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Reintroduction of freshwater macroinvertebrates: challenges and opportunities

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ABSTRACT

Species reintroductions – the translocation of individuals to areas in which a species has been extirpated with the aim of re-establishing a self-sustaining population – have become a widespread practice in conservation biology. Reintroduction projects have tended to focus on terrestrial vertebrates and, to a lesser extent, fishes. Much less effort has been devoted to the reintroduction of invertebrates into restored freshwater habitats. Yet, reintroductions may improve restoration outcomes in regions where impoverished regional species pools limit the self-recolonisation of restored freshwaters. We review the available literature on macroinvertebrate reintroductions, focusing on identifying the intrinsic and extrinsic factors that determine their success or failure. Our study reveals that freshwater macroinvertebrate reintroductions remain rare, are often published in the grey literature and, of the attempts made, approximately one-third fail. We identify life-cycle complexity and remaining stressors as the two factors most likely to affect reintroduction success, illustrating the unique challenges of freshwater macroinvertebrate reintroductions. Consideration of these factors by managers during the planning process and proper documentation – even if a project fails – may increase the likelihood of successful outcomes in future reintroduction attempts of freshwater macroinvertebrates.

Key words: invertebrate reintroduction, conservation, translocation, species management, population restoration, restoring diversity.

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CONTENTS

I. INTRODUCTION

Humans have profoundly altered freshwater ecosystems by overexploitation, habitat degradation, and pollution, all of which have contributed to the decline of native biodiversity (Allan & Flecker, 1993; Dudgeon *et al.*, 2006). In recent decades, there has been increasing emphasis on the restoration of freshwater ecosystems worldwide (Palmer, Menninger & Bernhardt, 2010; Haase *et al.*, 2013; Palmer, Hondula & Koch, 2014). Broad policy initiatives aiming at protecting aquatic life (e.g. the *Water Framework Directive* 2000/60/EC in Europe, or the *Clean Water Act* in the USA) have resulted in the widespread implementation of restoration with substantial financial costs (Bernhardt *et al.*, 2005). Often, projects have focused on restoring hydromorphological and physico-chemical properties of freshwater habitats [e.g. hydromorphological conditions (Bernhardt *et al.*, 2005), chemical pollutants (Skjelkvåle *et al.*, 2005)] or hydrological regimes of wetlands (Zedler, 2000), driven by the assumption that habitat improvement will lead to a corresponding restoration of previous species composition, population densities and community-wide functional traits (Palmer, Ambrose & Poff, 1997). Although subsequent evaluations often confirm an improvement in physico-chemical conditions and macro-scale morphological habitat quality (Palmer *et al.*, 2010), these improvements have rarely achieved the desired outcome for the aquatic community (Palmer *et al.*, 2010; Haase *et al.*, 2013). Benthic macroinvertebrates, in particular, often show no substantial increase in population densities, species richness or trait diversity in response to restoration activities (Palmer *et al.*, 2010; Louhi *et al.*, 2011; Pilotto *et al.*, in press).

Multiple factors may inhibit macroinvertebrate recolonisation following restoration, including deficiencies in water quality (Kail, Arle & Jähnig, 2012) associated with catchment land use (Harding *et al.*, 1998). In cases where water quality is good and the aquatic habitat attains a pre-disturbance state, dispersal and metapopulation dynamics play a significant role in determining recolonisation success (Clarke *et al.*, 2008; Tonkin *et al.*, 2014; Li *et al.*, 2016). Freshwater macroinvertebrates use a variety of active (e.g. upstream movement, aerial dispersal) and passive (e.g. downstream drift, bird-mediated dispersal) mechanisms to colonise both connected and spatially isolated freshwater systems (Williams & Hynes, 1976;

Bilton, Freeland & Okamura, 2001; Parkyn & Smith, 2011; Tonkin *et al.,* 2018). While some insect taxa with long-winged adult stages can disperse between catchments (Briers *et al.,* 2004; Macneale, Peckarsky & Likens, 2005; Geismar *et al.,* 2015; Li *et al.,* 2016), most stream macroinvertebrates largely disperse within the streambed or along the riparian corridor (Altermatt, Seymour & Martinez, 2013; Tonkin *et al.,* 2018). Such localised dispersal highlights the importance of nearby source populations for successful recolonisation (Tonkin *et al.,* 2014). However, as a consequence of large-scale pollution, habitat degradation (Feld & Hering, 2007) and hydrological alteration (Dunbar *et al.,* 2010), nearby species pools often no longer provide appropriate sources for recolonisation (Sundermann, Stoll & Haase, 2011; Tonkin *et al.,* 2014; Cañedo-Argüelles *et al.,* 2015; Stoll *et al.,* 2016).

The unfulfilled hopes of self-recolonisation in many restoration projects prompts the question of how the recovery of natural macroinvertebrate communities can be supported when appropriate source populations are lacking. One answer might come from the terrestrial realm, where reintroductions are commonly used as a tool for wildlife rehabilitation (Armstrong & Seddon, 2008; Seddon *et al.,* 2014), and hence also may be a valuable tool in freshwater restoration. Reintroduction is defined by the Species Survival Commission of the International Union for Conservation of Nature (IUCN/SSC, 2013, p. 3) as 'the intentional movement and release of an organism *inside its indigenous range* from which it has disappeared'. Reintroductions have most often been employed for the conservation of terrestrial vertebrates (reviewed in Seddon, Soorae & Launay, 2005) and, in freshwaters, for fishes (e.g. Fraser, 2008; George *et al.,* 2009; Cochran-Biederman *et al.,* 2015). By contrast, much less effort has been placed on the reintroduction of aquatic macroinvertebrates. This bias is likely due to freshwater macroinvertebrates having little direct economic value in many countries (except for some Astacidae), and few 'charismatic' freshwater macroinvertebrate species generating public attention [e.g. astacid crayfish (Souty-Grosset & Reynolds, 2009); pearl mussel, *Margaritifera margaritifera* (Degerman *et al.,* 2009); some dragonflies, (Lemelin, 2007)]. Another reason could be that several aquatic insect species tend to emerge *en-masse* prior to disturbance taking place (Sartori *et al.,* 1995; Cid, Ibanez & Prat, 2008; Málnás *et al.,* 2011; Bauernfeind & Soldan, 2012). Such observations may give conservation practitioners the subjective (but erroneous) impression that such species would once again reach high population densities following the removal of stressors that led to their decline (see Sections IV.1*a,f*). Furthermore, the magnitude of invertebrate declines has not been evaluated often, and only recently have quantitative long-term observations been published that report on massive declines of insect biomass (Hallmann *et al.,* 2017; Vogel, 2017). The growing attention on downward trends of invertebrate populations will likely create an increasing demand for methods and approaches to restore natural biodiversity, including reintroductions.

The success of macroinvertebrate reintroductions will depend on several intrinsic and extrinsic factors. Although extrinsic factors have classically received much attention in aquatic restoration biology (e.g. hydromorphological conditions or chemical pollutants), intrinsic factors are often neglected. Intrinsic factors include species-specific morphological, physiological, behavioural, and life-history traits that affect the ability of species to establish a self-sustaining population following colonisation. The complexity of many insect life cycles, including having both aquatic and terrestrial stages, highlights the need for a critical appraisal of research on this subject to date.

Here, we review the available literature on freshwater macroinvertebrate reintroduction efforts. The few previous reviews on this subject generally focused on local ('grey') literature and provided practical, group-specific recommendations [e.g. astacid crayfish (Souty-Grosset & Reynolds, 2009); unionid mussels (Cope & Waller, 1995; Degerman *et al.,* 2009)]. Our review aims to identify general mechanisms that might explain the success or failure of macroinvertebrate reintroductions. Our objectives are to: (*i*) provide an overview of the freshwater macroinvertebrate groups considered in reintroduction programs to date; (*ii*) assess whether some taxonomic groups have a higher probability of local population establishment following reintroduction; (*iii*) determine if successful population establishment is linked to specific intrinsic or extrinsic factors; (*iv*) discuss risks to resident ecological communities that may arise from species translocations and weigh these risks against the benefits of re-establishing desired species; and (*v*) provide recommendations for practitioners to improve the success of future reintroduction projects.

II. REVIEWING METHODS

To identify literature relevant to our review, we used the terms 'reintroduction', 'aquatic' OR 'limnic' OR 'freshwater' and 'invertebrate' OR 'macroinvertebrate' OR one of the following taxonomic group names ('Arachnida', 'Arthropoda', 'Astacidae', 'Bivalvia', 'Coleoptera', 'Crustacea', 'Diptera', 'Ephemeroptera', 'Gastropoda', 'Hemiptera', 'Hirudinea', 'Hydracarina', 'Hymenoptera', 'Insecta', 'Lepidoptera', 'Megaloptera', 'Mollusca', 'Neuroptera', 'Odonata', 'Oligochaeta', 'Plecoptera', 'Trichoptera', 'Tricladia') for *Google Scholar* and *ISI Web of Science* searches. We searched for additional studies by screening the bibliographies in publications identified during our search. We only considered studies that matched the definition of reintroductions and excluded those describing other kinds of species translocation, such as reinforcement or 'assisted colonisation', which describes the 'intentional movement and release of an organism *outside its indigenous range* to avoid extinction of populations of the focal species' (IUCN/SSC, 2013, p. 3).

According to the IUCN/SSC (2013), the objective of any reintroduction program is to re-establish a self-sustaining population. Therefore, it is important to assess if the population successfully reproduces in the new habitat for at least one generation. Conducting such assessments is challenging, however, for many macroinvertebrates. For example, pearl mussels are one of the longest-lived invertebrates known, reaching ages of >100 years (Bauer, 1992) and maturing at 10–15 years (Lopes-Lima *et al.,* 2017). For those studies that provided monitoring results over at least one generation, we classified reintroduction success into one of three categories: (*i*) *successful*: the released individuals reproduced and a new generation was observed, (*ii*) *partially successful*: the released generation survived, and (*iii*) *failure*: released individuals did not survive. Care needs to be taken when classifying reintroductions based on these criteria. Seddon (1999) cautioned against the danger of classifying a reintroduction as successful, since doing so may imply that neither new releases nor additional monitoring are necessary. Keeping this in mind, our classification was primarily intended to provide an estimate of population development during the time of monitoring. We tentatively suggest that success rates may actually be lower than implied by our results, as successful reintroductions are more likely to be published than failed projects.

III. CURRENT STATUS OF FRESHWATER MACROINVERTEBRATE REINTRODUCTIONS

Macroinvertebrates represent just three [$N = 2$ on dragonflies (Odonata) and $N = 1$ on semi-aquatic spiders (Araneae)] out of 290 reintroduction case studies summarised in the five compiled volumes of the IUCN 'Global Perspectives in Reintroduction Biology' series (Soorae, 2008, 2010, 2011, 2013, 2016). Overall, we identified 40 reintroduction attempts of 34 different freshwater macroinvertebrate species meeting the search criteria outlined above (Table 1). Of these studies, the largest number was conducted on unionid mussels ($N = 13$), followed by astacid crayfish ($N = 7$), stoneflies (Plecoptera; $N = 6$), dragonflies (Odonata; $N = 5$ and mayflies (Ephemeroptera; $N = 3$) (Table 1; Fig. 1A).

We found no reintroduction projects focusing on megalopterans (Megaloptera), dipterans (Diptera), worms (Oligochaeta), leeches (Hirudinea), water mites (Hydracarina), flatworms (Tricladia), aquatic butterflies (Lepidoptera), or aquatic beetles (Coleoptera). Furthermore, we were unable to retrieve detailed information on some reintroduction projects mentioned in previous reviews on astacid crayfish (Souty-Grosset & Reynolds, 2009) and unionid mussels (Cope & Waller, 1995; Degerman *et al.,* 2009) because these projects were either not properly cited or written in a language inaccessible to us.

Twenty-three studies provided post-release monitoring data for the duration of at least one generation. Of these studies, 65.2% were classified as successful, 8.7% as partially successful, and 26.1% as failures (Fig. 1B). We also found a high discrepancy in success rates among taxonomic groups. All reintroduction attempts of non-insect species were at least partially successful (reintroduced species survived and/or reproduced), but only 62.5% of insect reintroduction attempts were successful (0% partially successful, 37.5% failed). However, estimates of success rates can be influenced by a suite of factors, including variable recapture probabilities resulting from variable species dispersal strategies, more- or less-aggregated population distributions, and variable duration of catchability (i.e. aquatic individuals exhibiting a minimal size enabling capture) according to both species life cycle and sampling characteristics.

(1) Reintroduction of non-insect species

Existing crustacean reintroductions are restricted to the family Astacidae, with two studies reporting success and two studies reporting partial success (Table 1). For example, the noble crayfish (*Astacus astacus*) was successfully reintroduced after it had been eradicated by crayfish plague in Norway (Taugbøl, 2004) and Austria (Sint & Füreder, 2004). In Norway, several thousand adult and juvenile crayfish reproduced after four years across release sites (Taugbøl, 2004). This success indicated that the former cause of extinction (in this case the crayfish plague, caused by the leptolegniacean fungus *Aphanomyces astaci*) was correctly identified and eliminated, while appropriate habitat conditions were still present and enabled successful population establishment.

Unionid mussels have received the most attention in invertebrate reintroduction programs. Due to overharvesting, pollution, habitat degradation and arrival of invasive species, several unionid mussels have experienced drastic declines in their distribution range and rank amongst the most endangered animal taxa (e.g. in North America: Williams *et al.,* 1993; Ricciardi & Rasmussen, 1999). We noted that relocation of mussels (e.g. to protect them from construction projects) was more common than reintroductions (Cope & Waller, 1995). Nevertheless, 13 case studies described true reintroductions. In North America, *Actinonaias ligamentina*, *A. pectorosa*, *Amblema plicata*, *Epioblasma capsaeformis*, *E. rangiana*, *Fusconaia subrotunda*, *Medionidus conradicus*, *Pleurobema clava*, *Villosa nebula* and *V. vanuxemensis* were reintroduced. In Europe, the pearl mussel (*Margaritifera margaritifera*) received most attention (Degerman *et al.,* 2009). We could not evaluate the success of any of these unionid reintroductions, as all species have long life cycles (Lopes-Lima *et al.,* 2017), and monitoring periods (at least those mentioned in the literature) never exceeded one generation. However, high initial mortality of introduced specimens (e.g. Sheehan *et al.,* 1989) indicates that establishment might be difficult to achieve. For example, low survival rates were observed in reintroduction attempts of *M. margaritifera* in northern Europe, especially when individuals originated from another watercourse. Survival rates of *M. margaritifera* were much higher when specimens were translocated within the same watercourse (Degerman *et al.,* 2009), suggesting that local adaptation might be a crucial factor determining reintroduction success (see Section IV.1*e*). Furthermore, the complex life cycle of unionid mussels, which involves an obligatory parasitic phase on a host fish, likely have a vital influence on the success or failure of population establishment (see Section IV.1*a*).

Table 1. Overview of invertebrate reintroduction attempts

Taxonomic group	Species name	Location of water body	Habitat type	Accompanied by physical habitat restoration	Method of reintroduction	Monitoring over at least one generation	Reintroduction success	Comments and caveats	Life cycle	Reference(s)
Arthropoda										
Arachnida										
Araneae	*Dolomedes plantarius*	Europe, UK	Pond	No	Wild to wild/ lab to wild/	Yes (2 years later)	Successful			Smith *et al.* (2013)
Crustacea										
Decapoda	*Astacus astacus*	Europe, Norway	Stream	No	Wild to wild	Yes (over 10 years)	Partially successful		Hololimnic	Taugbøl (2004)
Decapoda	*Astacus astacus*	Europe, Austria	Stream	Yes (stream restoration before reintroduction)	Wild to wild/ lab to wild	No (over 4 months)	NA	Survived during short time of monitoring	Hololimnic	Sint & Füreder (2004)
Decapoda	*Astacus astacus*	Europe, Netherlands	Pond	No	Wild to wild	Yes (∼20 years later)	Successful (reproduced)		Hololimnic	Niewold (2002, 2003)
Decapoda	*Astacus astacus*	Europe, Germany	Stream	No	Juveniles from commercial breeder to wild	Yes (∼7 years later)	NA	In 8 of 13 streams high survival rates and egg-carrying females were observed	Hololimnic	HMUKLV & Hessen-Forst-FENA (2014)
Decapoda	*Austropotamobius pallipes*	Europe, UK	Stream	No	Wild to wild, but adults were kept in quarantine facility before release	No, (over ∼ 1 year)	NA	Observations of marked adults one year after release	Hololimnic	Rogers (2003)
Decapoda	*Austropotamobius pallipes*	Europe, Ireland	Lake	No	NA	Yes (∼7 years later)	Successful (reproduced)		Hololimnic	Reynolds & Matthews (1997) cited in Reynolds (1998)
Decapoda	*Austropotamobius pallipes*	Europe, UK	Stream	No	Wild to wild (source population from the same stream)	Yes (∼15 years later)	Partially successful		Hololimnic	Spink & Frayling (2010)
Insecta										
Ephemeroptera	*Oligoneuriella rhenana*	Europe, Germany	Stream	No (but improvement of water quality)	Wild to wild	Yes (over ∼10 years)	Failure		Merolimnic (winged adult stage)	Rupprecht (2009)
Ephemeroptera	*Ephemera danica*	Europe, UK	Stream	No	Wild to wild (larvae and eggs)	No (∼1 year later)	NA		Merolimnic (winged adult stage)	Bennett (2007)
Ephemeroptera	*Palingenia longicauda*	Europe, Germany	Stream	Yes (stream restored and water quality improved)	Wild to wild (larvae and eggs)	Yes (over 3 years)	Failure (T. Tittizer, personal communication)		merolimnic (Winged adult stage)	Tittizer *et al.* (2008)
Hemiptera	*Aquarius najas*	Europe, Finland	Stream	No	Wild to wild	Yes (∼ 3 months later)	Successful	Reproduced in 20 of 90 reintroduction sites	Merolimnic (winged adult stage)	Ahlroth *et al.* (2003)
Hemiptera	*Ambrysus amargosus*	North America, USA	Spring system	Yes (physical habitat restoration, including restoration of natural stream flow)	NA	Yes	Successful		Hololimnic	Fraser & Martinez (2002)
Odonata	*Coenagrion mercuriale*	Europe, UK	Ditch/ runnel	Yes (introduction of dams to avoid fast flow; implementation of a grazing regime avoiding runnels to be covered by encroaching vegetation)	Wild to wild	Yes (2 years later)	Successful		Merolimnic (winged adult stage)	Thompson (2010)

Table 1. Continued

Taxonomic group	Species name	Location of water body	Habitat type	Accompanied by physical habitat restoration	Method of reintroduction	Monitoring over at least one generation	Reintroduction success	Comments and caveats	Life cycle	Reference(s)
Odonata	*Leucorrhinia dubia*	Europe, Czech Republic	Pond	Yes (small ponds were artificially created)	Wild to wild (larvae)	Yes (15 years later)	Successful		Merolimnic (winged adult stage)	Dolný *et al.* (2018)
Odonata	*Nehalennia speciosa*	Europe, Germany	Pond	No	Wild to wild (adults)	Yes (1 year later)	Successful	Group of adult imagos was translocated. One adult observed 1 year later	Merolimnic (winged adult stage)	Mauersberger (1998)
Odonata	*Ischnura gemina*	North America, USA	Ditch	Yes (removal of riparian trees and shrubs; new ponds created)	Wild to wild	Yes (over ∼ 1 year)	Successful	Two generations observed, but populations did not persist over more than one year	Merolimnic (winged adult stage)	Hannon & Hafernik (2010)
Odonata	*Urothemis edwardsii*	Africa, Algeria	Lake	No	Wild to wild (larvae and eggs)	Yes (∼ 3 years later)	Successful		Merolimnic (winged adult stage)	Khelifa *et al.* (2016)
Plecoptera	*Acroneuria frisoni*	North America, USA	Stream	No	Wild to wild (eggs)	Yes (over ∼ 1 year)	Failure		Merolimnic (winged adult stage)	Chabot (2010)
Plecoptera	*Isoperla goertzi*	Europe, Germany	Stream	No (but improvement of water quality)	Lab to wild	Yes (over ∼ 10 years)	Failure		Merolimnic (winged adult stage)	Rupprecht (2009)
Plecoptera	*Isoperla oxylepis*	Europe, Germany	Stream	No (but improvement of water quality)	Lab to wild	Yes (over ∼ 10 years)	Failure		Merolimnic (winged adult stage)	Rupprecht (2009)
Plecoptera	*Isoperla grammatica*	Europe, Germany	Stream	No (but improvement of water quality)	Lab to wild	Yes (over ∼ 10 years)	Failure		Merolimnic (winged adult stage)	Rupprecht (2009)
Plecoptera	*Perla marginata*	Europe, Germany	Stream	No (but improvement of water quality)	Lab to wild	Yes (over ∼ 10 years)	Successful		Merolimnic (winged adult stage)	Rupprecht (2009)
Plecoptera	*Leuctra inermis*	Europe, Germany	Stream	No	Wild to wild (eggs)	Yes (> 20 years)	Successful	At least three generations observed but finally extinct	Merolimnic (winged adult stage)	Zwick *et al.* (2011)
Trichoptera	*Lepidostoma basale*	Europe, Netherlands	Stream	Yes	Wild to wild (larvae)	Yes (over ∼ 4 years)	Successful	New generations observed in subsequent four years	Merolimnic (winged adult stage)	P.F.M. Verdonschot & R.C.M. Verdonschot (unpublished data)
Mollusca Bivalvia										
Unionoida	*Actinonaias ligamentina*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ∼ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan, Neves & Kitchel (1989)
Unionoida	*Actinonaias pectorosa*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ∼ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)
Unionoida	*Amblema plicata*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ∼ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)

Table 1. Continued

Taxonomic group	Species name	Location of water body	Habitat type	Accompanied by physical habitat restoration	Method of reintroduction	Monitoring over at least one generation	Reintroduction success	Comments and caveats	Life cycle	Reference(s)
Unionoida	*Epioblasma capsaeformis*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild/ lab to wild/ infested host fish	No (over ~ 2 years)	NA	Survived during monitoring time	Hololimnic	Carey *et al.* (2015)
Unionoida	*Epioblasma rangiana*	North America, USA	Stream	No	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time	Hololimnic	Tiemann (2014)
Unionoida	*Fusconaia subrotunda*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)
Unionoida	*Margaritifera margaritifera*	Europe, Germany	Stream	Partially (increasing amount of gravel)	Wild to wild/ infested host fish	No (in the following years)	NA	No survival could be observed	Hololimnic	HMUKLV & Hessen-Forst-FENA (2014)
Unionoida	*Margaritifera margaritifera*	Europe, Russia	Stream	No	Wild to wild	No (over ~ 2 years)	NA	Survived during monitoring time, low mortality rates	Hololimnic	Ziuganov *et al.* (1994)
Unionoida	*Medionidus conradicus*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)
Unionoida	*Pleurobema clava*	North America, USA	Stream	No	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time	Hololimnic	Tiemann (2014)
Unionoida	*Pronodularia japanensis*	Asia, Japan	Stream	Yes	Wild to wild	No (over 4 years)	NA	continuous recruitment of juveniles	Hololimnic	Miura *et al.* (2018)
Unionoida	*Villosa nebulosa*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)
Unionoida	*Villosa vanuxemensis*	North America, USA	Stream	No (but improvement of water quality)	Wild to wild	No (over ~ 3 years)	NA	Survived during monitoring time, however, high mortality rates	Hololimnic	Sheehan *et al.* (1989)
Gastropoda										
Sorbeoconcha	*Io fluvialis*	North America, USA	Stream			Yes	Successful		Hololimnimc	Ahlstedt (1991)
Neritopsida	*Theodoxus prevostianus*	Europe, Hungary	Stream	No (but continuous availability of water restored)	Wild to wild	Yes (> 4 years)	Successful		Hololimnimc	Feher *et al.* (2017)

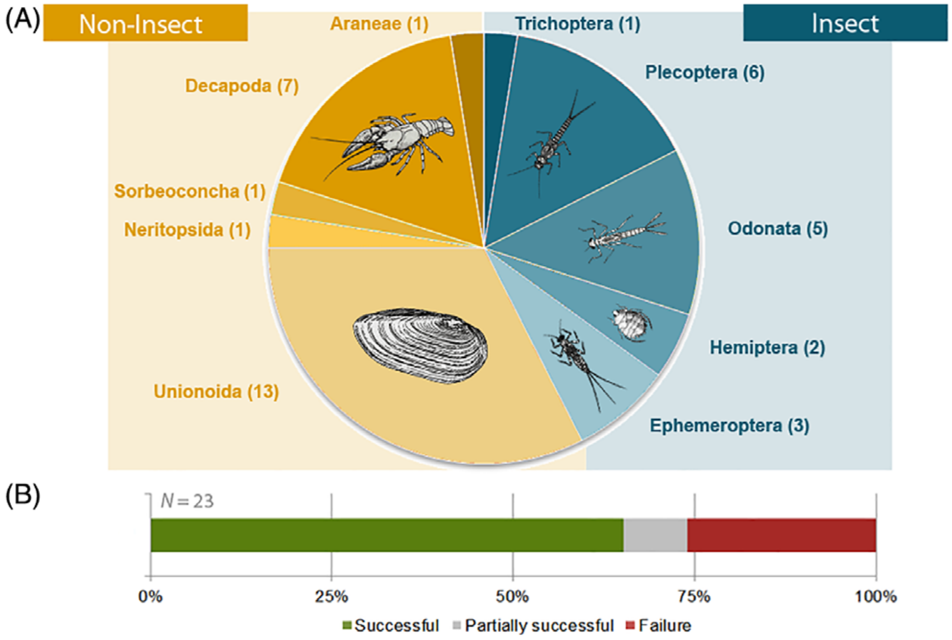


Fig. 1. (A) Overview of the 40 reintroduction attempts considered herein; numbers of studies per taxonomic group are given in parentheses. (B) Success rates of the introductions (calculated from the 23 studies that provided post-release monitoring over at least one generation).

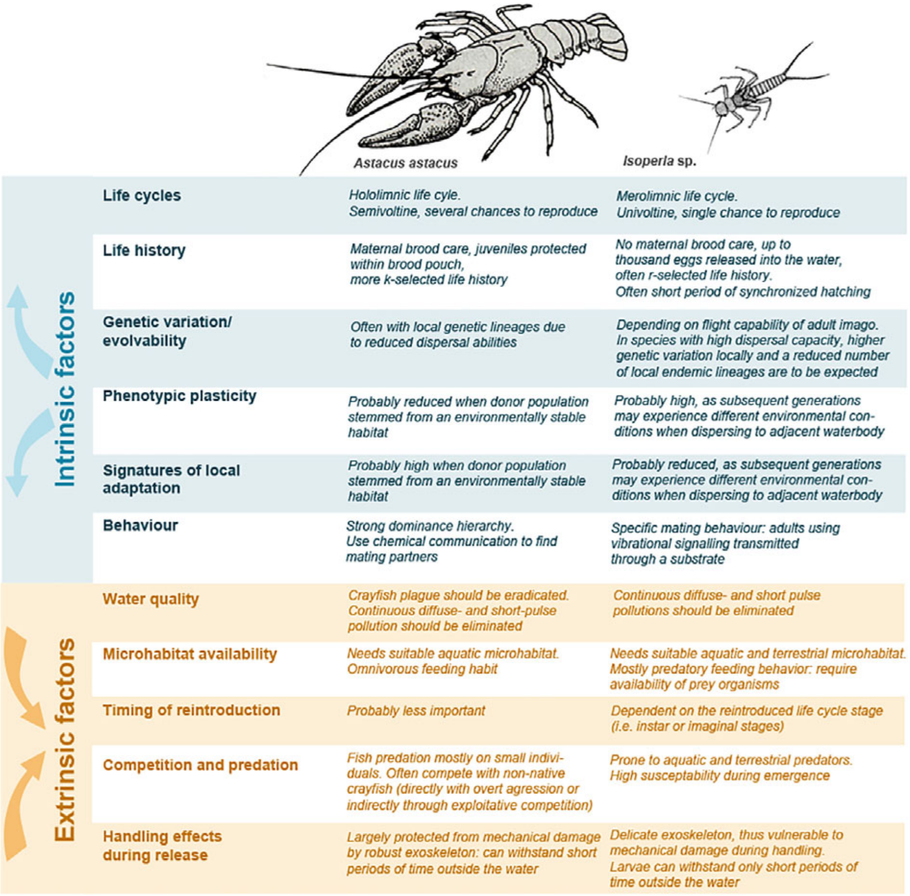
(2) Reintroduction of aquatic and semi-aquatic insects

We identified 16 studies on reintroductions of aquatic insects that provided monitoring for more than one generation, of which only half were assessed as at least partially successful (Table 1). For instance, the mayfly *Palingenia longicauda* (Palingeniidae; Ephemeroptera) was formerly widely distributed in Europe, but now occurs in only 2% of its former range (Tittizer *et al.*, 2008; Bálint *et al.*, 2012). Reintroductions of *P. longicauda* were attempted twice in the River Lippe (a tributary of the River Rhine in Germany), where this species still occurred by the end of the 19th century (Tittizer *et al.*, 2008). To reintroduce *P. longicauda*, a total of 9000 fertilised females were trapped during mating events at the River Theiß (Hungary). About 80 million eggs gained from these females were hatched in the laboratory. For the release in the River Lippe, plastic tubes (60 cm; 16 cm diameter) were inserted into the river bed. First-instar larvae were placed into the tubes to enhance settling on, and burrowing into the sediment and to avoid instant larval drift. Additionally, sediment corers were used to remove about 1200 first- and second-year larval stages from the bed of the River Theiß and released into the River Lippe. Stream type, macroinvertebrate species composition, water chemistry and bed sediment composition were previously compared between sites and judged to be sufficiently similar to support relocation (Tittizer *et al.*, 2008). Nevertheless, monitoring revealed no success, i.e. no emergence of *P. longicauda* from the River Lippe so far. Tittizer *et al.* (2008) suggested that substratum cohesiveness did not match exactly the donor river situation due to a higher per cent of sand in the Lippe.

An example of a successful reintroduction comes from the caddisfly *Lepidostoma basale* (Lepidostomatidae; Trichoptera). This species inhabits dead woody debris in slow-flowing sections of streams with stable discharge and good water quality, woody riparian vegetation and a relatively cool water temperature (Hoffmann, 2000). Larvae (2400 individuals) were released in a 7-km long lowland stream in the Netherlands (P.F.M. Verdonschot & R.C.M. Verdonschot, unpublished data). The stream was restored prior to reintroduction, which consisted of water-quality improvements through the removal of point-source pollution and physical habitat restoration. Four years following the introduction of *L. basale*, new generations were observed every year and the population expanded, both in up- and downstream directions from the initial release site. This study indicates that, if the specific habitat requirements of a given taxon are met, reintroductions of aquatic insect species are possible. However, a few years of post-release monitoring does not guarantee long-term success, as exemplified by the stonefly *Leuctra inermis* (Leuctridae; Plecoptera), which was reintroduced in the Breitenbach in Germany in 1986. Although adults were found in each of several years following reintroduction, the species eventually became extinct in the Breitenbach (Zwick *et al.*, 2011).

IV. FACTORS DETERMINING THE SUCCESS OF REINTRODUCTIONS

Why do some macroinvertebrate groups have a higher probability of establishment after reintroduction? In the



		Astacus astacus	*Isoperla* sp.
Intrinsic factors	Life cycles	Hololimnic life cyle. Semivoltine, several chances to reproduce	Merolimnic life cycle. Univoltine, single chance to reproduce
	Life history	Maternal brood care, juveniles protected within brood pouch, more k-selected life history	No maternal brood care, up to thousand eggs released into the water, often r-selected life history. Often short period of synchronized hatching
	Genetic variation/ evolvability	Often with local genetic lineages due to reduced dispersal abilities	Depending on flight capability of adult imago. In species with high dispersal capacity, higher genetic variation locally and a reduced number of local endemic lineages are to be expected
	Phenotypic plasticity	Probably reduced when donor population stemmed from an environmentally stable habitat	Probably high, as subsequent generations may experience different environmental conditions when dispersing to adjacent waterbody
	Signatures of local adaptation	Probably high when donor population stemmed from an environmentally stable habitat	Probably reduced, as subsequent generations may experience different environmental conditions when dispersing to adjacent waterbody
	Behaviour	Strong dominance hierarchy. Use chemical communication to find mating partners	Specific mating behaviour: adults using vibrational signalling transmitted through a substrate
Extrinsic factors	Water quality	Crayfish plague should be eradicated. Continuous diffuse- and short-pulse pollution should be eliminated	Continuous diffuse- and short pulse pollutions should be eliminated
	Microhabitat availability	Needs suitable aquatic microhabitat. Omnivorous feeding habit	Needs suitable aquatic and terrestrial microhabitat. Mostly predatory feeding behavior: require availability of prey organisms
	Timing of reintroduction	Probably less important	Dependent on the reintroduced life cycle stage (i.e. instar or imaginal stages)
	Competition and predation	Fish predation mostly on small individuals. Often compete with non-native crayfish (directly with overt agression or indirectly through exploitative competition)	Prone to aquatic and terrestrial predators. High susceptability during emergence
	Handling effects during release	Largely protected from mechanical damage by robust exoskeleton: can withstand short periods of time outside the water	Delicate exoskeleton, thus vulnerable to mechanical damage during handling. Larvae can withstand only short periods of time outside the water

Fig. 2. Overview of intrinsic and extrinsic factors that can promote or hamper success of macroinvertebrate reintroductions, exemplified by the noble crayfish (*Astacus astacus*) and stoneflies of the genus *Isoperla*.

following sections, we address this question by providing an overview of intrinsic and extrinsic factors that can promote or hamper reintroduction success, some of which are unique to the reintroduction of macroinvertebrates (Fig. 2).

(1) Intrinsic factors

Intrinsic factors describe species- or population-specific traits and include (*i*) effects of life cycles, (*ii*) life-history differences, (*iii*) differences in genetic variation/evolvability of introduced populations, (*iv*) effects of phenotypic plasticity, (*v*) signatures of local adaptation, and (*vi*) behavioural differences between populations, including acquired (learned) differences.

(*a*) *Effects of life cycles*

While non-insect species (e.g. crustaceans and molluscs) are mostly introduced as juveniles or adults that may carry sperm in their reproductive tracts (Bauer, 1986) or may be selfing (Jarne & Städler, 1995), insects are often translocated as larvae (i.e. before they are able to reproduce). The sensitivity of invertebrates to environmental stressors, such as heavy metal pollution, may be greater during early stages of development compared to later stages (Williams *et al.*, 1986). In addition, translocated insect larvae have to complete their life cycle in the new habitat and have only a single chance to breed following emergence, which increases the risk of reintroduction failure due to environmental stochasticity (Wilbur, 1980). Therefore, the probability of successful population establishment after reintroduction could be linked to the (species-specific) complexity of their life cycle and the life stage that is transferred.

While limited information is available from studies monitoring reintroduction success, some can be inferred from research on invasive species. Interestingly, a general pattern in reintroductions matches the pattern documented for invasive species; even though aquatic insects are the dominant group of freshwater invertebrates – more than 60% of all freshwater animal species are insects (Balian *et al.*, 2008) – only very few freshwater insects become invasive (e.g. some culicid mosquitoes; Medlock *et al.*, 2012). This 'paradox in biological invasions' (Fenoglio *et al.*, 2016) is illustrated by the fact that no plecopterans or megalopterans and very few trichopterans and ephemeropterans have become successful invaders (De Moor, 1992; Strayer, 2010; Salles *et al.*, 2014). By contrast, non-insect groups such as crustaceans and molluscs are amongst the most successful aquatic invaders (reviewed in Hänfling, Edwards

& Gherardi, 2011). A comparison between reintroductions and invasions needs to be treated with caution, though, as the low number of invasive aquatic insects could be explained by (*i*) the rarity of intentional translocation by humans (due to low economic interest) and (*ii*) the lack of adaptations that allow them to survive during passive transport (e.g. no euryhaline tolerance, and little ability to adhere to vessels; Williams & Williams, 1998; Sakai *et al.*, 2001). However, the bias towards non-insect invertebrate invaders implies that species with less-complex, entirely aquatic (hololimnic) life cycles have an advantage in terms of successful population establishment compared to aquatic insect species with their more complex life cycle, which often comprise both aquatic and terrestrial life stages (merolimnic; Hubendick, 1962; Tonkin *et al.*, 2014).

The hololimnic life cycle of most non-insect macroinvertebrates seems to be a beneficial trait for reintroduction, as it usually offers the ability to reproduce multiple times per year, allowing the loss of a brood due to stochastic events such as physical disturbances to be balanced by producing a replacement clutch in the same or next season (Brittain & Eikeland, 1988; Townsend, 1989; Mackay, 1992). By contrast, reintroducing aquatic insects with a complex merolimnic life cycle poses a challenge. For example, due to the short duration of their adult phase, many ephemeropteran species have synchronised their hatching and rely on the simultaneous emergence of a large number of adults to find mating partners (Bauernfeind & Soldan, 2012). This requires an even higher number of larvae to be introduced, as only a very small fraction of larvae reaches emergence, and only a fraction of the emerged adults mate successfully (Werneke & Zwick, 1992; Huryn & Wallace, 2000). Reduced reproductive success beyond a certain threshold, due to low population densities of breeding adults, is also known as the ‘Allee effect’ (Dennis, 1989; Courchamp, Clutton-Brock & Grenfell, 1999), indicating that a certain density threshold has to be achieved in order to increase the chances of population establishment. Indeed, many recently extinct or endangered insect species that are typical of large rivers show mass emergences and short but synchronised flight periods (Sartori *et al.*, 1995; Cid *et al.*, 2008; Málnás *et al.*, 2011; Bauernfeind & Soldan, 2012). While minimum population sizes or densities necessary for sustaining populations are usually not known, even slight reductions of swarming stages could lead to abrupt species losses within the whole catchment. Consequently, it is most unlikely that enough larvae of these species can be introduced to allow successful mating flights.

Nevertheless, hololimnic life cycles can also be highly complex. All Unionoida have unique and complex life cycles involving parasitic larvae (Lopes-Lima *et al.*, 2017). For example, the freshwater pearl mussel, *M. margaritifera*, requires glochidia to be inhaled by suitable host fishes, where they live encysted as obligate gill parasites. Only sea trout (*Salmo trutta* f. *trutta*), brown trout (*Salmo trutta* f. *fario*) and Atlantic salmon (*Salmo salar*) are suitable hosts. Therefore, the conservation of those fishes is also central in conservation attempts of this endangered mussel (Geist, 2010). The situation is even more complex as different fish strains have different susceptibilities to infection, and specimens that have already been exposed to infection are immune to further infection (Degerman *et al.*, 2009; Geist, 2010; Taeubert *et al.*, 2010). This example illustrates that irrespective of taxonomic group (insect/non-insect), reintroduction of macroinvertebrates becomes increasingly challenging with increasing life-cycle complexity.

(*b*) *Life-history differences*

Some life histories are beneficial in terms of reintroduction, especially those that enable reproduction at low population densities or include the protection of offspring. For example, freshwater decapods as well as amphipods have evolved maternal brood care and carry their eggs and hatched juveniles within a ventral brood pouch. This strategy involves substantial maternal energy expenditure and costs in terms of losing time for growth and further reproduction, but enables offspring to withstand harsh environmental conditions and provides protection from predators (Thiel, 2000), which might be beneficial in the early stages of population establishment. Beyond brood care in Crustaceans, some mayflies are ovoviviparous and nymphs hatch immediately after egg deposition (Brittain, 1982), but the nymphs are not guarded by the parents.

Other examples come from decapods, such as brachyuran crabs, which are able to store sperm packets in the female spermatheca. This means that even if only a single female survives the reintroduction process, it has the potential to reproduce successfully and thus, colonise new habitats (Christy, 1987). Likewise, parthenogenesis is widespread among crustaceans (mostly in Branchiopoda, Ostracoda and Isopoda; Gruner, 1993) or in the gastropod genus *Potamopyrgus* (Neiman, Jokela & Lively, 2005) and self-fertilization common in some freshwater snails (e.g. *Ancylus fluviatilis*; Städler, Loew & Streit, 1993).

(*c*) *Standing genetic variation and evolvability*

Populations can experience novel selective regimes to which they can adapt in two distinct ways: *via* selection on pre-existing genetic variation – which is usually considered to be the fastest way of adapting to altered selective regimes – and *via* selection on new mutations (Barrett & Schluter, 2008). If an insufficient number of individuals or an already bottlenecked population is released, this might result in increased rates of inbreeding and loss of genetic diversity (and thus, reduced evolvability of the population). Moreover, inbreeding depression can bring about a direct and immediate loss in fitness (Keller & Waller, 2002). Considering the evolvability of populations is of particular importance as climate change is predicted to affect multiple levels of biological organisation in freshwater ecosystems, thereby altering selective regimes (Chown *et al.*, 2010; Woodward, Perkins & Brown, 2010; Jourdan *et al.*, 2018). Effects of genetic variation in reintroduction biology are, however, not specific to freshwater macroinvertebrates, and detailed reviews and empirical studies are available (Armstrong & Seddon, 2008; Jamieson, 2011; Tracy *et al.*, 2011; Weeks *et al.*, 2011).

(*d*) *Phenotypic plasticity*

The role of phenotypic plasticity in the ecology and evolution of freshwater organisms that live in variable environments has received considerable attention in recent years (Ghalambor *et al.*, 2007; Murren *et al.*, 2015; Schneider & Meyer, 2017). Classic examples of inducible phenotypic responses to environmental conditions come from studies on water fleas (genus *Daphnia*), where juveniles produce neck-teeth, helmet-like structures, or elongated spines on the dorsal surface of the carapace in response to predator presence (Dodson, 1989). Merolimnic insects with complex life cycles and good dispersal ability (e.g. Culicidae or Odonata) can experience starkly divergent environmental conditions during their (aquatic) larval stages (Wilbur, 1980; Palmer & Poff, 1997; Johansson, 2002). However, since imagos might move between water bodies for oviposition, successive generations often experience different environmental conditions; therefore, plastic responses to the environment in larval life histories, morphology and behaviour are to be expected (reviewed in Benard, 2004). For example, merolimnic insects show considerable variation in size at metamorphosis in response to environmental conditions [Plecoptera (Taylor, Anderson & Peckarsky, 1998); Ephemeroptera (Peckarsky *et al.*, 2001); Diptera (Jourdan *et al.*, 2016*a*)].

In the context of reintroduction, the similarity of environmental conditions between source (donor) site, and reintroduction (recipient) site(s) needs to be considered. For example, if donor larvae stem from a predator-free or a laboratory environment, they might not have produced the morphological (Johansson, 2002) and behavioural traits (Wisenden, Chivers & Smith, 1997) necessary to avoid predators present at the release site. Once the first generation survives in the new habitat, however, environmentally induced phenotypic plasticity is, of great advantage since the next generation can produce the favoured phenotypic optimum (Ghalambor *et al.*, 2007). Adaptive phenotypic plasticity is therefore a crucial component during initial population establishment and increases the probability of establishment.

(*e*) *Signatures of local adaptation*

By contrast, species with reduced dispersal capacities often have a higher degree of local adaptation. For example, populations of the amphipod *Gammarus pulex* from ponds with and without predatory fish show heritable differences in anti-predator responses (i.e. increased refuge use in co-evolved populations; Åbjörnsson, Hansson & Brönmark, 2004). Similarly, intraspecific variation in resistance to pollutants was reported for *G. pulex* where populations exposed to metal pollution had a higher metal tolerance than populations from unaffected sites (Maltby & Crane, 1994; Khan *et al.*, 2011). This highlights the importance of choosing appropriate source populations for reintroductions. For example, if the source population stems from a pristine habitat that never experienced anthropogenic pollution, short peaks of pollution are likely to have a substantial effect on a reintroduced population.

(*f*) *Behavioural deficiencies*

The behaviour of reintroduced individuals/populations can affect reintroduction success, including mate-finding tactics. For example, mass emergence within species probably evolved to minimise individual predation risk (Allan & Flecker, 1989), and for these species traits associated with finding a mate will not be under strong selection (Kokko & Rankin, 2006). However, if few individuals are reintroduced, finding a mate can become a problem in such species. By contrast, many Plecoptera and Trichoptera evolved complex mate-finding strategies using vibrational communication (Ziegler & Stewart, 1977; Virant-Doberlet & Cokl, 2004). Such signals act as reproductive isolating mechanisms, helping females to recognise conspecific males over some distance. In general, the use of such forms of communication and mate-searching behaviour increase the chance of finding a mating partner at low population densities (Hissmann, 1990). However, within-species variation was observed as well (e.g. in temporal characteristics, such as duration and repetition time; Sandberg, 2011). Empirical studies on causes of intraspecific variation of vibrational communication in Plecoptera and Trichoptera are still lacking, but it is likely that local biotic and abiotic conditions cause this variation (e.g. due to character displacement induced by a congeneric species; Henry, 1994). Therefore, similar recommendations for reintroductions apply as formulated for phenotypic plasticity and local adaptation (see Sections IV.1*d*,*e*).

(2) **Extrinsic factors**

(*a*) *Water quality*

The most-straightforward explanation for reintroduction failure may be that the water quality requirements of the reintroduced species are not met. Even if local input of pollutants is eliminated at the restored river section, input of pollutants further upstream *via* point and non-point sources can affect downstream communities (Liess & von der Ohe, 2005). Furthermore, although micropollutants and pharmaceutical compounds are often not considered in water-quality assessments due to the difficulty and cost involved in their measurement (Schwarzenbach *et al.*, 2006; Verlicchi, Al Aukidy & Zambello, 2012), they can have clear biological consequences on regional stream macroinvertebrate diversity (e.g. Beketov *et al.*, 2013).

Generally, continuous diffuse pollution is easier to detect by monitoring programs than unpredictable and short-pulse disturbances. For example, surface run-off after heavy rain can cause high peaks of insecticide loads in streams that are often not reflected in daily average measurements or monthly point samples but result in short (~1 h) pulses of acute pesticide contamination (Liess *et al.,* 1999). Such short, intense pollution events might strongly affect reintroduction success, especially when sensitive taxa are reintroduced (Morrissey *et al.,* 2015). For example, nymphs of reintroduced *Ephemera danica* were killed by a pollution incident at an upstream site but survived at a second reintroduction site further downstream (Bennett, 2007), probably due to dilution effects.

(*b*) *Microhabitat availability*

Another important reason for reintroduction failure is habitat restoration not meeting the criteria required by the species. Suitability of microhabitat covers the whole life cycle, spanning from suitable microhabitat for oviposition (e.g. suitable substratum; Blakely *et al.,* 2006), to the spatial and temporal availability of appropriate food resources even when strong competitors are present (Kohler & Wiley, 1997), refugia from predation (Rader & McArthur, 1995) and appropriate conditions for mate finding and reproduction (see also Section IV.1*f*). Special awareness is needed whenever species with complex life cycles are reintroduced (see Section IV.1*a*), in which habitat requirements may be substantially different between juvenile and adult life stages. Stream restoration may have focused on aquatic conditions, but neglected the terrestrial environment. The importance of removing anthropogenic disturbances in both aquatic and terrestrial surroundings can be illustrated by behavioural observations on swarming *P. longicauda* mayflies in the River Tisza (Hungary): upon approaching a bridge, upstream-flying mayflies turned back because the bridge disrupted the horizontally polarizing channel guiding their flight above the river (Málnás *et al.,* 2011). Such a disruption cannot explain the abovementioned failure of *P. longicauda* reintroduction in Germany (as no swarming was observed at all), but it shows the diversity of anthropogenic disturbances affecting species reintroductions.

(*c*) *Timing of reintroduction*

The timing of reintroductions will affect the outcome of reintroduction projects through a suite of factors, including the flow regime of the recipient system and ambient air temperature during transport. Streams from different ecoregions can have considerably different flow regimes, ranging from highly predictable seasonal flows in continental climates to often unpredictable, aseasonal flows in oceanic climates (Bonada, Rieradevall & Prat, 2007; Tonkin *et al.,* 2017). In predictable environments, such as in snowmelt-driven streams, which experience floods from spring snowmelt and droughts during autumn and winter (Lytle & Poff, 2004), release timing can be tailored to suit the conditions. In such systems, the early summer months most likely offer suitable conditions for reintroductions. As soon as air temperatures increase substantially, however, the maintenance of suitable temperatures during transport becomes increasingly difficult and aerial exposure of aquatic invertebrates is more damaging than during the cold season (see also Section IV.2*e*). In other systems, where high-flow disturbances are unpredictable and severe in terms of timing and magnitude, the outcome of reintroduction success is likely controlled by the abiotic forcing of the recipient system. In such systems, tailoring the timing of reintroduction to the flow regime is difficult due to the unpredictability of local climatic conditions. Here the outcome will be affected by stochastic events such as the occurrence of extreme weather conditions and deviations in average temperatures that affect life-cycle duration and the survival of the reintroduced species (Leigh *et al.,* 2015; Woodward *et al.,* 2016).

(*d*) *Competition, predation and facilitation*

While streams are often highly dynamic systems characterised by pronounced fluctuation in physico-chemical conditions (Poff *et al.,* 1997), there is little doubt that biotic interactions also play a role in shaping stream community structure (McAuliffe, 1984; Townsend, 1989; Kohler & Wiley, 1997). Biotic and abiotic habitat conditions combined are classically referred to as the 'habitat templet' (Southwood, 1977). This concept considers the habitat as a templet for ecological responses and thereby emphasises the linkage between local habitat conditions and life-history and other species-specific traits that predict population ecological parameters (Townsend & Hildrew, 1994). The role that biotic interactions play in determining the outcome of reintroduction projects is likely to be highly context-dependent, with many factors regulating their relative influence, including reintroduction timing, the flow regime of the recipient system, and the trait space available in the recipient community. For instance, if high-flow disturbances are unpredictable and severe in terms of timing and magnitude, the outcome of reintroduction success is more likely controlled by the abiotic forcing of the recipient system, and less so by biotic interactions, such as competition, predation, or facilitation. By contrast, if the flow regime of the donor system is more stable or predictable, biotic interactions may become more important, depending on how intra-annually variable the flow regime is and the time of year. Streams with seasonally disrupted flows through drying events (Acuña *et al.,* 2014) may exhibit strong intra-annual variation in the strength of biotic interactions, as competition for space and resources may intensify during the drying phase (Dewson, James & Death, 2007). Moreover, if the sequence of drying and re-wetting is predictable, such as in Mediterranean climates, the likelihood of finding distinct communities between different seasons is high (Tonkin *et al.,* 2017), which requires careful attention to potential interactions between the reintroduced species and the seasonally distinct local community.

Finally, merolimnic invertebrate species may be particularly susceptible to predation because (*i*) aquatic insects are especially vulnerable to fish predation when rising to the surface at the time of emergence (e.g. Makino *et al.,* 2001), and (*ii*) emerged insects are a substantial prey for terrestrial predators, such as birds, bats or spiders (with losses of up to 90% due to predation; Huryn & Wallace, 2000; Baxter, Fausch & Saunders, 2005). This high susceptibility to predators and thus, naturally high losses, further emphasises the need to reintroduce a sufficiently high number of individuals to ensure mating success.

(*e*) *Handling effects during release*

Reintroduction projects face several logistical challenges, from field collection to transport and, finally, release into their new habitat. So far, there is only sporadic species-specific guidance regarding the handling, sampling and transportation of aquatic invertebrates (e.g. pearl mussel; Degerman *et al.,* 2009). Different taxa and life stages are likely to require different methodological approaches to ensure success. Sampling methods range from collecting sessile organisms (e.g. mussels; Degerman *et al.,* 2009), using aerial insect nets to sample winged adult stages (e.g. Odonata; Hannon & Hafernik, 2010), net sampling of aquatic life stages (e.g. crayfish *Austropotamobius pallipes*; Reynolds, 1998), collection of sediment with burrowing larvae (e.g. *P. longicauda*; Tittizer *et al.,* 2008), to passive sampling techniques (e.g. by introducing enclosed natural substrata to donor streams, which are transferred to the recipient system after colonisation). In the latter case, target species depend on the chosen substratum types but are always more than one taxon (Dumeier, Lorenz & Kiel, 2018). In general, the level of stress to which the animals are exposed during handling will be essential in determining the success of reintroductions of species by affecting their physiological condition. For example, due to the narrow oxygen tolerance of many aquatic invertebrates (Verberk & Bilton, 2013), it is essential to ensure that the oxygen concentration during transport is appropriate. This can be achieved by using ‘breathing bags’ which enable gas exchange and the usage of Styrofoam boxes to keep temperatures low (Tittizer *et al.,* 2008). In all cases, handling time and aerial exposure should be kept as short as possible (e.g. Cope & Waller, 1995).

Finally, an additional risk during the release procedure is considerable passive downstream drift of animals. This might be of particular importance for species that are not adapted to withstand strong flow velocity (e.g. burrowing species) and therefore prone to passive drift and resultant risk of predation. Accounting for this, Tittizer *et al.* (2008) used plastic tubes to enable *P. longicauda* larvae to burrow into the substratum without drifting away. Another possibility to prevent immediate drift is moving and releasing species within their preferred substratum, which provides shelter in the new habitat (Dumeier *et al.,* 2018), but also increases the risk of transferring other (non-target) species (see Section V). Furthermore, during release it is most important that environmental conditions in the recipient habitats are as closely matched as possible to those in the donor habitat (and in the transport containers) to prevent environmental ‘shocks’. After cooling the transport medium, for example, a proper acclimatisation period is required before specimens are finally released into the new habitat. However, studies quantifying survival rates during transport and establishment are lacking so far.

V. RISKS AND OPPORTUNITIES OF MACROINVERTEBRATE REINTRODUCTIONS

(1) Translocation of pathogens and invasive species

Translocation of species from one habitat to another always carries the risk of co-transferring undesirable pathogens or invasive species. One well-known example of parasite translocation is the crayfish plague fungus, *Aphanomyces astaci* (Leptolegniaceae; Saprolegniales), a severe pathogen of freshwater crayfish that was introduced to Europe by American crayfish species including *Pacifastacus leniusculus*, *Orconectes limosus* and *Procambarus clarkii*. While American crayfish are partly resistant to the fungus, they transfer the disease to susceptible native European crayfish species, which had devastating effects on European crayfish populations, such as the noble crayfish, *Astacus astacus* (Dièguez-Uribeondo & Söderhäll, 1993; Vennerström, Söderhäll & Cerenius, 1998; Westman, 2002). While the crayfish plague is now usually taken into consideration when planning translocations of freshwater organisms (Wittwer *et al.,* 2018), several other pathogens are not part of public discussions and might be overlooked by practitioners. For instance, amphipods carry a wide range of parasites and transferred individuals can also transport their parasites to the new habitat, as shown for the microsporidian *Fibrillanosema crangonictidae* and their amphipod host *Crangonyx pseudogracilis* (Slothouber Galbreath *et al.,* 2004). Although it is still uncertain if this parasite is transmittable to other amphipod species (Slothouber Galbreath *et al.,* 2004), this example illustrates that translocation of target species bears the risk of also introducing pathogens.

Transferring wild-caught species to the recipient habitat also involves the risk that non-target species will be transferred. This can either be certain divergently evolving lineages of native species (see Section V.2) or invasive species. The latter is a growing problem in many freshwater ecosystems worldwide. The accidental transfer of invasive species can affect local communities as they may prey on native species, compete for resources or alter ecosystem processes, finally leading to a decline of indigenous biodiversity (reviewed by Sakai *et al.,* 2001).

(2) Significance of the evolutionary history of species and populations

Genetic studies frequently reveal that supposedly widespread single species in reality comprise species complexes (Bickford *et al.,* 2007; Pfenninger & Schwenk, 2007; Janzen *et al.,* 2017; Fišer, Robinson & Malard, 2018). For example, the above-mentioned white-clawed crayfish, *Austropotamobius pallipes*, has gone through several taxonomic revisions, nowadays being considered as a species complex consisting of the two threatened crayfish species *A. pallipes* and *A. italicus* (Fratini *et al.,* 2005). Fratini *et al.* (2005) described strong intraspecific genetic variation in *A. italicus*, with four genetically distinct clades (or subspecies) occurring in Italy. The authors emphasise that reintroduction attempts should be conducted with extreme caution, since not only the two *Austropotamobius* species but also the four *A. italicus* subspecies are genetically and taxonomically separate units (i.e. evolutionarily significant units, see Ryder, 1986) and require independent conservation plans.

Studies on the freshwater shrimp *Paratya australiensis* illustrate what can happen when genetic variation not naturally present is introduced into another population (Hancock & Hughes, 1999; Hughes *et al.*, 2003). *P. australiensis* was translocated between pools from two different Australian subcatchments, with the aim to use fixed allele differences between populations to monitor movements of translocated adults, subsequent larvae, and juveniles (Hancock & Hughes, 1999). After only seven years, representing seven generations, the resident genotype was extinct at one of the sites. This was explained by a mating preference of all females (both translocated and resident) for translocated males (Hughes *et al.*, 2003). This example demonstrates the potential risk of mixing populations with significant intraspecific variation, because they may eliminate locally adapted ecotypes and change evolutionary trajectories within species.

Guidelines for the protection of threatened species advocate the identification of evolutionarily significant units (Ryder, 1986; Moritz, 1999). Weeks *et al.* (2011) considered the evolutionary implications of moving genetic clades (or species) from donor into recipient streams. Their assessment of risks and benefits of such translocations highlights the need for population-genetic screening of donor populations and recipient communities. Conservation of biodiversity not only between but also within species should be a priority goal to retain the intraspecific variation and thus the evolutionary potential for adaptation to future changes in the environment.

(3) Opportunities

Three major motivations should justify reintroduction attempts: (*i*) reintroducing a locally extinct species helps restore the natural biodiversity. This can be of special importance, as certain aquatic invertebrates can act as keystone species or ecosystem engineers in aquatic ecosystems (Covich, Palmer & Crowl, 1999). Local extinction of these keystone taxa can have dramatic consequences for the affected ecosystem for many reasons, including their key position in local food webs with strong effects on downstream nutrient flux (reviewed by Covich *et al.*, 1999; Moore, 2006). For example, either local extinction or replacement of macroinvertebrate shredder species can significantly alter decomposition rates and hence nutrient transfer to higher trophic levels (Gessner *et al.*, 2010; Jourdan *et al.*, 2016*b*). Also, the introduction of mussels increases filter-feeding capacity and can change water clarity and alter primary production rates (Strayer *et al.*, 1999). Gaps or deviations in functional-trait-distribution patterns in the recipient community in comparison to donor communities could be an important guideline when selecting species for reintroductions. In many cases these functionally important species are not the most visually appealing ones but their effects are (e.g. improved water clarity), which in turn can be helpful to establish strong public or political support. Furthermore, reintroduced species can help re-establish other species through facilitation, and niche overlap eventually renders the community more resistant by providing insurance effects under changing environmental conditions (Loreau *et al.*, 2001). Finally, a restored natural biodiversity strengthens the communities' resistance against invasive species by re-occupying vacant niches (Leuven *et al.*, 2009). (*ii*) Reintroducing a locally extinct and threatened species facilitates conservation plans for the species, as the risk of going extinct is reduced with every vital population. (*iii*) Reintroductions might create the public and political support necessary to undertake habitat restoration or to conduct species protection measures. Especially in those cases where a species can serve as a 'flagship' or 'umbrella' species, this might help to protect the entire ecosystem (Simberloff, 1998).

VI. RECOMMENDATIONS FOR PRACTITIONERS

Macroinvertebrate reintroduction is a promising tool to restore the natural biodiversity in freshwater ecosystems and will likely be applied more frequently in the future. We recommend to consider a reintroduction only if natural recolonisation appears to be impossible or can be expected to be exceedingly slow. Generally, for practical applications, we recommend following the framework for reintroductions provided by the IUCN/SSC (2013). Furthermore, we strongly recommend considering the following points for the reintroduction of freshwater invertebrates.

(1) Planning the reintroduction

Practitioners should make sure that all necessary knowledge of the candidate species is gathered, including its biotic and abiotic habitat needs, its current and historical distribution, its interspecific relationships and its basic biology (see Section IV.1). Specifically, the stressors that caused the previous extirpation should be correctly identified and removed (see Section IV.2). This is especially important for species with complex life cycles, as suitable conditions for each life stage have to be considered (see Section IV.1*a*). After the full array of possible hazards both during collection and transport, and after the release of specimens is assessed, the reintroduction can be conducted. The reintroduction then should be repeatedly conducted during different seasons and years to reduce the risk of stochastic events (see Section IV.2*c*).

(2) Selection of target species and populations

As outlined in Section V.3, the restoration of ecosystem functioning might be one of the reasons that justify a reintroduction (Loreau *et al.*, 2001). Therefore, the community-wide distribution of functional traits (and the absence of certain traits; see Covich *et al.*, 1999; Statzner & Beche, 2010) might be a useful criterion to select appropriate target species.

Ideally, nearby reference systems with natural, undisturbed conditions should be selected (e.g. Hawkins & Yuan, 2016), and the functional trait composition of those communities, as well as the target (recipient) community, should be evaluated. Trait classification for each species can be compiled from online databases (e.g. freshwaterecology.info database; Schmidt-Kloiber & Hering, 2015). Assessing the functional diversity of the reference systems (i.e. the breadth of functions performed by all species in the community; Petchey & Gaston, 2006) can be achieved by estimating multidimensional trait space, where species are plotted along synthetic axes capturing a combination of functional traits (Maire *et al.,* 2015). If some key traits are missing in the target habitat, species representing those traits may receive priority for reintroduction. However, the highly context-dependent nature of functional diversity makes it difficult to generalise any conclusions about species values (Petchey & Gaston, 2006). This again highlights that *nearby*, ecologically similar (but undisturbed) systems should be used to compare functional trait spaces – a situation that unfortunately is no longer given in many urbanised and agriculturally transformed areas (Allan, 2004; Grimm *et al.,* 2008).

Practitioners should be aware of different evolutionary units of the target species (see Section V.2), especially when lineages do not show major phenotypic differences (Fišer *et al.,* 2018). This is of particular importance in freshwater species with reduced dispersal abilities, as the geological evolution of drainage systems and their catchment areas plays a significant role in explaining genetic differentiation between populations (Alp *et al.,* 2012). As a result, cryptic species diversity in aquatic invertebrates is often high (Fišer *et al.,* 2018). If monitoring prior to the reintroduction cannot exclude that some remaining individuals of the target species persist in the system, the reintroduction project could *de facto* result in a reinforcement project (*sensu* IUCN/SSC, 2013), thereby substantially increasing the risk of mixing historically isolated populations. Hybridisation between previously independently evolving genotypes not only bears the risk of potential outbreeding depression (Edmands, 1999), but also jeopardises the integrity of evolutionarily independent lineages (see Section V.2). This is of particular importance when considering that reintroduced populations might become self-sustaining in the future and may act as source populations for both down- and upstream dispersal into other stream sections that were themselves not parts of the reintroduction campaign (e.g. Taugbøl, 2004).

Molecular taxonomy provides a tool by which cryptic diversity can be uncovered (Palsbøll, Berube & Allendorf, 2007; Fišer *et al.,* 2018), and analyses of this kind have now become rather inexpensive and fast. We emphasise the need to use a combination of mitochondrial and nuclear DNA markers to assess intraspecific diversity and historic range distributions [e.g. for different species of crayfish see Fratini *et al.,* 2005, Dawkins & Burnham, 2013 and Schrimpf *et al.,* 2014]. Generally, the founder population(s) selected for a reintroduction should be the genetically closest to the original wild population, and museum samples or environmental samples stored in laboratories may provide a wealth of information if a given taxon is extinct on a larger scale (Wandeler, Hoeck & Keller, 2007; Bálint *et al.,* 2012). If no genetic information is available from the extinct population, the founder population should preferably stem from the same catchment or at least the closest geographic neighbour population, ideally considering the phylogeographic structure observed in related taxa if such information is available.

(3) Avoiding pathogen and parasite transmission

Possible co-transfer of pathogens and parasites (see Section V.1) highlights the importance of careful selection of individuals to be released so as to maximise the reintroduction success while minimising harm to the recipient community. The introduction of the crayfish plague fungus, *Aphanomyces astaci*, provides an example of the devastating effects of novel pathogens. Even if this example does not involve a reintroduction, it demonstrates that practitioners should thoroughly study the available literature on host–parasite relationships of their target species. Specimens with externally visible parasites or signs of disease should be avoided when selecting donors. However, in many cases, the context-dependent expression of virulence would require extended quarantine times in the laboratory, which is simply not feasible for many aquatic invertebrates and carries its own risks (see Section IV.1*d*). When infections cannot be detected by external inspection, molecular screening of pathogens might be helpful (Wittwer *et al.,* 2018). Nevertheless, such screening can barely cover the vast number of possible candidate pathogens and parasites, and in most cases not all individuals of the target species can be screened. Moreover, such procedures may increase handling stress (see Section IV.2*e*) or even require haemolymph (or other) samples to be taken (unless environmental DNA is being assessed; Bohmann *et al.,* 2014).

Given these constraints, selecting a donor population within the same catchment as the recipient site represents a simple rule of thumb to reduce the risk of transferring allochthonous pathogens or parasites. This risk is illustrated by a study on snail-schistosome interactions using population-genetic data on the freshwater snail *Bulinus globosus* and its trematode parasite *Schistosoma haematobium* (Davies *et al.,* 1999). The study found geographic isolation of parasite lineages between catchments even though schistosomes spend large parts of their life cycle within highly mobile definitive mammalian hosts. The isolation of parasite populations between catchments demonstrates that a translocation between catchments increases the risk of introducing allochthonous parasite lineages.

(4) Post-reintroduction monitoring

We encourage practitioners to document and report their reintroduction attempts comprehensively. The project design should consider the life-cycle length of the target species and thus the fact that project evaluation is only possible after more than one generation-length (which can be more than 10 years in some species; Lopes-Lima *et al.,* 2017). Adequate post-reintroduction monitoring should provide detailed information of the reintroduction methods and origin of donor individuals, and offer short- and long-term monitoring results like breeding success, survival and dispersal rates. Sutherland *et al.* (2010) provided standards for documenting and monitoring reintroduction projects, and even though these were specifically established for bird reintroductions, they can be readily applied to aquatic invertebrate reintroductions (see Feher *et al.,* 2017). Successful monitoring of reintroduced invertebrates, however, involves specific challenges and may be increasingly difficult with increasing habitat size, increasing dispersal ability and decreasing body size of the target species. Ideally the monitoring procedures applied should be less susceptible to technical changes over time (e.g. changes in monitoring staff), such as the potential use of DNA metabarcoding-based identification of macroinvertebrate samplings (Elbrecht *et al.,* 2017) or environmental DNA extracted from water and sediment samples (Thomsen *et al.,* 2012; Bohmann *et al.,* 2014).

VII. CONCLUSIONS

(1) Due to the growing importance of reintroductions as a management tool (Armstrong & Seddon, 2008), broad guidelines have been developed for conservation-based reintroductions (IUCN/SSC, 2013). Our literature review revealed that freshwater macroinvertebrate reintroductions are not yet frequently undertaken – or at least not reported in international scientific journals – and often detailed information is missing. We therefore encourage practitioners to document and report their reintroduction attempts comprehensively. Publication bias, such as where negative reintroduction outcomes remain unpublished, is likely giving a false impression of overall success rates.

(2) In contrast to the widespread and common practice of reintroducing vertebrates, reintroduction efforts involving freshwater invertebrates present unique challenges, such as when life stages differ in their specific habitat requirements. In general, life-cycle complexity appears to represent an important aspect that can hamper reintroduction success if not properly accounted for.

(3) Multiple, partly interacting factors affect reintroduction success. Our overview of key intrinsic and extrinsic factors that potentially influence the outcomes of macroinvertebrate reintroductions serves as a starting point with the aim of assisting future reintroduction management and developing taxon-specific guidelines.

(4) The reintroduction of species always bears the risk of transferring non-target species or genetically divergent lineages within species that are not necessarily detectable by visual inspection due to a lack of morphological differentiation. Therefore, decisions about where, when and how to reintroduce species for conservation purposes should always consider all potential risks and opportunities.

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