

GROUND BEETLES AND ROVE BEETLES ASSOCIATED WITH TEMPORARY PONDS IN ENGLAND

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Introduction

To date, research on the ecology and conservation of wetland invertebrates has concentrated overwhelmingly on fully aquatic organisms. Many of these spend part of their life-cycle in adjacent terrestrial habitats, either as pupae (water beetles) or as adults (mayflies, dragonflies, stoneflies, caddisflies and Diptera or true-flies). However, wetland specialist species also occur among several families of terrestrial insects (Williams & Feltmate 1992) that complete their whole life-cycle in the riparian zone or on emergent vegetation. Eyre & Lott (1996) listed 441 terrestrial invertebrate species which characteristically occur in riparian habitats along British rivers. Most of these species belong to two families of predatory beetles: the ground beetles (Carabidae) and the rove beetles (Staphylinidae). The prevalence of these two families in beetle assemblages is repeated in a wider range of temperate wetland types (Krogerus 1948; Obrtel 1972; Kohler 1996), where, usually, rove beetles are the most species-rich terrestrial family. Both groups have carnivorous larvae and adults, feeding on a wide range of other insects and small invertebrates (Bauer 1974, 1991) or scavenging on dead insects and cast skins washed up at the water's edge (Hering & Plachter 1997). However, some rove beetles (e.g. *Bledius* species) feed on algae (Herman 1986).

Many species of carabid and staphylinid beetles that live in wetland habitats are recognised to have significance for nature conservation (Shirt 1987; Hyman 1992, 1994). This article briefly reviews aspects of the ecology of wetland ground and rove beetles, in order to examine whether temporary ponds have potential significance for their conservation.

Diversity of ground and rove beetles around ponds

There are few published references on the diversity of terrestrial beetles specific to ponds. However, recent work in Leicestershire, England, has revealed some interesting patterns. In 1999, the species diversity of six invertebrate groups was studied in 30 ponds and their margins across three landscape types: farmland on boulder clay, residential areas in a river valley, and recreational areas on siliceous rocks in a semi-upland area. The ponds

Table 1. Six groups of macroinvertebrates sampled in 30 ponds in Leicestershire, during 1999. Columns give numbers of samples containing each group (N), total number of species found in the survey (S), average species-richness per sample (α -diversity), and (β -diversity ($\beta = (S/\alpha) - 1$). Stray non-wetland species of ground and rove beetles are eliminated from totals.

Group	N	S	α -diversity	β -diversity
Water beetles (adult)	29	70	13.23	4.29
Ground & rove beetles (adult)	28	93	10.47	7.88
Water bugs (adult)	23	19	2.70	6.04
Dragonflies (larvae)	22	10	1.53	5.54
Water snails	17	10	1.13	7.82
Leeches	16	5	0.90	4.56
All groups	30	207	27.93	6.41

Table 2. Species of ground and rove beetles recorded from riparian zones at four or more sites in a survey of 30 ponds in Charnwood, Leicestershire.

Carabidae	Staphylinidae	
<i>Agonum fuliginosum</i>	<i>Atheta graminicola</i>	<i>Parocynusa longitarsis</i>
<i>Bembidion articulatum</i>	<i>Carpelimus bilineatus</i>	<i>Philhygra elongatula</i>
<i>Bembidion assimile</i>	<i>Carpelimus rivularis</i>	<i>Philhygra malleus</i>
<i>Bembidion biguttatum</i>	<i>Deinopsis erosa</i>	<i>Philhygra volans</i>
<i>Bembidion dentellum</i>	<i>Gnypeta rubrior</i>	<i>Quedius maurorufus</i>
<i>Bembidion guttula</i>	<i>Lathrobium brunripes</i>	<i>Stenus bifoveolatus</i>
<i>Bembidion lunulatum</i>	<i>Mocyta fungi</i> agg.	<i>Stenus binotatus</i>
<i>Pterostichus nigrita</i>	<i>Mycetota laticollis</i>	<i>Stenus boops</i>
<i>Stenolophus mixtus</i>	<i>Myllaena gracilis</i>	<i>Stenus cicindeloides</i>
	<i>Myllaena infuscata</i>	<i>Stenus junco</i>
	<i>Myllaena intermedia</i>	<i>Stenus picipennis</i>
	<i>Oxypoda elongatula</i>	<i>Stenus pubescens</i>

ranged in character from large permanent waterbodies to small seasonal features. Adult water beetles formed the largest component of the species list at most ponds (Table 1). They had the highest average α -diversity (species richness per site) of any single group and comprised on average 47% of the total number of species recorded at each pond. However, adult riparian ground and rove beetles were the most species-rich group in the dataset for the entire survey. They contributed 45% of all species recorded and also outnumbered the aquatic groups at some individual sites. A short-list of the commonest ground and rove beetles is given in Table 2. β -diversity, a measure of the differences between sites, was highest among the riparian beetles, closely followed by water snails.

Narrow habitat requirements and poor dispersive capabilities have been cited as possible correlates of high β -diversities (Shmida & Wilson 1985; Harrison et al. 1992). Low efficiency in colonising isolated ponds may be an explanation for the observed high β -diversity of aquatic snails, which were found to be more species-rich in the river valley where sites are closer and connected by ditch systems facilitating dispersal. However, the same argument cannot be used for the terrestrial ground and rove beetles, as many of the species recorded here seem to be proficient at colonising new sites. Only a small proportion of the riparian beetles recorded in the study are habitually short-winged (e.g. *Agonum fuliginosum* and *Stenus boops*), and some of these produce occasional full-winged morphs which can be efficient dispersers (den Boer 1977). Habitat specificity is a more likely explanation of high β -diversity in riparian beetles than poor dispersive ability. If so, ground and rove beetles would be a suitable group upon which to base a classification of ponds into habitat types. Furthermore, their sensitivity to environmental variables makes them good candidates to indicate the effects of pond management on biodiversity..

Temporary ponds considered as a habitat for ground and rove beetles

In order to investigate habitat specificity further and to determine whether there may be a specialist fauna of temporary ponds, a Detrended Correspondence Analysis (DCA) was performed on 112 samples of ground and rove beetles taken from 112 ponds of many different types in lowland England between 1985 and 2000. Fig. 1a shows the ordination scores obtained, arranged according to the two most important axes of variation in species composition. The most important axis of variation (axis 1) is related to the organic nature of the substratum, with high-scoring samples on this axis taken from ponds with peat substrata, and low scoring samples from ponds on mineral substrata. The 31 samples from temporary ponds are distributed more

or less evenly along this axis, reflecting the fact that they provide habitat for beetles associated with many different types of substratum.

By contrast, all samples of beetles from temporary ponds have high scores on axis two, the second most important axis of variation, which is related to hydrology. This suggests that temporary ponds have a characteristic fauna of ground and rove beetles. However, other pond types also score highly on axis 2, in particular those situated in river floodplains, where they are subject to seasonal fluctuations in water level. Consequently, a specialist beetle fauna of temporary ponds cannot be identified from this ordination. We can only identify a fauna that has specialist requirements which can be met by temporary ponds as well as other pond types. It is likely that these requirements are connected with an ability to breed in substrata exposed by receding water levels in the spring.

Fig. 1b shows the ordination scores for beetles of national conservation importance. Nationally scarce species are distributed throughout the ordination space, indicating that they can occur in any type of pond. However, the national Red Data Book species recorded in the dataset all have high scores on either axis 1 or axis 2. Consequently, they are more likely to be found either in peaty ponds or in ponds of an ecological type that includes temporary ponds. Therefore, some temporary ponds have the capacity to support populations of species that are of national importance for conservation.

Table 3 lists the species of national conservation status that were recorded in temporary ponds within the dataset. Several ground beetle species, such as *Bembidion clarki*, *Pterostichus gracilis* and *Agonum livens*, are relatively numerous around permanent reservoirs that have large draw-down zones, as well as at the margins of temporary ponds. This supports the hypothesis that many species associated with temporary ponds are dependent on seasonal fluctuations in water levels rather than total drying out of open water.

In general, less is known about the ecology of the rove beetles listed in Table 3. Little has been published on the habitats of *Stenus longitarsis* in Britain, but Horion (1963) described its preference for peat and, in particular, damp heath and moorland in Central Europe. In 1999, I found single specimens in two temporary pools in the New Forest, one of them ephemeral following heavy rainfall. Between 1989 and 1992, I recorded *Calodera uliginosa* in large numbers from several seasonal pools and also a river bank on Loughborough Big Meadow, Leicestershire. The only other published British records come from the River Stour in Hampshire, where it was found abundantly for two years (Harwood & Williams 1928) before seeming to disappear, as happened also in Leicestershire. A single specimen of *Calodera rufescens* was also found in Loughborough Big Meadow at one of the shallow

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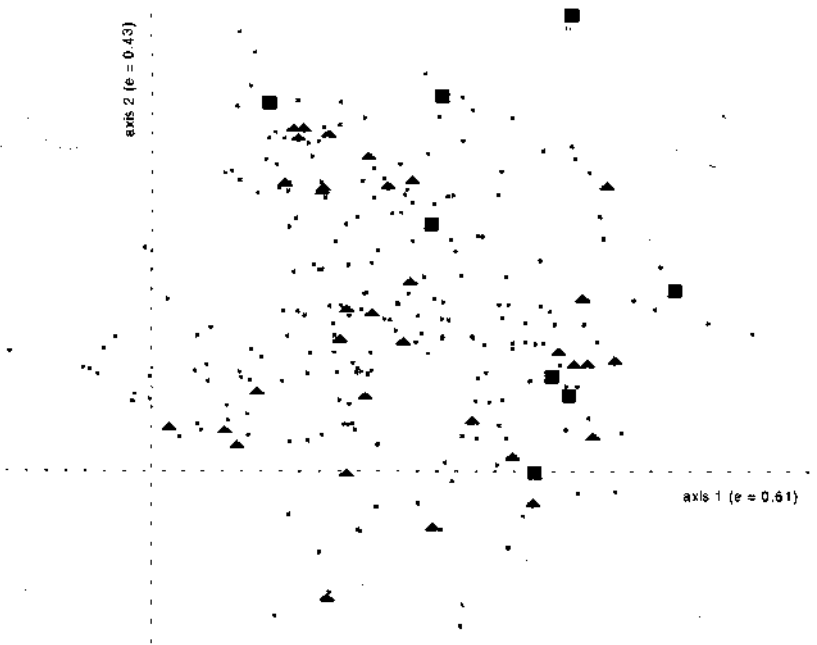
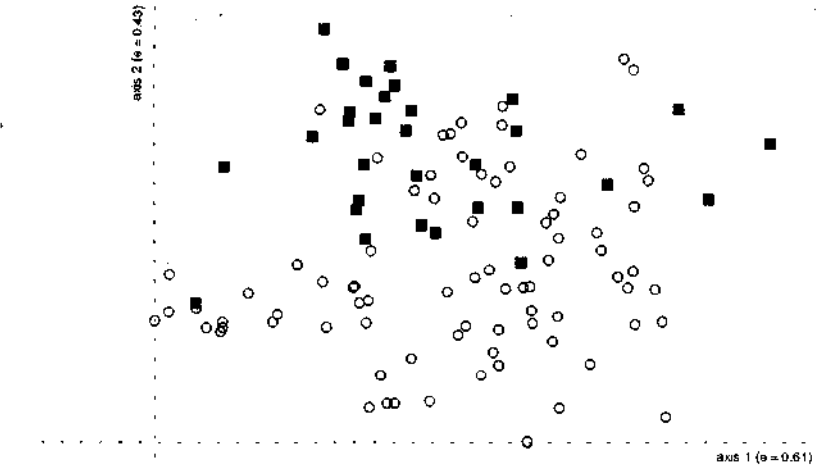


FIG. 1. (a) (*left, above*): DCA ordination plot of samples of ground and rove beetles taken from 112 ponds in lowland England. Solid squares represent 31 samples taken from temporary ponds; open circles represent permanent ponds. Low scoring samples to the left of axis 1 are from ponds on mineral substrates subject to disturbance by excavation, intensive grazing or frequent scouring by floods. High scoring samples to the right of axis 1 are from relatively undisturbed ponds on organic substrata. Low scoring samples on axis 2 are from sites with a constant water source such as a spring. High scoring samples on axis 2 are from ponds with large seasonal fluctuations in water level, (b) (*left, below*): DCA ordination plot of 238 individual species from 112 ponds in lowland England. Large solid squares represent eight provisional or designated national red data book species, and solid triangles represent 42 nationally scarce species as listed by Hyman (1992, 1994). Axes 1 and 2 are the same as those shown in (a).

seasonal pools. This rove beetle has been more widely recorded in Britain (Hyman 1992), although it is often confused with *C. riparia*. In general, *Calodera* species breed in early spring (Assing 1996), and the species that are rare in Britain tend to be more common in eastern Europe. *Schistoglossa viduata* was recorded from a temporary pond on Thompson Common, Norfolk, but its typical habitat is emergent tussocks in ponds and it cannot be regarded as a particularly characteristic species of temporary ponds.

The habitat specificity of carabids and staphylinids can be linked to variations in life-histories, hibernation strategies, behaviour and morphological adaptations. These aspects are briefly considered in the following sections, including their possible importance for certain species in relation to temporary ponds.

Life-histories of ground and rove beetles

In northern Europe, ground beetles rarely if ever go through more than one generation per year (Lindroth 1949). Within this constraint, certain types of life-history appear to offer a selective advantage in the wetland environment. Murdoch (1967) studied the life-histories of 21 wetland ground beetles in marshes in Britain and found that all but one were spring-breeders that habitually overwintered as adults. Furthermore, he examined data on Scandinavian ground beetles and found that only 11 out of 124 wetland species were autumn-breeders with overwintering larvae. He suggested that larvae are vulnerable to inundation during the winter, whereas adults can escape more easily into hibernation quarters. However, Andersen (1968) reported high survival rates of eggs, larvae and pupae of riverbank species during submersion and recorded a higher survival rate for larvae than adults.

Table 3. Twenty-four ground and rove beetles of national conservation status recorded from 31 temporary ponds in lowland England between 1985 and 2000. Conservation status is taken from Hyman(1992, 1994).

Family	Species	National conservation status
Staphylinidae	<i>Stenus longitarsis</i>	Red Data Book (indeterminate)
Staphylinidae	<i>Calodera rufescens</i>	Red Data Book (insufficiently known)
Staphylinidae	<i>Calodera uliginosa</i>	Red Data Book (insufficiently known)
Staphylinidae	<i>Schistoglossa viduata</i>	Red Data Book (insufficiently known)
Carabidae	<i>Acupalpus consputus</i>	Nationally scarce
Carabidae	<i>Agonum livens</i>	Nationally scarce
Carabidae	<i>Badister dilatatus</i>	Nationally scarce
Carabidae	<i>Bembidion clarki</i>	Nationally scarce
Carabidae	<i>Bembidion fumigatum</i>	Nationally scarce
Carabidae	<i>Bembidion gilvipes</i>	Nationally scarce
Carabidae	<i>Pterostichus anthracinus</i>	Nationally scarce
Carabidae	<i>Pterostichus gracilis</i>	Nationally scarce
Staphylinidae	<i>Calodera riparia</i>	Nationally scarce
Staphylinidae	<i>Dochmonota clancula</i>	Nationally scarce
Staphylinidae	<i>Gabrius bishopi</i>	Nationally scarce
Staphylinidae	<i>Gabrius velox</i>	Nationally scarce
Staphylinidae	<i>Gnypeta ripicola</i>	Nationally scarce
Staphylinidae	<i>Gnypeta velata</i>	Nationally scarce
Staphylinidae	<i>Myllaena elongata</i>	Nationally scarce
Staphylinidae	<i>Myllaena kraatzii</i>	Nationally scarce
Staphylinidae	<i>Oxyteta exoleta</i>	Nationally scarce
Staphylinidae	<i>Oxytelus fulvipes</i>	Nationally scarce
Staphylinidae	<i>Philhygra hygrobia</i>	Nationally scarce
Staphylinidae	<i>Platystethus nodifrons</i>	Nationally scarce

Nevertheless, adult mobility may be important for avoiding mortality from prolonged inundation during the winter, especially in sites that have large seasonal fluctuations in water levels such as temporary ponds.

Krogerus (1948) conducted field observations of developmental stages when he studied the insect fauna of a Finnish lake margin whose seasonal water levels were affected by snow-melt. The ground beetles were nearly all spring-breeders, but did not arrive at the breeding site until late May or June. Numbers built up very quickly, with strong migrations from hibernation sites on the warm days. Some species arrived one week later than others. Young larvae first appeared in June close to the water margin. As the water level dropped, the adults moved with it and most died off several weeks later. The larvae lived deep within the soil and did not move from a zone which became progressively drier and more remote from the water margin. By July, remaining adults were concentrated near the water's edge, young larvae were found higher up the bank and older larvae were found higher still. Pupation took place in flat depressions on mud under a thin layer of moss. Adults emerged from their pupation site in August. Mass emergences often followed heavy rain. The soft, freshly moulted adults waited in dry areas high up on the bank until they had developed hard cuticles, and then moved down to the water margin before migrating to hibernation sites in September. It is easy to imagine that this pattern of exploiting the shoreline of a lake with receding water levels could apply to temporary ponds as well.

Anyone who has sampled riparian or wetland ground beetles in Britain will know that, for most species, spring is their main period of activity when they can be most easily captured. At this time of year they congregate in breeding assemblages on sediments exposed by falling water levels. Rove beetles are also active in the same areas in the spring, but there is a tendency for some species to persist through to the late summer and autumn, and several species appear to have a longer breeding season than ground beetles. By contrast, sampling in the winter is often relatively unproductive.

It is not known whether the domination of spring-breeders among riparian ground beetle assemblages is repeated among rove beetles. Methodically collected information on riparian rove beetles is lacking, although Horion (1963, 1965, 1967) gives records of many riparian and wetland species overwintering as adults. On the other hand, Steel (1970) reported that riparian species of *Lesteva* breed in autumn and overwinter as larvae.

Hibernation strategies of ground and rove beetles

In his study of a Finnish lake, Krogerus (1948) found that in winter, most species of ground beetles and rove beetles on the lake shore occurred in large

numbers in leaf litter among willow scrub above marginal areas. Only a few species were found by the water's edge and these were often washed up into the willow scrub by winter floods. Palmén (1945) observed that some shore habitats such as extensive reedbeds growing in shallow water do not lose their summer fauna in the winter. He investigated overwintering in six beetle species which spent the summer in a reedbed growing in the shallow margins of an almost freshwater inlet of the Baltic Sea, and found that the ground beetle *Agonum fuliginosum* moved higher up the bank to an area dominated by sedge during the autumn. There was also a partial migration of the rove beetle *Paederus riparius* to the sedge zone. Other beetles, together with some *Paederus riparius*, stayed throughout the winter in the inundated reedbed. Several small beetles, including many rove beetles, were found sheltering in hollow reed-stems in ice (Palmén 1949). Laboratory experiments suggested that the presence of litter is important in enabling many beetles to survive freezing conditions underwater (Palmén 1945, 1949). In an Oxfordshire marsh, *Agonum* and *Pterostichus* were found hibernating in rotten logs and grass tussocks on site, although some individuals washed out by winter floods moved to grass tussocks in surrounding grassland (Murdoch 1966).

In his Finnish lake, Krogerus (1948) failed to find some species during the winter and concluded that they overwintered some distance away. There were few species in this group but they included many of the larger species. He reported isolated instances from elsewhere in Finland in which some of these (*Blethisa multipunctata*, *Pterostichus minor*, *P. nigrita* and *Agonum versutum*) were found in leaf litter c.1 km from the nearest wetland. In Sweden, Lindroth (1942) concluded that the wetland ground beetle *Oodes gracilis* flies away from its summer habitat in order to hibernate. In England, I have found large numbers of the small rove beetle *Platystethus cornutus* hibernating in woodland leaf litter over 100 metres from the margins of a large reservoir, where it had presumably bred.

Thus ground and rove beetles appear to have two main hibernation strategies: either they stay at or adjacent to the breeding site, or they fly away to separate hibernation quarters. It is unclear how either of these strategies might confer any particular selective advantages in the temporary pond environment and it seems likely that habitat quality in the surrounding landscape is a more important factor.

Morphological adaptations for running, burrowing and climbing

Evans (1990) identified two adaptations in body shape that are frequently found in riparian ground beetles. *Rapid runners* (e.g. *Elaphrus*) have long thin legs and are able to sprint over the ground surface. *Powerful burrowers* (e.g.

Dyschirius) have much shorter legs and so are much less mobile above ground. However, their powerful leg muscles enable them to burrow into the ground. Similar body forms are found among rove beetles; *Bledius* and *Carpelimus* burrow into soft sediments, whereas several species of *Stenus* and *Ischnopoda* have long legs and could be classified as *rapid runners*. These adaptations are well-suited to sparsely vegetated ground like that found on sediments exposed by falling water levels.

On the other hand, a third group of ground beetles classified by Evans as *strong wedge-pushers* (e.g. *Pterostichus*) are well equipped for activity in deciduous litter which requires pushing against vegetative obstacles (Evans & Forsythe 1984). The long thin body-shape of rove beetles, especially those with shorter legs (e.g. *Lathrobium*), is also well suited to moving through fissures in the ground and tangled vegetation in litter and tussocks.

Well vegetated biotopes such as fens contain several species of ground and rove beetles that are capable of climbing plants. *Demetrius* and several *Stenus* spp. found in fenland have enlarged tarsal segments similar to those of leaf beetles and weevils which are habitual plant-climbers. Some *Quedius* and *Hygromoma* are adept at climbing the vertical walls of glass tubes. Landry (1994) found that, out of four species of *Agonum* in a Canadian lakeside fen, *A. nigriceps* had the highest climbing ability and also the longest tarsi. He associated this climbing ability with a preference on the part of *A. nigriceps* for flooded areas with tall emergent vegetation.

It might be expected that the ability to climb emergent vegetation is not very useful in the environment of temporary ponds. However, *rapid runners* and *powerful burrowers* should prosper on exposed mineral substrata in temporary ponds. When the substratum is composed of or covered by organic matter, we might expect *strong wedge-pushers* or rove beetles with short legs to be favoured.

Behavioural adaptations to survive submersion by floods

The ability of ground and rove beetles to survive submersion in water depends on the species, the temperature of the water and the presence or absence of refuges such as litter or air pockets in the substratum (Palmen 1945, 1949). While some fenland beetles such as *A. thoreyi* and *Paederus riparius* survive flooding by clinging to submersed vegetation and becoming torpid (Palmen 1945), many other wetland species actively seek to escape the advancing waters. On riverbanks, burrowing adults and larvae usually remain in the substratum during flooding, but surface-active species retreat up the bank as the flood advances (Andersen 1968). Joy (1910) identified four types of active locomotion over the water surface to escape from submersion. Firstly, several

rove beetles in the subfamily Steninae, and the ground beetle *Agonum albipes*, can skim over the water surface. In order to do this they secrete a substance which lowers the surface tension behind them and propels them forward. Some *Stenus* and *Bembidion* swim with their legs, whereas other species of *Stenus* raise themselves above the water surface and walk. Joy also observed the rove beetle *Gnypeta carbonaria* raising itself above the surface, with its abdomen held aloft like a sail to be propelled by the wind. Some *Bembidion*, *Bledius* and *Gnypeta* can fly from the water surface when air temperatures are relatively high (Andersen 1968).

When on the water surface, some species orientate themselves toward the largest dark object on the horizon, which is usually the bank (Jenkins 1960; Andersen 1968). Zulka (1994) reported that several ground beetles associated with floodplains were relatively fast at reaching the bank when stranded on water. However, Joy (1910) noted that several *Quedius* and many smaller rove beetles are very poor at moving on water and his observations of huge numbers of beetles in flood litter deposited on river banks suggests that many individuals escape submersion passively, by clinging onto fragments of vegetation.

Behavioural adaptations to escape floods are probably of greatest utility in river channels where flooding events are less predictable, more frequent and more severe than in temporary ponds. More passive behavioural responses to submersion are probably adequate for survival in most temporary ponds.

Conclusions

Temporary ponds in lowland England support a rich fauna of wetland/terrestrial ground and rove beetles, equivalent in number of species to the corresponding aquatic beetle fauna, and can be used as a habitat by beetles of national importance for nature conservation. There is a wide variation in species composition between temporary ponds with mineral substrata and those with peaty substrata. The beetles that occur by temporary ponds are probably adapted, through their life-histories and larval habits, to sites with seasonal reductions in water level.

The environmental conditions favoured by ground and rove beetles at temporary ponds are repeated around the margins of larger permanent waterbodies and in ponds subject to flooding in river floodplains. Some species of the rove beetle genus *Calodera* may be particularly associated with temporary pools in floodplains, but their ecology is poorly understood and needs further investigation.

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