Article

Ephemerum cohaerens, an exquisite survivor of functional alluvial habitats

here is a significant number of bryophytes that are most often found in artificial habitats. In the 20th century, rapid urbanization and exploitation of natural resources throughout Western Europe have profoundly altered the natural habitats of mosses and liverworts. Recording of bryophytes in cities and artificial habitats has increased dramatically in the last few decades, and has significantly improved our knowledge of the artificial ecology of bryophytes.

Tortula muralis is ubiquitous and abundant on concrete, mortared walls and roof tiles but is often present in only modest quantity on calcareous rock outcrops in France or other parts of Europe. Riccia crystallina is found on compacted, fine-textured substrates in gardens, but also in the inundation zone of natural ponds. In cities, Syntrichia papillosa is observed growing on concrete, but it is a typical epiphyte of Quercus in natural Mediterranean areas. Pseudocalliergon lycopodioides is often found in oligotrophic fens, but also in China clay quarries in France. Leptodictyum riparium is found growing at the base of deciduous shrubs in alluvial forests and also in greenhouses and on sloping tarmac roads. For such species, it is not difficult to explain occurrences in artificial habitats as chance colonization of secondary ecological niches.

On the other hand, some species have artificial habitats as their primary niches. *Grimmia*

Many bryophytes are now so familiar to us in man-made habitats that it is often difficult to understand what their natural habitat would be without human intervention. **Vincent Hugonnot** and colleagues takes a look at one such species, *Ephemerum cohaerens*, familiar (although rare) to French and British bryologists from the inundation zone of artificial reservoirs.

crinita is almost always found on mortared walls in churchyards in southern France. Many bryophytes are adapted to arable land and some particular species are difficult to spot outside this anthropogenic habitat (for example Dicranella staphylina and Didymodon tomaculosus). In southern France, Leptophascum leptophyllum is only observed along heavily disturbed paths in or near urban areas, whilst its British occurrences are in arable fields in the south. Rhynchostegium rotundifolium is a specialist of castle walls and is never found in natural biotopes in France, whereas its two British populations are both adjacent to lanes. In these cases, the original and natural habitat can be rather difficult to trace. It is not difficult to see G. crinita as a typical inhabitant of calcareous outcrops, but it is in



 E. cohaerens.
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fact almost never observed in such a situation (Greven 2011). One could wonder where *Rhynchostegium rotundifolium* was growing before human settlement.

The study of the original habitats of synanthropic bryophytes (ecologically associated with humans) can be a stimulating research area. A population growing in an artificial habitat cannot be considered precisely equivalent with a natural one, and it is a well-established fact that populations are liable to genetic modification following colonization events. From a management perspective, a good understanding of natural habitats may be crucial for an accurate conservation action plan.

Ephemerum cohaerens (Hedw.) Hampe is typically linked with artificial reservoirs in France and in the UK, so its natural habitat is somewhat obscure. We focused on this species because of its rarity worldwide and because it could be a useful tool in a conservation context.

The distribution of E. cohaerens

Following the recent taxonomic revision of Holyoak (2010), six species of the genus *Ephemerum* are known to occur in Europe. *E. cohaerens* is one of the rarest species and is included in the *Red Data List of European Bryophytes* with the status 'Vulnerable' (ECCB 1995). It is also listed in the *British Red Data Books mosses and liverworts* (Church *et al.*, 2001), on the revised UK Red List (Hodgetts, 2011) and in other countries' Red Data Books. This species has a wide but discontinuous range in the Holarctic, being mentioned in Eastern North America (Bryan & Anderson 1957; Crum & Anderson 1981; Bryan 2005), in Asia (China and Japan; Bryan 2005) and Europe, where it extends from Spain to The Netherlands, and from the United Kingdom to Poland. A recent French distribution map showed a great scarcity of the species in France (Hugonnot *et al.*, 2005).

The inundation zone of reservoirs as a habitat for *E. cohaerens*

The inundation zone of reservoirs provides important habitats for mosses (Atherton et al., 2010). Alternative flooding and exposure are characteristic of the margins of water bodies (Ellenberg, 1988; Rodwell, 2000), whilst open and moist, fine-textured substrates are most characteristic. E. cohaerens shows special adaptations to this peculiar habitat, such as rhizoidal tubers (Pressel et al., 2005), fast growth and abundant production of large spores (50–90 μ m) that enable it to cope with specific seasonal constraints (alternating cycles of waterlogging and drying). As it has been demonstrated that the spore bank is of utmost relevance in the strategy of Physcomitrium sphaericum (Furness & Hall, 1981), it is likely to play a major role in the case of E. cohaerens too. In Europe, this species is mostly recorded as growing on the margins of artificial water bodies (Hill *et al.*, 1994; ECCB, 1995; Ahrens in Nebel & Philippi, 2000; Dierssen, 2001; Infante & Heras, 2005). Rarely the species grows in stubble fields (Delarze *et al.*, 1998) and exceptionally in a *Schoenus nigricans* mire (Rogeon, 1975). Very little is known regarding the nutrient

 status of the habitats although they are reputedly naturally quite eutrophic (Rodwell, 2000).

The example of Rhône river valley (France)

Ongoing bryological surveys in south-eastern France surprisingly revealed that *E. cohaerens* is rather frequent in artificial gravel pits in the Rhône valley, while totally absent at the margins of the fluctuating Rhône channel or connected lateral arms of the river. This led the authors to search for explaining factors. *E. cohaerens* appears strictly located within the Rhône flood plain,



between the main channel and adjacent hill slopes (Figs 1 & 2). Our repeated attempts to find the species in the river channel bed failed, even though apparently suitable microhabitats of bare and moist substrates are very frequent.

Seven *E. cohaerens* populations have been discovered recently. In view of the scarcity of abandoned and unforested gravel pits in

 ▽ Fig. 2. Photographs of the localities of *E. cohaerens*.
 1, Ain confluence; 2, Miribel-Jonage; 3, Tournon sur Rhône; 4, Canal de Montélimar. the Rhône river valley we are confident that these figures reflect the genuine abundance of the species. Only one population is not in an artificial reservoir. With regard to bryophyte assemblages, it is worth noting the occurrence of other ephemeral species as *Aphanorrhegma patens*, *Bryum klinggraeffii* and several liverworts (*Aneura pinguis, Riccia cavernosa*) that are typical inhabitants of water-body margins (Table 1). The distance between the populations and the main channel is very variable, from more than 1 km to 100 m (Table 1). Notwithstanding



Locality	No. of	Habitat	Associated species	Water input	Distance from the
	populations				main channel (m)
1 – Ain confluence	1	Oxbow lake	Bryum pseudotriquetrum	Groundwater +	750
			Calliergonella cuspidata	rainfall inputs	
			Leptodictyum riparium		
2 – Miribel-Jonage	4	Artificial	Aneura pinguis	Groundwater +	1,100
		reservoir:	Bryum gemmiferum	rainfall inputs	
		gravel pit	Bryum pseudotriquetrum		
			Calliergon cuspidatum		
			Cratoneuron filicinum		
			Drepanocladus aduncus		
			Leptodictyum riparium		
			Pellia endiviifolia		
			Philonotis calcarea		
			Pohlia melanodon		
3 – Tournon sur	1	Artificial	Barbula unguiculata	Groundwater +	150
Rhône		reservoir:	Bryum argenteum	rainfall inputs	
		gravel pit	Bryum pseudotriquetrum		
			Hygroamblystegium varium		
			Leptobryum pyriforme		
			Leptodictyum riparium		
			Pellia endiviifolia		
4 – Canal de	1	Artificial	Aphanorrhegma patens	Groundwater +	100
Montélimar		reservoir:	Bryum klinggraeffii	rainfall inputs	
		gravel pit	Dicranella schreberiana		
			Dicranella staphylina		
			Leptobryum pyriforme		
			Oxyrrhynchium hians		
			Riccia cavernosa		

Table 1. Characteristics of the populations of E. cohaerens

their distance from the main channel, all populations have developed on alluvial deposits left by the past meanderings of this large, mature river.

Natural versus artificial stations

E. cohaerens populations were encountered in two distinct ecological situations. The vast

majority of them (6 out of 7) are located at the margins of water bodies located in abandoned gravel pits. These artificial reservoirs have a very low connectivity to the Rhône and are only fed by aquifers that provide nutrient-poor waters. The population located around the dynamic confluence of the Ain and Rhône is the only one in a natural situation. However, it is remote from the main channel, dominated by groundwater seepage and rainfall inputs, and is only connected during major flood events.

Significantly, in the Rhône valley, *Hippuris* vulgaris and Nitella hyalina are two common and typical oligotrophic associates. For charologists, it is a well-known fact that some species of *Chara* or Nitella are restricted to localities with clear water and very low nutrient content (Krause, 1981; Simon & Nat, 1996).

From a general point of view, in a naturally functioning river valley, channel dynamics lead to dramatic changes in stability and create bare habitats when meanders are cut off to form oxbow lakes. The water quality in the active channel is very different from the underground water infiltrating from the river or from the ground (phreatic) water table of abandoned channels. In the Rhône river valley mesotrophic communities are replaced by oligotrophic ones towards the margin of the floodplain (Bornette & Amoros, 1991). In strongly man-influenced river valleys, such as the Rhône, large-scale connectivity does not allow oligotrophic vegetation to develop. Instead, hydrological isolation provides optimal conditions for oligotrophic amphibious bryophyte communities to grow. In a sense, E. cohaerens could well be considered as a powerful indicator of hydrological isolation from flooding by water from the main river channel. Here, phreatic artificial reservoirs are ecological refugia for E. cohaerens.

The distribution of *E. cohaerens* in Baden-Württembergs (Ahrens in Nebel & Philippi, 2000; Meinunger & Schröder, 2007) and older mentions of the species (Limpricht, 1890) closely reflect the dependence towards large functional hydrosystems, another example being the Rhine in Vanderpoorten *et al.* (1995). A recent survey in south-western France suggests that *E. cohaerens* could be more widespread than previously realized in reservoirs of the Garonne valley where a frequent associate is *Riccia cavernosa* (Celle *et al.*, 2010). This is at odds with observations in the UK, however, where records come from five reservoirs and an artificial lake in England, none of which is associated with a large river. It is also at odds with the nine Irish populations, most of which come from the margins of fluctuating natural loughs.

Lessons for site management

Regarding site management, oligotrophic waters are essential for the maintenance and expansion of E. cohaerens, so nutrient enrichment should be controlled. The aggregated effects of chemical inputs (human sources of nitrogen, phosphorus and other pollutants) and the prevailing transport of fine sediment in river channels have greatly contributed to water quality deterioration. The improvement of overall water quality is usually only conceivable at a catchment scale and is therefore beyond the reach of most site managers. However, the observations from France emphasize the need to maintain oligotrophic conditions at the British and Irish sites, and raise concerns for the Sussex population, which is a very popular site for feeding ducks and swans.

It is not recommended to favour the creation of new gravel pits because quarry owners do not need our recommendations to severely exploit available natural resources: new gravel pits will continue to appear here and there in the Rhône valley. Hence the best way to conserve dynamic populations of *E. cohaerens* there is surely to favour a return to a more natural functioning. The subtle balance between re-energization of the river and management of human pressures is difficult to attain, and remains to a large extent illusory. Experiments in Switzerland (Cosandey & Rats, 2007) showed nevertheless that the re-energization of riparian habitats was possible at the local level, without an increase in exposed alluvium.

E. cohaerens is unable to tolerate shade, so encroachment by riverine shrubs and trees should be kept at a minimal level and planting totally precluded. Paradoxically, water eutrophication and vegetation succession are only problematic in artificial hydrosystems: in natural hydrosystems, the spontaneous rejuvenating effects of cyclic flooding are regular phenomena. Today, in the Rhône valley, recreation of regressive successions in already existing gravel pits requires expensive intervention.

Life traits of *E. cohaerens* (large quantities of tubers and spores) seem advantageous in a strongly man-influenced valley. It is highly probable that significant numbers of spores are carried from one artificial pond to another by migrating birds, and that is also likely to be the case in the British reservoirs and Irish loughs. Studies involving the life span of spores buried in the sediment are urgently needed to determine with accuracy the optimal frequency of seasonal water fluctuations of artificial ponds.

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Erratum

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On p. 13 of the above article, the photographs were incorrectly labelled. The correct labelling of these photographs is shown here.

The Editor and author apologize for this error.

> Orthotrichum rogeri. Michael Lüth

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> Orthotrichum philibertii. Michael Lüth