length, even though a permanent hatching of young nymphs was recorded. Other insect taxa remained too rare to find similar abundance patterns.

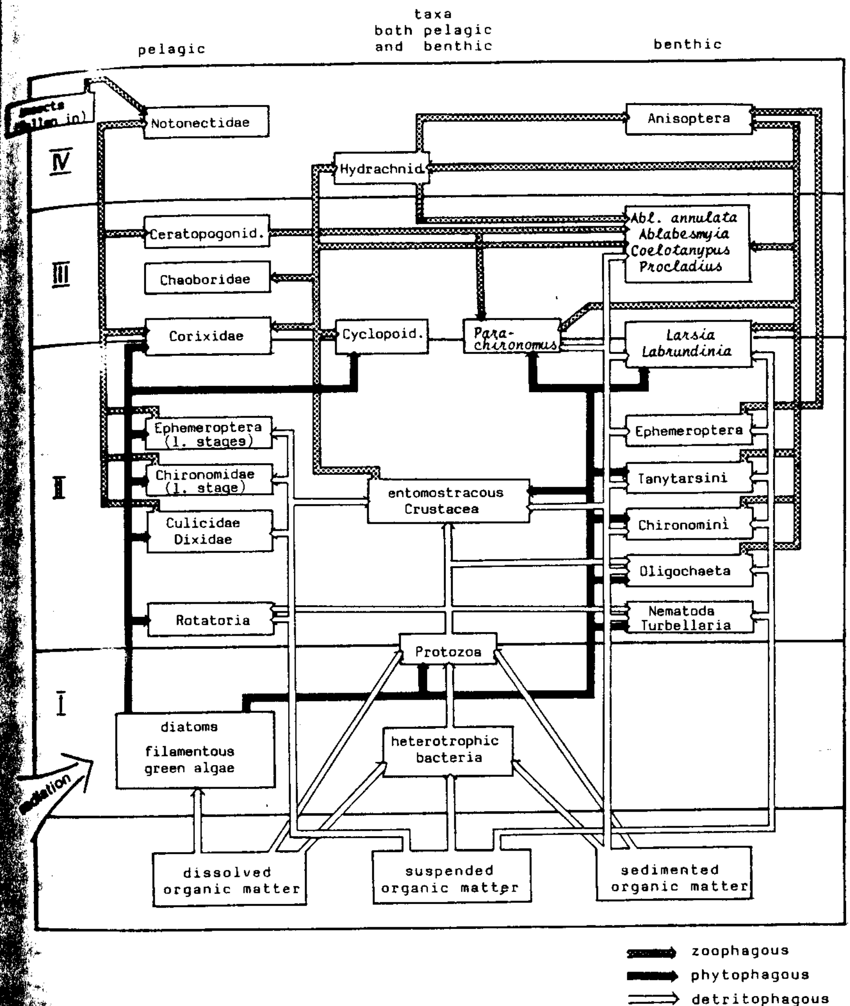


Fig. 2. Qualitative scheme of the food web (for explanation see the text).

concept is widely accepted, but there have been only a few attempts at testing its validity (Drury & Nisbet 1973, Fisher et al. 1982). Comparison of the nine evaluated attributes show that trends in small waters of the terra firme generally agree with Odum's predictions, whereas those in the várzean small water coenoses are often divergent (in Table 3 Odum's numeration is given in parenthesis).

(1) The benthic yield was always high in comparison with natural waters. Apart from the early successional stages, this results from the fact that the studied pools were largely closed systems.

Table 3. Comparison of the present results with Odum's (1969) predictions.

| ecosystem attributes | postulated by Odum (1969) | results of present research: terra firme | | várzea | |
|---|---|---|---|---|---|
| 1. ( 4.) $P_n$ (yield) | high | high | + | high | + |
| 2. ( 5.) food chain | linear; mainly grazing | web-like; mainly grazing | — + | linear; mainly detritus feeders | + — |
| 3. ( 6.) total organic matter | small, increases | increases | + | increases | + |
| 4. ( 8.) species diversity | low, increases | increases | + | increases | + |
| 5. (12.) niche spezialisation | broad | broad (in dominants) | + | narrow (in dominants) | — |
| 6. (14.) life cycles | short, simple | short, simple | + | short, simple | + |
| 7. (17.) role of detritus in nutrient regeneration | unimportant | unimportant | + | important | — |
| 8. (18.) growth form | r-selection | r-selection | + | r-selection | + |
| 9. (22.) stability (resistance to external pertubations) | poor | poor | + | short-term increase | — |

\+ agreement, — divergence.

(2) During the three months the trophic relations in the várzean communities remained linear. In the terra firme, on the other hand, the young coenoses developed a complex foodweb within a few weeks. The latter disagrees with Odum's concept. However, the findings that almost all primary consumers among the terra firmean colonizers fed on algae, agree with it. In contrast, in the várzean small waters, which were comparatively heterotrophic (low primary production Nolte 1986), the foodchains were mainly based on detritus. Odum considers detritus an unimportant source in early successional stages [see also (7) in Table 3] without distinguishing autotrophic and heterotrophic systems. The present study shows that such a generalization is unadmissable.

(3) As Odum predicts, the total standing crop increased with time. In the closed systems no output of organic matter, but a steady production, was seen.

(4) The number of colonizing taxa increased with time. However, in response to the dominance of a single species (e.g. *C. notatus, Larsia* spec.) the diversity index did not always increase.

(5) In agreement with Odum, the dominant colonizers from the terra firme were generalists (food, substratum, water quality), with the exception of Tanytarsini. In the várzea, on contrary, besides Tanytarsini the eudominant *C. notatus* is specialized to biotope structures (waterquality, substratum), so that a broad ecological valence cannot be generalized for all colonizers.

(6, 8) Life cylces of all colonizers are short and simple and they are r-selected taxa.

(9) Odum defines the stability of a system as its resistance to external perturbations. As pointed out earlier, young várzean communities show comparatively simple organizational patterns (foodchain, trophic levels, abundance dynamics). This is understood to represent adaption to the pulse stability of the floodplains. In agreement with Fisher et al. (1982) it has to be stated that



Odum's prediction that early successional stages are always more susceptible to perturbations than older systems cannot be generalized. Particularly when resistance to perturbations (fluctuations in water level) is the criterion for stability (Odum), relative stability is intrinsic to less complex systems, since a rapid attainment of previous community status following perturbation is permitted.

The present results agree only in part with Odum's (1969) concept. This supports the doubt, first expressed by Drury & Nisbet (1973), toward the applicability of one theory on detailed community-attributes to all existent ecosystems. The resulting demands for a generalization of Odum's concept (Drury & Nisbet 1973, Fisher et al. 1982) reduce its value by the introduction of non-specific criteria.

Odum's concept is undoubtly a useful framework in empirical succession analysis. But as a consequence of the present results, and of studies of succession in other limnetic, marine and terrestrial systems (e.g. Fisher et al. 1982, Schoener 1974, Drury 1956), it appears inappropriate for certain biotopes. Therefore a subdivision of systems with distinct basic attributes is proposed, prior to application of Odum's criteria, which can then be modified to a form more suitable to that subdivision (for example, in a developing heterotrophic system, it is not justified to demand that the food chain be primarily based upon grazers). With recognition of the nature of one such subdivision (e.g. more autotrophic or more heterotrophic systems, or communities recruited from constant or pulse stable biotopes), it should be possible to apply appropriate specific ecosystem attributes.

## Summary

Short-term succession of aquatic communities was studied in the Amazonian floodplains (várzea) and in the rain-forest (terra firme) with the aid of experimental pools. Attributes of the colonizing insect communities of both biotopes are compared in terms of their composition, abundance dynamics, standing crop and complexity of their trophic relations. In the three series of experiments, Chironomidae always colonized the pools with most species (out of 9—12 genera, Table 1), contributing up to 93 % of the benthic standing crop (várzea, Table 2). Terra firmean colonizers showed continuous abundance fluctuations during the three month period [esp. Tanytarsini, Chironomini, Tanypodinae (Fig. 1) and Baetidae], whilst dominant várzean colonizers showed high initial density peaks with subsequent well-balanced abundances [esp. Tanytarsini (Fig. 1) and Polymitarcidae (*Campsurus notatus*)]. During the three month period the terra firmean small water communities became predator dominated (Libellulidae, Tanypodinae, Notonectidae) in terms of biomass (about 72 %, Table 2), and their trophic relations were complex and weblike after only eight weeks (Fig. 2). The várzean communities, in contrast, consisted of primary consumers, mainly feeding on detritus (Polymitarcidae, Chironominae). Here the food chain remained linear and secondary consumers (Tanypodinae) never exceeded 4 % of the benthic standing crop. These distinct community-attributes are understood to represent adaption to the constant terra firmean and pulse stable várzean biotope.

The present findings are compared with the succession concept of ODUM (1969). Attributes of terra firmean communities largely agree with ODUM's concept, but várzea coenoses often show divergences (Table 3). Therefore, a subdivision of ecosystems with distinct basic patterns is proposed, before attributes specific to early successional stages can be classified.

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