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Freshwater Reservoir, Ecological Traps and Source-Sink Dynamics

Nina Melendez [1], Virginie M. Stevens [1] and Michel Baguette [1,2,*]

[1] Centre National de la Recherche Scientifique, SETE Station d'Ecologie Théorique et Expérimentale, CNRS UAR 2029, 09200 Moulis, France
[2] Institut Systématique, Evolution, Biodiversité (ISYEB), UMR 7205 Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 75241 Paris, France
* Correspondence: michel.baguette@mnhn.fr

Abstract: Odonata are biodiversity indicators that adequately represent many aquatic and semi-aquatic animal species. We recorded over two field seasons a rich lentic community of Odonata (18 species) in a large artificial freshwater reservoir (ca. 55 ha) built 40 years ago. The release of water from the dam in summer for crop irrigation leads to the desiccation of large parts of the reservoir, which prevents the reproduction of half of the species of this Odonata community. We identify two adaptations that allow eight species to cope with desiccation, i.e., a precocious breeding period allowing the emergence of adults before the retreat of water, or a delayed adult emergence due to egg diapause from oviposition to the end of winter. The reservoir acts thus as an ecological trap for individuals of 10 species that developed elsewhere and were attracted to the site without successfully breeding there. As consequence of the local population extinction at each generation, the presence of individuals of these 10 species at the reservoir depends on source-sink population dynamics in the landscape. In the context of global warming that encourages the creation of artificial freshwater reservoirs, the multiplication of such sinks could threaten the persistence in the landscape of species maladapted to desiccation.

Keywords: freshwater ecosystem; biodiversity; desiccation; Odonata; dragonfly; damselfly; dispersal; metapopulation; lotic community; lentic community

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1. Introduction

Freshwater ecosystems cover only ~0.8% of the Earth's surface but support almost 6% of the diversity of all described existing species [1]. Freshwater is unquestionably considered the most vital natural resource for both biodiversity and humanity, yet directly threatened by various human activities from land cover changes to urbanization, through water provision aiming at maximizing human access to water [2]. Indeed, the management of freshwater resources often focuses on human water security rather than on natural ecosystem integrity and biodiversity conservation [3]. Changing climate is among the most challenging threats to water biodiversity [4]. Among various impairments to freshwater ecosystem functioning linked to climate change, humans try to mitigate shifting temperature and precipitation by constructing reservoirs to store water and enhance irrigation capacity for crop cultivation [4]. The raising of dams on watercourses not only alters flow regimes and prevents or disrupts the free movement of aquatic organisms [4], but also creates temporary lentic ecosystems whose impact on biodiversity is still poorly known. The creation of freshwater reservoirs in a landscape could be seen as a mitigation measure for the drainage and destruction of many ponds, marshes or wet meadows resulting from the intensification of agriculture—wetland loss is three times as high as forest loss [3]. However, the question remains to assess the real effectiveness of these artificial freshwater ecosystems in terms of hosting biodiversity.

Here, we address this question by focusing on a water reservoir in the French Pyrénées. This reservoir captures two watercourses and retains water that is released from the dam during the three driest months in summer for irrigation of crops in the watershed below the reservoir. During summer, the flow of the two watercourses feeding the reservoir is very low. When the water is used for irrigation, the reservoir does not dry completely. Due to the gentle slope of the reservoir, at the end of the water release period, the shore of the reservoir recedes locally by 150 m, thus exposing vast surfaces previously covered with water. These surfaces are then gradually submerged again during the abundant autumn rains, which swell the flow of the two watercourses. To investigate the consequences of this large-scale desiccation on biodiversity, here we focus on the local community of Odonata, i.e., those adult damselflies and dragonflies that fly and try to reproduce around the reservoir. Species of Odonata are frequently used as biodiversity indicators for the following reasons: they are reasonably diverse and benefit from a rather well-established and stable taxonomic framework; they have a complex life cycle with larvae living underwater, whereas adults are aerial but depend on aquatic habitat for breeding; both stages are predaceous; they constitute all at once a keystone, umbrella and flagship group; they are easily accessible and amenable to quantitative sampling by standardized techniques (e.g., [5]).

We monitored around the reservoir adult presence, age-teneral (freshly metamorphosed) or adult individual—and behavior of damselflies and dragonflies during two flight seasons. We compiled from existing databases the species-specific traits of Odonata habitat selection to identify which species were attracted to this artificial lentic ecosystem in an area previously strictly visited by lotic species. Then, for each of the lentic species we extracted from the databases phenological and behavioral traits to predict which species of this lentic community should be able to cope with the reservoir desiccation. Specifically, we compare the requirements of each species in terms of egg-laying site, resistance to desiccation and speed of development with the presence or the absence of water during the different periods of their life cycle. Finally, we compared these predictions to the indices of successful reproduction that we recorded in the field, i.e., the presence of newly emerged adults that reveals that the species has managed to complete its lifecycle in this artificial lentic ecosystem. We acknowledge that our study is local and concerns only one reservoir. However, at this state of knowledge, we are not aware of no other studies that address this crucial research question.

2. Materials and Methods

2.1. Study Site

The reservoir of Mondély (43° 03′ 08″ N, 1° 26′ 16″ E, Figure 1) is located in France, in the Occitanie region, more precisely at the foothill of the Pyrénées in the Ariège deparment. This water impoundment was created in 1980 by building a dam on the Lèze river that has an upstream watershed of 13.6 km^2. Its surface ranges between 51.3 ha and 56.6 ha according to seasonal water release. Its maximum depth is 23.7 m for a maximal water capacity of four million m^3. The reservoir is used to irrigate 1700 ha of crops in the downstream watershed of the Lèze valley. Water release from the dam is decided by the managers of the reservoir (SMHVL: Syndicat Mixte d'Aménagement Hydraulique de la Vallée de la Lèze) according to the water requirements of crops.

Figure 2 shows the debit of water released each month from the dam during the years 2019, 2020 and 2021; water is released between May and October. Figure 2 illustrates that the peak of water release does not occur at the same time each year: there is a shift of approximately 4 weeks between 2019 and 2020 on the one hand, and 2021 on the other hand.

Damselflies and dragonflies were monitored in a creek of 2 ha located at the western part of the reservoir (Figure 1) and enclosed between two watercourses that were former tributaries of the Lèze river. This sampling site was chosen because due to its gentle slope the water level recedes 150 m during the summer months of June, July and August, which increases the emerged part of the study site by 1.25 ha (Figure 3). During periods of strong water release, the water recedes extremely quickly, in less than a week. When the water level is at its minimum, the confluence between the two Lèze tributaries emerges. Over the whole reservoir, this site is the part where the emerged area is the most important during summer. Moreover, the creek has a natural character that the few other gently sloping banks of the site do not have because they have been fitted out for swimming and nautical activities, which generates there a very high tourist load from May to October. Our study area is thus the only suitable place for Odonata reproduction around the reservoir, by its shallow depth and absence of disturbance by humans.

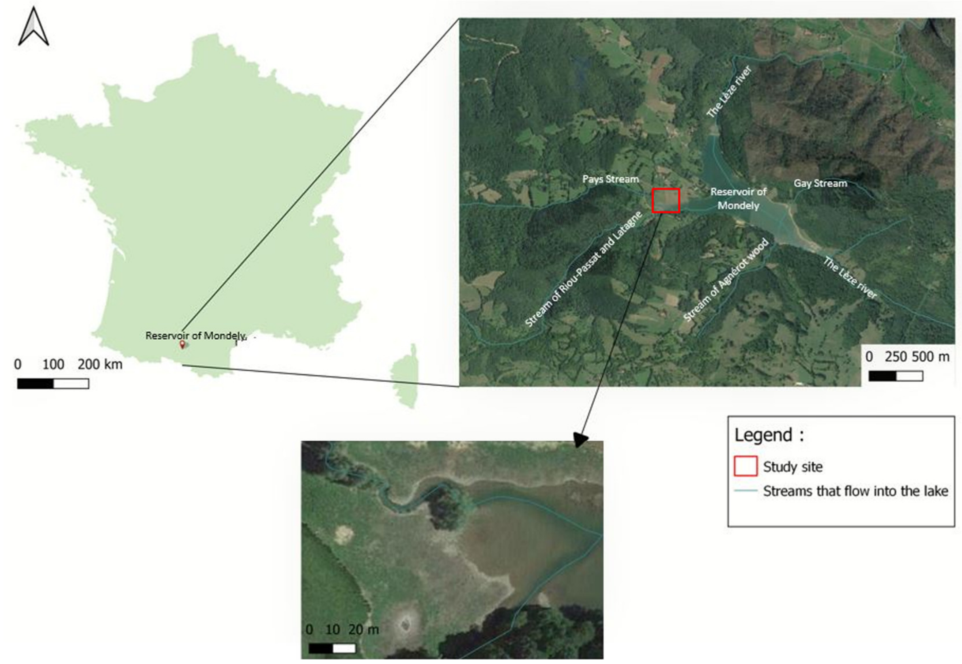

Figure 1. Map of the Mondély reservoir showing the location of the study site (red rectangle). The dam is visible at the upper side of the reservoir.

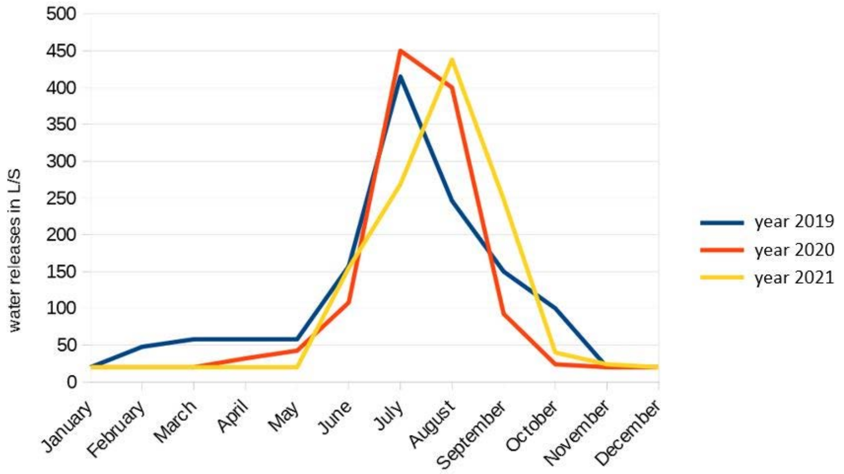

Figure 2. Dynamics of water release at the Mondély reservoir dam during the period 2019–2021 (data courtesy of the SHMVL).

The vegetation of the majority of the site can be attached to the group of eutrophic wet meadows. In particular, the area that emerges each summer is dominated by the water mint (*Mentha aquatica*). The vegetation of three depressions located to the west and northwest of the site can be linked to *Typha* low marshes and aquatic vegetation. The edges of the Lèze tributaries are occupied by narrow, non-continuous strips of trees dominated by willows and alders.

Figure 3. Emerged (**left** panel) and submerged part (**right** panel) of the study site showing the extent of the desiccated area between June and August.

2.2. Sampling Methods

Adult damselflies and dragonflies were monitored by performing modified Pollard's walk [6] on the accessible parts of the study site (Figure 4). This method is widely used to estimate the relative abundance and diversity of butterflies and has been adapted to Odonata. Observation surveys are carried out along fixed transects. Adult damselflies and dragonflies were observed in a 5 m strip on both sides of the transect, while walking a slow and steady pace and their identity and numbers were recorded. The route taken between transects during each sampling session is shown in Figure 4. Routes are modified to follow the variation of the water level (Figure 4).

Figure 4. Map of the location of the Pollard walks in the study site. Transects are following the course of the water retreat during summer. White and orange traits indicate transect walked during the flood or the desiccation of the creek, respectively.

Each time a species new to the community was observed, it was photographed so that its identification could be confirmed with certainty. For each individual encountered, the observer noted its behavior, looking for signs of reproduction (mating, egg-laying) and its age (teneral or adult). Tenerals are adult individuals freshly hatched from their larvae that can be recognized by their pale colors and their soft integuments (see Figure 5c, *Aeshna affinis* teneral male). Adult damselflies and dragonflies were sampled during two calendar years beginning in July 2020. Sampling visits were performed two or three times a month, weather permitting, between July and November in 2020, between February and November in 2021 and between April and June in 2022, which provided a total of 53 visits.

(**a**)

Figure 5. *Cont*.

(**b**)

Figure 5. *Cont.*

(**c**)

Figure 5. (**a**) Odonata species recorded in the Mondély reservoir (1). From left to right and top to bottom. *Lestes barbarus* (Fabricius, 1798) female, *Chalcolestes viridis* (Vander Linden, 1825) ovipositing

pair, *Sympecma fusca* (Vander Linden, 1820) ovipositing pair, *Calopteryx virgo* (L., 1758) displaying male, *Platycnemis pennipes* (Pallas, 1771) male, *Ischnura elegans* (Vander Linden, 1820) mating pair, *Enallagma cyathigerum* (Charpentier, 1840) mating pair, *Coenagrion puella* (L., 1758) ovipositing pair. (**b**) Odonata species recorded in the Mondély reservoir (2). From left to right and top to bottom. *Erythromma lindenii* (Selys, 1840) ovipositing pair, *Pyrrhosoma nymphula* (Sulzer, 1776) ovipositing female, *Ceriagrion tenellum* (de Villers, 1789) male, *Aeshna mixta* (Latreille, 1805) ovipositing female, *Aeshna affinis* (Vander Linden, 1820) ovipositing female, *Anax imperator* (Leach, 1815) ovipositing female, *Boyeria irene* (Fonscolombe, 1838) male, *Cordulegaster boltonii* (Donovan, 1807) female. (**c**) Odonata species recorded in the Mondély reservoir (3). From left to right and top to bottom. *Libellula quadrimaculata* (L., 1758) male, *Libellula depressa* (L., 1758) male, *Orthetrum cancellatum* (L., 1758) male, *Sympetrum sanguineum* (Müller, 1764) ovipositing pair, *Sympetrum fonscolombii* (Selys, 1840) male, *Sympetrum striolatum* (Charpentier, 1840) male, *Sympetrum meridionale* (Selys, 1841) male, *Aeshna affinis* (Vander Linden, 1820 teneral. All photographs were taken in Mondély, except *C. virgo meridionalis* and *P. pennipes*, from the nearby Arize valley, and *Ceriagrion tenellum*, from Mazère (Ariège). Photographs by Michel Baguette, all rights reserved.

2.3. Odonata Life History Traits

Species-specific habitat preferences and life history traits were extracted from existing databases [7,8]. First, we investigated whether each species recorded on the study site prefers lotic, lentic or mixed water bodies. Next, for each lentic species we recorded a suite of life-history traits to investigate the possible completion of its life cycle by coping with the summer desiccation of the creek. We compiled the following traits: female egg-laying strategy, larval location, female egg-laying time, egg hatching time and larval development time. Female egg-laying strategy is subsumed by the type of substrate in which females lay their eggs: either underwater (endophytic or exophytic), or aerial (endophytic or in muddy soil). Larval location provides information on the habitat selection of larvae. The timing of the species' life cycle is described by the period during which females lay their eggs, the eggs hatching time, including the possibility of diapause, and the time required for the development of the larvae, from egg-hatching to the metamorphosis of the adult. This analysis provides us with a subset of candidate lentic species potentially having a stable reproductive population in the reservoir.

3. Results

Table 1 presents the composition of the Odonata community recorded on the study site over the period 2020–2022. Adults of the 23 species recorded in Mondély are illustrated in Figure 5. Counting data performed during the field surveys were aggregated over each flight seasons. Numbers in Table 1 reflect the mean abundance of the species over the 3 flight seasons. We also mention in Table 1 the records of breeding attempts, either the observation of mating or of egg-laying females, and the records of tenerals, i.e., these newly emerged adults that unambiguously demonstrate that the species has completed its life cycle in the study area.

Among this community of 23 species of adult damselflies and dragonflies, 2 (*Calopteryx virgo* and *Cordulegaster boltonii*) are strictly lotic species living in streams and small rivers. Their presence is certainly to be related to the tributaries of the Lèze river surrounding the study site, where all adults of both species have been recorded. Three species are considered as having mixed preferences for lotic and lentic water bodies. Adult of two of these three species (*Platycnemis pennipes and Boyeria irene*) were represented by only one individual in our data set, with no cue of reproduction detected. Adults of the third one (*Pyrrhosoma nymphula*) were scarce, but we observed an ovipositing female (Figure 5b).

The 18 remaining species are thus strictly lentic species that are attracted to the reservoir. Among these 18 species, our life history trait compilation (Table 2) indicates that one of them (*Sympecma fusca*) has the possibility of completing its life cycle before the beginning of the desiccation. The two species of the genus *Sympecma* are the only Odonata that overwinter as adults in Western Palearctic. Adults of *S. fusca* emerge in May-July in our study area and leave the water surroundings. They come back to the study site from February onwards and begins to reproduce at this time. During the desiccation period of the reservoir, this species is at the adult stage but in pre-reproductive period outside the study area. *Chalcolestes viridis* is another species of damselfly with a particular life cycle. Adults breed from August onwards, i.e., at the peak of the desiccation period. Females lay their eggs at 100–150 cm high into aerial, thin shoots of soft trees such as willows (*Salix* sp.) surrounding water. The egg stage is long (5–6 months), then the larval hatches and drops into the water where its development is rapid (6–8 weeks). After emergence, the adults undergo a protracted, pre-reproductive, summer diapause (up to 3 months) before mating and ovipositing. During the desiccation period of the reservoir, this species is at the egg stage sheltered in shoots of trees overhanging the study area. *Lestes barbarus* has a life cycle closely related to the previous species. Adults mate between June and August, and females lay their eggs in aerial vegetation, in thin shoots of large herbaceous species (*Juncus* sp., *Carex* sp., . . .). Eggs hatch after several months, the larval development is fast, whereas there is no summer diapause after adult emergence unlike the previous species but a classical pre-reproductive period. During the desiccation period of the reservoir, this species is at the egg stage sheltered in shoots of large herbaceous species. Females of *Aeshna affinis* oviposit in July-August in the study area. Tenths of ovipositing females were observed alone or in tandem, and all of them lay their eggs in mud. Eggs hatch after 6–7 months, and the subsequent development of the larva last about 3 months. During the desiccation period of the reservoir, this species is at the egg stage sheltered in mud. Four species of *Sympetrum*, i.e., *S. fonscolombii*, *S. meridionale*, *S. sanguineum* and *S. striolatum* have the potential to cope with the summer desiccation. Adults of these four species are on the wings and breed during or after of the peak of water retreat (from mid-May to mid-September for *S. fonscolombii*, from June to September for *S. meridionale*, from June to October for *S. sanguineum*, and from June to November for S. striolatum). Females of these four species lay their eggs in shallow water or in mud. The eggs of *S. fonscolombii* laid in May either will undergo a direct development and produce a new adult generation that will emerge in September or enter in diapause during winter and will hatch at the end of winter, to produce the spring adult generation. Similarly, the eggs of *S. striolatum* will hatch directly or can enter diapause to produce the new adult generation the next June. All eggs of *S. meridionale* and *S. sanguineum* enter in diapause, hatch at the end of winter and produce a single adult generation the next June.

According to this analysis of the species' life cycles, the 8 species listed above should be able to cope with the desiccation of the study site during summer. Conversely, the remaining 10 species seem not be able to develop permanent population on the site, as for all of them the water retreat occurs their larval development, while their larvae do not have the possibility of escaping. During our surveys, teneral individuals were found for six species (Table 1), all of them being among the eight candidate species to perform their life cycles despite the desiccation. For the two remaining candidates for which no teneral individuals were found (*Lestes barbarus* and *Sympetrum meridionale*), it is worth noticing that reproduction cues were observed (egg laying for *L. barbarus*, mating for *S. meridionale*). The lack of teneral detection could be explained by their low to very low adult abundance on the study site, but we cannot exclude that they do not reproduce locally. There is also a small probability that we missed certain species as tenerals, especially if individuals of those species have strongly synchronized hatching occurring in the time interval between our sampling sessions. Searching for exuviae would have been helpful to solve this issue, but it revealed to be difficult to find exuviae in a site with moving shore.

Table 1. Abundance and reproduction index of the 23 species of damselflies and dragonflies recorded in Mondély. Reproduction index indicates whether reproduction clues of the species were observed in the study site. For each species, we mentioned the most indicative clue of reproduction observed, using the rule teneral > egg laying > mating > no reproduction clue observed.

Species	Abundance Class	Reproduction Index
Calopteryx virgo meridionalis	**2**	**-**
Lestes barbarus	**1**	**E**
Lestes viridis	**4**	**T**
Sympecma fusca	**4**	**T**
Ischnura elegans	**2**	**M**
Enallagma cyathigerum	**3**	**M**
Coenagrion puella	**3**	**E**
Erythromma lindenii	**2**	**E**
Pyrrhosoma nymphula	**1**	**E**
Ceriagrion tenellum	**1**	**-**
Platycnemis pennipes	**1**	**-**
Aeshna mixta	**2**	**E**
Aeshna affinis	**2**	**T**
Anax imperator	**1**	**E**
Boyeria irene	**1**	**-**
Cordulegaster boltonii	**1**	**E**
Libellula quadrimaculata	**2**	**-**
Libellula depressa	**1**	**E**
Orthetrum cancellatum	**1**	**-**
Sympetrum striolatum	**4**	**T**
Sympetrum fonscolombii	**3**	**T**
Sympetrum sanguineum	**3**	**T**
Sympetrum meridionale	**1**	**M**

Abundance class cumulated over the field visits—**1**: 1–5 adults. **2**: 6–25 adults. **3**: 26–125 adults. **4**: 126–625 adults. Reproduction index—**-**: nothing. **M**: Mating. **E**: Egg-laying. **T**: Teneral adults.

Table 2. Egg-laying strategy, larval location, egg-laying time, egg hatching time and larval development time of the 18 lentic species observed in Mondély. Mixed larval location means that larvae occur both on sediments and on vegetation. Data from references [7,8].

Species	Egg-Laying Strategy	Larval Location	Egg Laying/Hatching Time	Larval Development
Lestes barbarus	Out of water, endophytic	On sediments	June–August/4–21 weeks	4–8 weeks
Lestes viridis	Out of water, endophytic	On sediments	August–September/28–32 weeks	8–12 weeks
Sympecma fusca	In water, endophytic	On sediments	April–May/3–6 weeks	8–12 weeks
Ischnura elegans	In water, endophytic	On vegetation	June–September/1–3 weeks	2–3 weeks/40–50 weeks
Enallagma cyathigerum	In water, endophytic	On vegetation	June–August/2–3 weeks	40–50 weeks
Coenagrion puella	In water, endophytic	On sediments	June–July/3–5 weeks	24–40 weeks
Erythromma lindenii	In water, endophytic	On vegetation	June–July/	24–48 weeks
Ceriagrion tenellum	In water, endophytic	On sediments	July–August/3–4 weeks	36–72 weeks
Aeshna mixta	In water, endophytic	Mixed	August–September/winter diapause (28–36 weeks)	16–20 weeks
Aeshna affinis	Out of water, in mud or endophytic	No data	August/ winter diapause (28–36 weeks)	12 weeks

Table 2. *Cont.*

Species	Egg-Laying Strategy	Larval Location	Egg Laying/Hatching Time	Larval Development
Anax imperator	In water, endophytic	On vegetation	June–September/3–6 weeks	12–100 weeks
Libellula quadrimaculata	In water, exophytic	Mixed	June–July/2–7 weeks	52–156 weeks
Libellula depressa	In water, exophytic	On sediments	June–July/1–5 weeks	52–104 weeks
Orthetrum cancellatum	In water, exophytic	On sediments	July–August/5–6 weeks	52–156 weeks
Sympetrum striolatum	Out or in water, exophytic	On sediments	August–September/4 weeks or after winter diapause	20 weeks
Sympetrum fonscolombii	In water, exophytic	On sediments	June–September/1–3 weeks	Direct development or winter diapause
Sympetrum sanguineum	Out or in water, exophytic	Mixed	July–August/winter diapause	6–10 weeks
Sympetrum meridionale	Out or in water, exophytic	Mixed	August–October/winter diapause	8–16 weeks

4. Discussion

The current species pool of damselflies and dragonflies currently censused in the Occitanie region (South-Western France) amounts to 73 species [9]. The richness of the Odonata community of our 2 ha study site bordering the Mondély reservoir (23 species) could thus be considered as rather low. However, the ecosystem diversity of Occitanie is very high, from glacial relict peat bogs in altitude to brackish fens along the Mediterranean coast, through large rivers such as the Aude, the Hérault or the Garonne. The different communities of Odonata specialists associated with each of these ecosystems contribute to increase the regional species pool. In fact, the community of Mondély is a respectable species assemblage representative of the low altitude water bodies of Occitanie [9].

Among these 23 species, 18 are lentic specialists that were attracted in the area by the construction of the dam and the resulting flooding of the reservoir. Damselflies and dragonflies have a complex life cycle, during which newly emerged adults engage in a pre-reproductive period and leave the water bodies where the larvae developed. At the end of this time, which is variable among species mature adults wander through the landscape in search of suitable breeding sites that they locate using a suite of species-specific, hierarchical cues [10]. Given this high vagrancy of adults, it is therefore not surprising that lentic damselflies and dragonflies have colonized the artificial reservoir of Mondély especially because the construction of the reservoir dates back more than 40 years ago.

What our study shows, which was unexpected, is that more than half of these lentic species attracted to the reservoir seem not able to develop a local population on the site. The key point is the rapid water retreat resulting in the rapid emergence of a large area of land previously occupied by shallow water. Our analysis of species' life cycle shows that 8 species have the potential to survive to this fast desiccation process. These species have either a precocious breeding period allowing the emergence of adults of the new generation before the retreat of water, or conversely a delayed adult emergence due to egg diapause from oviposition to the end of winter, and then a rapid larval development. We indeed found tenerals for six out these eight species that indicate the full completion of their life cycle on site. Adults of the remaining 10 species are thus attracted to the site and attempt to reproduce there but they seem to fail—we did not record any teneral of these species, whereas egg-laying females were observed for some of them. It is worth investigating to what extent the traits we identified as potential driver of resistance to desiccation could be plastic and/or rapidly evolve to allow the completion of the life cycle for each of these 10 species. Moreover, further investigation of this phenomenon could be to sample benthic community to search for larvae on the study site during the period there is water. In this way, we could rule out indisputably less parsimonious hypotheses as to the absence of these species than the summer desiccation of the site, such as predation or competitive exclusion.

Ecological traps occur when "good animals love bad habitats" [11], which is probably the case here for adults of these 10 species. Ecological traps result from errors in habitat assessment by individuals due to some mismatch between the environmental cues they use to select habitats and the actual quality of the habitat [11,12]. Ecological traps result thus from maladapted individual behavioral processes resulting in low adult survival and/or reproductive success [13]. As the fitness of individuals caught in ecological traps is, by definition, lower than that of those settled in normal habitats [14], we expect that consequences of these individual processes on population and metapopulation dynamics will occur [12,15]. Given their lifestyle where adult females must anticipate during their aerial life the aquatic conditions favorable to the development of young stages, Odonata are poorly equipped to escape ecological traps. The analysis of behavioral sequences of habitat selection used by female Odonata indeed indicates the use of a hierarchical process, first to locate a water body in which to lay eggs, then to select a suitable part of this water body to find the required substrate for egg-laying, and finally to choose the best egg-laying substrate (e.g., [10]) This hierarchical process of habitat selection entails the use by the female of a succession of different stimuli (visual, tactile, thermal and perhaps olfactory) according to a binary decision-making process (e.g., [10]). The evolution of these behavioral sequences to cope with the existence of ecological traps is probably possible, but the key question is whether it could occur in a time frame compatible with the rate of current environmental changes.

The most probable consequences of the summer desiccation of the Mondély reservoir on the 10 species that are trapped there is a source-sink metapopulation dynamics [16] at the landscape scale. Those damselfly and dragonfly adults that are attracted into the Mondély reservoir acting as a demographic sink had to have developed elsewhere in sources, i.e., in water bodies allowing their full development from eggs to adults. These water bodies had to be located into the "vagrancy range" of immature adults wandering through the landscape during their maturation phase.

Besides small pools up- and down-stream of the two watercourses feeding the reservoir, there is only a single large (66 ha) water body located at ca. 2.5 km as the crow flies from Mondély. This water body of Filleit also serves as a water reservoir for irrigation, but its desiccation in summer is much lower than in Mondély. We thus suggest that those adults of the 10 species that cannot complete their life cycle in Mondély could at least from some of them come from Filleit. Unfortunately, the current state of knowledge of Odonata life histories is sorely lacking data on adult dispersal: the current databases on European Odonata traits either does not address movements and dispersal [7] or mention movements and dispersal as a binary trait according to adult migration [8]. This black box about dispersal strongly limits the understanding of Odonata spatial dynamics in comparison with butterflies that are alternative iconic insects with a much more detailed understanding of their dispersal data [17,18]. Anyway, large scale landscape genetic studies [19,20] would be very helpful to solve the issue of the geographic origin of the species colonizing Mondély at each generation, and more generally to provide insights on the spatial scale of Odonata metapopulations, which has a great potential value for the design of conservation measures.

Whatever their origin damselfly and dragonfly adults of 10 species seem trapped in a demographic sink in Mondély. At the landscape scale, metapopulation dynamics of species facing such source-sink systems can be affected in two ways, with rather different consequences for species conservation. Firstly, if individuals spend all their adult lifetime and waste all their reproductive effort in the sink, the dynamics of the metapopulation can be negatively affected, which can threaten its persistence in the landscape [15,16]. The key parameter is thus the ratio at each generation between the productivity of adults in source habitat vs. the loss of adults in sinks. Given the high spatial and temporal variability of insect demography, only long-term studies would inform on the stability of such source-sink systems. Landscape genetic studies mentioned above could also be very helpful here, in identifying which local populations in the landscape act consistently as sources of first-generation migrants, making them priorities for conservation action. Secondly, damselfly and dragonfly adults confronted to the degradation of their habitat due to its fast desiccation can take the decision to leave the site to find out better conditions elsewhere. In such a situation, the reservoir can act as a stepping stone for those individuals that disperse further from the source [15]. If these individuals manage to locate a suitable habitat and breed there, such movements can be beneficial for the persistence of the species in the landscape by leading to the (re)colonization of empty habitats or the reinforcement of small populations (e.g., [21]). However, the probability of these appealing theoretical events has apparently never been measured in the field.

These two scenarios are not mutually exclusive, i.e., they can affect the same species depending on the year: as shown in Figure 2, the peak of the desiccation period of the reservoir is variable according to the year, which can differentially influence the reproduction of the species. Anyway, we expect dragonflies to have a better chance of being able to locate a new habitat according to scenario 2 because their abilities of movement and therefore of exploration are higher than those of damselflies. Finally, we want to stress that the existence of a source-sink dynamics could preclude the apparition of evolutionary responses to desiccation. Indeed, the incessant flow of genes from source populations to sinks should limit the establishment of a life cycle adapted to desiccation, or even the perception by adults that a body of water is in fact an ecological trap.

5. Conclusions

To our best knowledge, our study is the first to address the consequences of the summer desiccation of an artificial freshwater reservoir on Odonata biodiversity (but see [22] for a thorough review of the consequences of winter desiccation on multiple taxa). Here, we report the presence of a rich lentic community of Odonata (18 species) in a large reservoir (ca. 55 ha) over 40 years old. Odonata are biodiversity indicators that adequately represent the many aquatic and semi-aquatic species. The release of water from the dam in summer for crop irrigation leads to the desiccation of large parts of the reservoir, which prevents the reproduction of more than half (10/18) of the species in the Odonata community. We identify two different adaptations that allow eight species to cope with desiccation, i.e., either a precocious breeding period allowing the emergence of adults of the new generation before the retreat of water, or a delayed adult emergence due to egg diapause from oviposition to the end of winter. The reservoir acts thus as ecological trap for individuals of these 10 species that developed elsewhere and were attracted to the site. As consequence of the local population extinction of these 10 species at each generation, the presence of individuals at the reservoir is suggestive of source-sink population dynamics in the landscape. In the current context of global warming that leads to severe changes in the precipitation regime and encourages the creation of artificial freshwater reservoirs, the multiplication of such sinks could threaten the persistence in the landscape of species maladapted to desiccation. The question remains about (1) the evolution of traits allowing those species to adapt to such environmental changes, and (2) the apparition of species adapted to such habitats that move northwards taking advantage of global warming. The current northward shift in Europe of several North African dragonfly species is a strong signal in this direction.

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