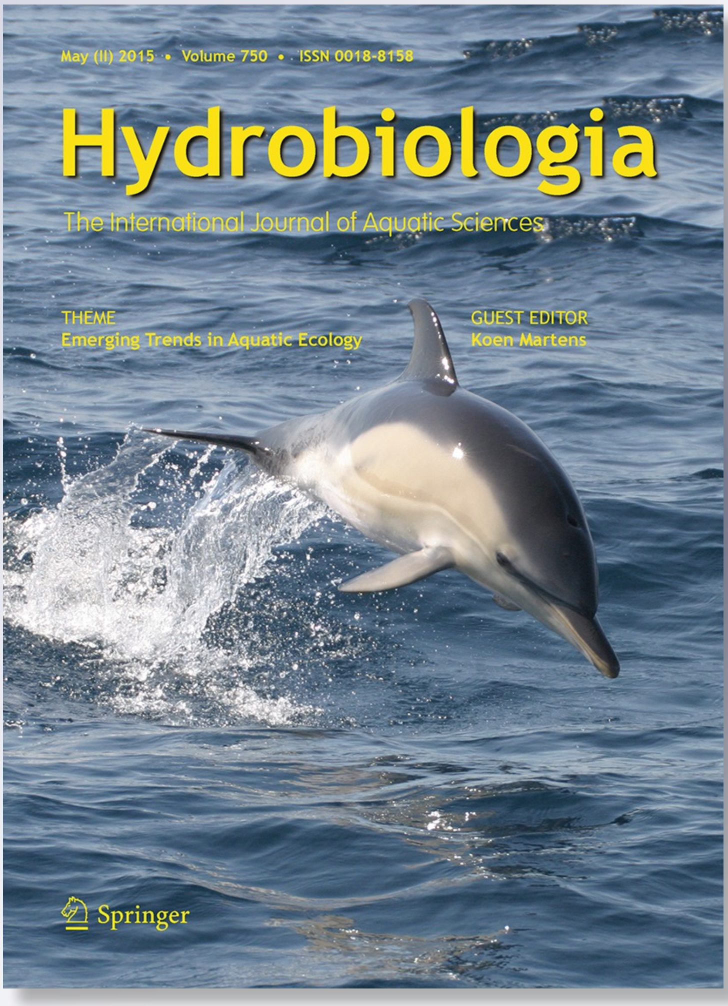
How do freshwater organisms cross the "dry ocean"? A review on passive dispersal and colonization processes with a special focus on temporary ponds

Giulia Incagnone, Federico Marrone, Rossella Barone, Lavinia Robba & Luigi Naselli-Flores

Hydrobiologia
The International Journal of Aquatic Sciences

ISSN 0018-8158
Volume 750
Number 1

Hydrobiologia (2015) 750:103-123
DOI 10.1007/s10750-014-2110-3



Hydrobiologia (2015) 750:103–123
DOI 10.1007/s10750-014-2110-3

TRENDS IN AQUATIC ECOLOGY

Review Paper

How do freshwater organisms cross the "dry ocean"? A review on passive dispersal and colonization processes with a special focus on temporary ponds

Giulia Incagnone · Federico Marrone ·
Rossella Barone · Lavinia Robba ·
Luigi Naselli-Flores

Received: 15 July 2014 / Revised: 28 October 2014 / Accepted: 2 November 2014 / Published online: 13 November 2014

Abstract Lakes and ponds are scattered on Earth's surface as islands in the ocean. The organisms inhabiting these ecosystems have thus developed strategies to pass the barrier represented by the surrounding land, to disperse and to colonize new environments. The evidences of a high potential for passive long-range dispersal of organisms producing resting stages inspired the idea that there were no real barriers to their actual dispersal, and that their distribution was only limited by the ecological characteristics of the available habitats. The development of genetic techniques allowed to criticize this view and revealed the existence of a more complex and diverse biological scenario governed by an assortment of historical and ecological factors. In this paper, we review the literature related to the passive dispersal of organisms producing resting stages among inland lentic ecosystems, with special emphasis to temporary ponds, which represent "isolated" ecosystems both in space and in time, and are characterized by high levels of biological diversity. The existence of a sharp decoupling between "dispersal potential" and "actual establishment rates" is stressed, thus urging a definitive overcome of the so-called "Everything is Everywhere" hypothesis in order to gain a proper understanding of the biogeography and ecology of inland water organisms.

Keywords Dispersal vectors · Biogeography · Dispersal-gene flow paradox · Priority effect · Monopolization hypothesis · Cosmopolitanism paradigm

Introduction

To explain the biosphere concept, Vladimir Vernadskij described the surface of our Planet as covered by a continuous layer of a multitude of (micro)organisms (Vernadsky, 1998). Although he was mainly interested in the processes that these organisms perform in shaping and moulding the Earth's surface, one question may arise from this perspective: how do the organisms distribute and colonize the entire Planet's surface? Since the mid-eighteenth century, Biogeography has been studying the patterns of species distribution across geographical areas and through geological time. However, even if well-established hypotheses on the distribution patterns of species on

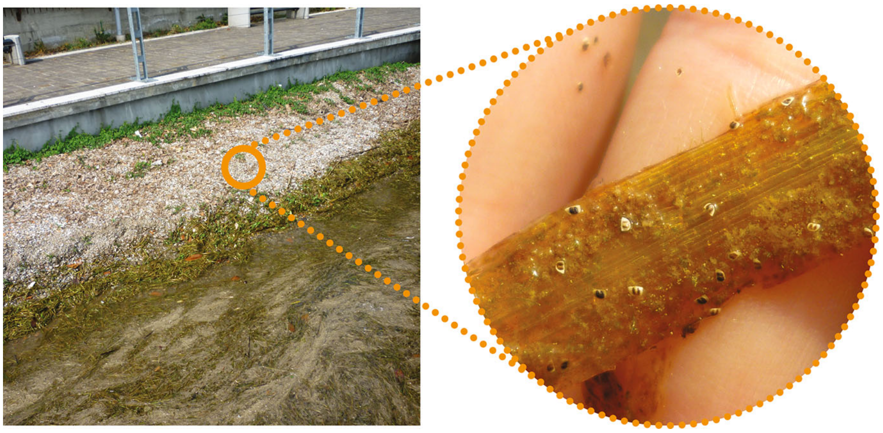
---

Guest editor: Koen Martens / Emerging Trends in Aquatic Ecology

G. Incagnone · R. Barone · L. Robba ·
L. Naselli-Flores (✉)
Dipartimento di Scienze e Tecnologie Biologiche,
Chimiche e Farmaceutiche – Sezione di Botanica ed
Ecologia Vegetale, Università di Palermo, Palermo, Italy
e-mail: luigi.naselli@unipa.it

F. Marrone
Dipartimento di Scienze e Tecnologie Biologiche,
Chimiche e Farmaceutiche – Sezione di Biologia Animale
ed Antropologia Biologica, Università di Palermo,
Palermo, Italy

Fig. 1 Ephippia of cladocerans coating the stranded aquatic vegetation and the shores of Lake Iseo (Northern Italy) in early spring (photos by Federico Marrone)



continents exist, it is more difficult to explain these patterns on geographical or biological islands, especially on the most remote and isolated ones (Whittaker & Fernández-Palacios, 2007). In this frame, inland lentic water bodies can be considered a special case of "biological islands" scattered across the land masses (Ripley & Simovich, 2009), and the distribution patterns of their biota, depending on dispersal abilities and colonization successes, are not fully clarified yet (Shurin et al., 2009).

The organisms inhabiting inland water ecosystems have developed diverse active and passive strategies to pass the barrier represented by the surrounding land, disperse and colonize new environments. The most effective strategy to achieve dispersal is the production of resting stages. These (also called akinetes, cysts, ephippia, statoblasts, spores, seeds in different group of organisms) are dehydrated dormant stages of the cell or of the embryo that show no measurable metabolism and are enveloped in a highly protective cover (Wells et al., 1997; Dumont & Negrea, 2002). Prokaryotes, unicellular eukaryotes, and small multicellular organisms less than 2 mm in length (microorganisms sensu Fontaneto & Brodie, 2011) have been generally considered to have a cosmopolitan distribution because of their minute sizes and their ability to form resting stages which facilitate dispersal by wind and migrating animals. In this review, the passive dispersal mechanisms of microorganisms and of larger ones (e.g. some calanoid copepods, large branchiopods, stoneworts, mosses, quillworts, vascular plants) producing resting stages in the same size range (100–600 μm) of microorganisms will be discussed.

A high potential for long-range passive dispersal of these organisms is supported by the very high population sizes which microorganisms can attain (up to an order of magnitude of $10^9\ l^{-1}$) and by the "astronomical numbers" of resting stages (Foissner, 2006) produced by the larger ones (Fig. 1). This potential is also supported (i) by the very fast colonization of newly formed water bodies (see Maguire, 1963; Jenkins & Buikema, 1998; De Meester et al., 2002; Audet et al., 2013, and references therein) and historically (ii) by the rapid recolonization of the faunally depleted central and northern regions of the northern hemisphere after the last Pleistocene glacial event, which is genetically mirrored by the "southern richness vs. northern purity paradigm" of the Holarctic biota (Hewitt, 2000; Marrone et al., 2010).

Such evidences for a long time inspired the idea that there were no real barriers to the dispersal of resting stage producing aquatic organisms. Their distribution (i.e. the actual presence of a given taxon in a given site) should therefore only be limited by the ecological characteristics of the available habitats themselves. Accordingly, the differences observed in the biota could be explained by the selective pressures operated by the environment only (see Martiny et al., 2006). This idea, known as the "Everything is Everywhere (EiE) hypothesis", was already sustained by Darwin (1859), and then formally defined at the beginning of the twentieth century; it can be efficaciously summarized by the renowned statement of the Dutch microbiologist L.G.M. Baas Becking: "*Everything is everywhere, but the environment selects*" (see Williams, 2011 for a review).

From a genetic perspective, according to the "EiE hypothesis", an extensive gene flow among populations should grant the genetic homogeneity of the species throughout their whole extensive distribution ranges, actually preventing the occurrence of allopatric differentiation among populations and, eventually, of allopatric speciation. Therefore, freshwater microorganisms should belong to a few, widely spread (i.e. subcosmopolitan to cosmopolitan) species, and these should be characterized by the absence of genetic structuring throughout their whole wide distribution areas, each of them actually acting as a single, immense, potentially panmittic population ("Cosmopolitanism Paradigm").

However, according to Foissner (2006), the "EiE" hypothesis is not falsifiable, thus cannot be considered a true scientific theory. At the base of this hypothesis there is likely our poor ability in distinguishing the different biological units based on morphology only (e.g. Pfenninger & Schwenk, 2007; Packer et al., 2009), which also hampers our ability to estimate how dispersal is in fact realized (Fontaneto & Brodie, 2011). Moreover, the knowledge about the autoecology of several organisms, which can offer important clues in species identification, is still inadequate (Kristiansen, 1996, 2008; Padisák et al., 2009).

Although some studies seem to support the EiE hypothesis (cfr. Finlay, 2002; Audet et al., 2013), the recent development and spreading of genetic techniques offered an additional tool that, coupled with a better understanding of the morphological and ecological features of organisms, allowed to criticize the EiE hypothesis even for bacterial communities (e.g. Roberts & Cohan, 1995; Green & Bohannan, 2006; Martiny et al., 2006; O'Malley, 2007; Fierer, 2008; Foissner & Hawksworth, 2009 and literature therein) and established phylogeography as a new discipline aimed at studying biogeographical patterns under a genetic perspective (Avise et al., 1987; Hickerson et al., 2010).

One important step to understand aquatic microorganisms distribution is to investigate their passive dispersal potential and the factors that can make effective a dispersal event, allowing thus the actual colonization of a new ecosystem (Bohonak & Jenkins, 2003). This is not an easy task: some ecological groups such as (phyto)plankton have cryptic dispersal methods (Shurin et al., 2009), and rare or even singly occurring dispersal events, although biologically significant, may remain undetected (Bilton et al., 2001). Moreover, dispersal often occurs through multiple processes and vectors (Higgins et al., 2003). In this review, we will put a special focus on temporary water bodies, since these ecosystems represent biodiversity hotspots (Williams et al., 2001; Zacharias et al., 2007) and their functioning and conservation strictly depends on the dispersal and colonization abilities of their biota (Sahuquillo & Miracle, 2013; Marrone et al., 2013; Korn et al., 2013). Moreover, temporary ponds, alternating flooded and dry phases, add the duration of their ponding phase as a further temporal dimension to their "insular features" (Ebert & Balko, 1987; Naselli-Flores & Barone, 2012). In addition, these ecosystems provide important services in terms of aquatic biodiversity-conservation since they (i) supply recruits of (micro)organisms to permanent waters and eventually constitute "reservoirs" of biodiversity enhancing the success of restoration measures in aquatic ecosystems subject to high human impacts (Moustaka-Gouni et al., 2012), and (ii) favour the observed northward movement of species as a response to climate change (Céréghino et al., 2014). In spite of this, the number of temporary ponds has been drastically reduced in the last decades due to climate change, to the increased demand of land for agriculture and urban development, and to the overexploitation of water resources (e.g. Stoch & Naselli-Flores, 2014). This trend strengthens an increasing geographical isolation of temporary ponds, and may enhance both local and global extinction of species (Florencio et al., 2014).

Understanding patterns of passive dispersal and colonization as well as the mechanisms through which the gene flow among temporary ponds' populations might occur can therefore contribute to preserve these ecosystems and their striking inter- and intra-regional biological diversity.

Passive dispersal mechanisms

Although papers documenting passive dispersal of adult microcrustaceans, water mites and plants are available in the literature (Dahms, 1995; Di Sabatino et al., 2004; Allen, 2007; Frisch & Green, 2007; van Leeuwen et al., 2013; Bruckerhoff et al., 2014), passive dispersal mechanisms more generally require the production of resting stages able to survive unfavourable environmental conditions and to act as

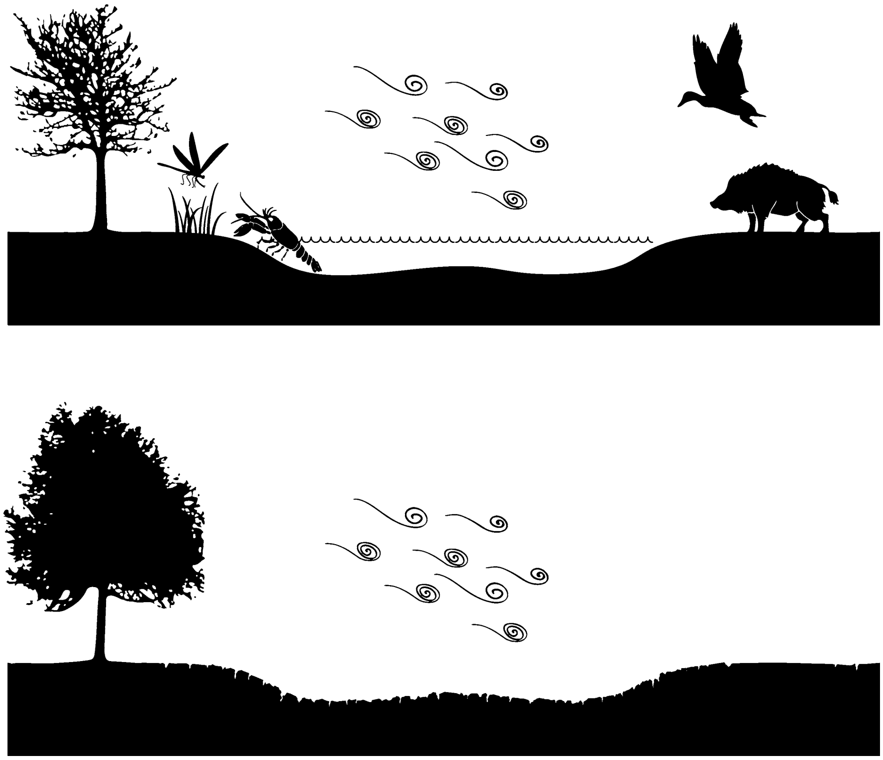


Fig. 2 Dispersal vectors acting on freshwater organisms during the water phase (*above*) and the dry phase (*below*) of a temporary pond

dispersal propagules, functionally performing as plant seeds (see Van Damme & Sinev, 2013). Resting stages are the most important propagules for many aquatic taxa (Rundle et al., 2002) and are easily transported by different physical and biological vectors (Fig. 2) on short and long distances, even though the existence of a direct relationship between the ability of producing resting stages and dispersal efficiency is controversial (Schulz et al., 2012; De Bie et al., 2012; Heino, 2013).

Several papers were published in the last years, estimating the potentiality of physical and biological agents in favouring dispersal of resting stages. In a recent paper, Rogers (2014) showed that resting stages directly dispersed by vectors that specifically move between suitable habitats (like aquatic birds—see Fig. 3) have a greater chance to effectively colonize a new habitat than those randomly dispersed by wind. However, the information contained in the scientific literature is sometime contradictory with some authors suggesting that wind can be more effective than animals as dispersal vector and some other stating the opposite (e.g. Cohen & Shurin, 2003; Allen, 2007).

These contrasting results may suggest that local environmental conditions may favour one or more dispersal vectors and that the effectiveness of dispersal flows may vary depending on both vector and propagule properties (Vanschoenwinkel et al., 2008a). In addition, it has to be highlighted that the majority of the examined studies investigated the potential dispersal and not its effective realization (i.e. a successful colonization event). However, irrespective of the vector, dispersal certainly occurs and the existing

Fig. 3 *Himantopus himantopus* preying on the notostracan *Triops cancriformis* in a Mediterranean temporary pond (Photo by Cristiano Liuzzi)

studies on colonization have shown that new, artificially created ponds are quickly colonized by aquatic organisms (Audet et al., 2013) and that these new communities may have a species diversity comparable to that of older, well-established ones (Louette & De Meester, 2005). In this article, we briefly review the principal outcomes from the studies on dispersal vectors available in the scientific literature.

Dispersal by physical vectors

The action of wind on temporary ponds can potentially disperse microorganisms or resting stages both from water during the wet phase (Sharma et al., 2007), and from soil during the dry phase (Graham & Wirth, 2008). Wind-mediated dispersal is known as anemochory. As regards microalgae, not only resting stages but also vegetative cells can be released from water by bubble-burst processes generated by the action of the wind on the water surface (Hamilton & Lenton, 1998). Due to their small dimensions, phytoplankton taxa can be trapped in the water bubbles and transported by the wind. Several species produce mucilages (Reynolds, 2007) and have cell walls that can act as a protection coating, allowing short-distance dispersal (Chrisostomou et al., 2009). Phytoplankton belonging to cyanobacteria, chlorophytes, diatoms, cryptophytes and euglenophytes have been described as air-dispersed algae (Sharma et al., 2006) and this set of taxa has been reported quite consistently in aerobiological investigation worldwide (see the review by Genitsaris et al., 2011a). The dispersal of vegetative phytoplankton cells has been documented on short distances (1 km) by Chrisostomou et al. (2009) who found that although small cells (width <5 μm) were most easily dispersed, also large organisms (e.g. *Fragilaria capucina*) or colonies (*Microcystis aeruginosa* of >1,000 cells per colony) can be subjected to air dispersal depending on the wind speed. However, Genitsaris et al. (2011b) in an analogous investigation pointed out the possibility of long-distance dispersal of both vegetative cells and resting stages. This latter hypothesis was based on the lack of close suitable aquatic ecosystems as a source for the microorganisms recorded in a set of water containers designed to collect airborne algae.

In contrast to the above cited results, Vanschoenwinkel et al. (2008b) report the absence of crustacean resting stages dispersal by wind among temporary rock pools when they are experiencing their ponding phase. According to these authors, biological vectors are the only effective dispersal agents during the wet phase in temporary ponds. Conversely, during the dry phase, wind causes erosion of soil by detaching particles from its surface and moving zooplankton resting stages even when it blows at low speed (Graham & Wirth, 2008).

Soil erosion due to the action of wind is one of the main environmental concerns in the Mediterranean area (Hill et al., 1994) and the multi-millennial history of intensive land use in this region may have had a role in the dispersal and colonization events that led to the forest-to-scrub transition in the mid-Holocene (Collins et al., 2010). A similar effect on the vegetation might well have taken place in the Mediterranean area even before the Holocene: according to Pretus (1990), the grazing impact exerted by the Balearic dwarf goral *Myotragus* sp. in the Pleistocene caused a land clearing and favoured the colonization of the Balearic islands by, and the long-time persistence of, steppic crustacean taxa in the temporary water bodies of the archipelago.

Several studies have investigated the importance of egg banks in the dry sediments of temporary ponds (e.g. Thiéry, 1997; Brendonck et al., 1998; Mura, 2004, 2005) and the role of the wind in the dispersal of zooplankton, large branchiopods eggs and other invertebrates (Baujard & Martiny, 1994; Cáceres & Soluk, 2002; Graham & Wirth, 2008 and literature therein). As already reported for phytoplankton, the effectiveness of the dispersal of these animals seems to be linked to the distance among sites. Jenkins & Underwood (1998) found that only a few bdelloid rotifers could be dispersed by wind when ponds were located 80 km apart. Conversely, Champeau & Thiery (1990) suggested a transport of crustacean eggs by Saharan winds across the Mediterranean Sea. They hypothesized a South-North gradient in the species distribution as a consequence of the different fallout rates of the resting stages because of their size (mass). Eggs of about 600 μm (like those of the notostracan *Triops* sp.) might reach Sicily and Balearic Islands from the Maghreb, while smaller ones (≈100 μm), such as those of calanoid copepods, might be transported further north and reach central Italy, Corsica and southern France. However, this hypothesis is not supported by a meta-analysis aimed at investigating the role of the size of the dispersing stages in determining the achievable dispersal distances in active and passive disperser:

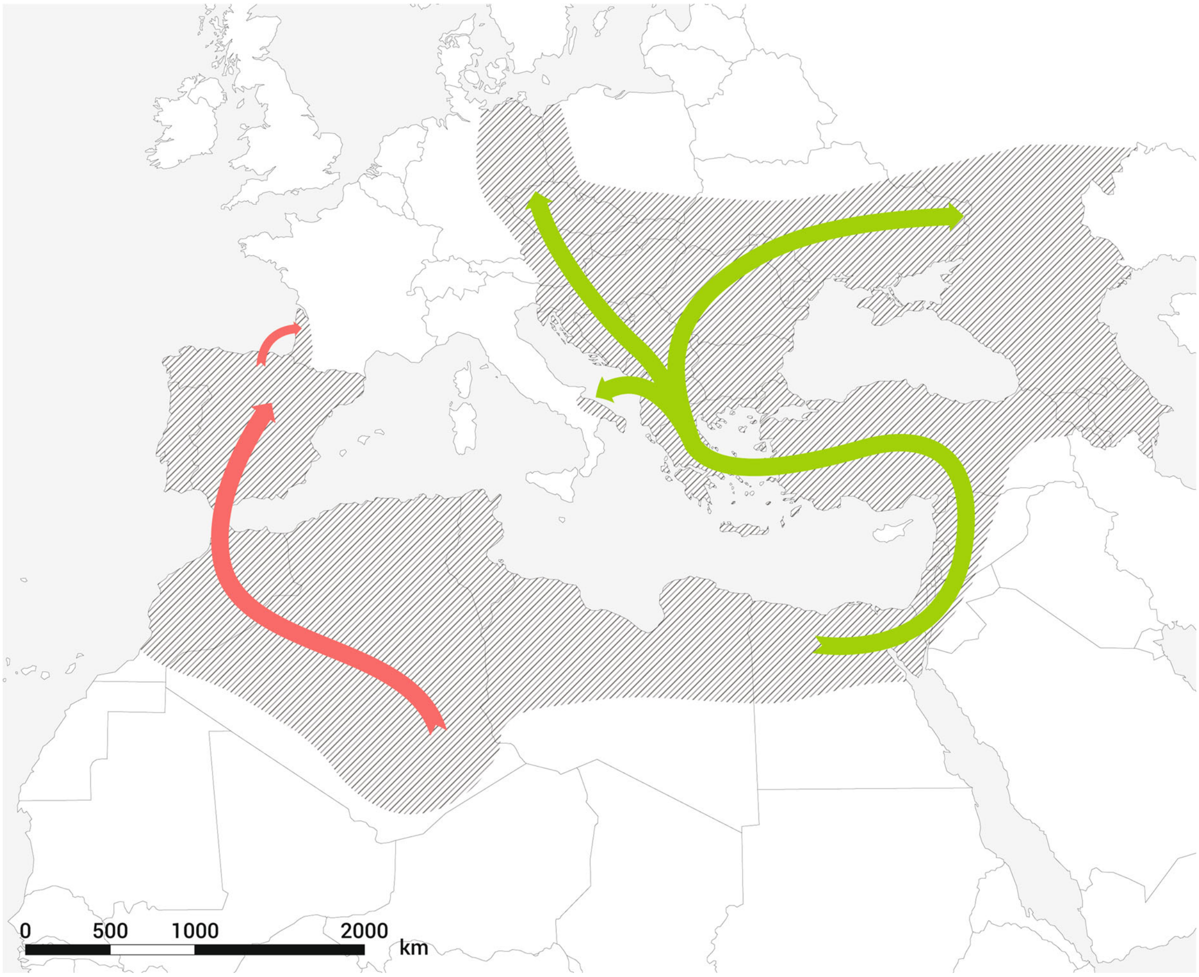


Fig. 4 Combined distribution pattern of the calanoid copepod *Neolovenula alluaudi* and of the anostracan branchiopod *Streptocephalus torvicornis* (for more details see the text). Both physical (wind) and biological (migrating birds) vectors are likely involved in determining this pattern. The arrow from Spain to French Aquitaine was added on the basis of the results by Cellamare et al. (2010)

according to Jenkins et al. (2007), passively dispersed propagules are less efficient on long distance than active disperser, and their dispersal distances do not depend on the propagule mass.

However, as shown by Alfonso & Belmonte (2013) for *Neolovenula alluaudi*, actual dispersal is likely due to mechanisms other than wind; this is in agreement with the biogeographical patterns of the anostracan *Streptocephalus torvicornis* pointed out by Dumont et al. (1995). These two crustacean species have a "pincers-like" distribution in the Mediterranean area (Fig. 4); they are both widely distributed in the Maghreb and in Spain (but without passing the Pyrenees barrier) from the West side and in the Middle East and Balkan Peninsula up to the Pannonian plain from the East. In Italy, both these species are present in Apulia (likely having arrived from the nearby Balkan Peninsula) but not in Sicily or in the rest of Peninsular Italy; this limits the hypothesis of a South–North dispersal primarily driven by wind (or by migratory birds: see next chapter) across the central Mediterranean Basin as further supported by the absence in Sicily of several inland water crustacean taxa able of passive dispersal and which are widespread in northern Tunisia (Marrone et al., 2009).

Overflows after heavy rain were demonstrated to be effective in mediating propagule dispersal among rock pool metacommunities (Vanschoenwinkel et al., 2008a; Meier & Soininen, 2014) and dispersal by surface waters (hydrochory) like that occurring in floodplains or during the rice-fields inundation (e.g. Frisch et al., 2005; Akasaka & Takamura, 2012; Van Leeuwen et al., 2013, and references therein) can also be important. However, this mechanism is not treated here in detail because its action is quite obvious.

Dispersal by biological vectors

A variety of animals has been described as dispersal vector of a wide array of freshwater organisms through a process called zoochory. The list of these vectors should include also humans but, because of the peculiar way in which humans may act as dispersal agents, their role will be examined in a dedicated subchapter.

The role of waterbirds as dispersal vehicles for resting stages among freshwater sites has been documented in several arid zones (e.g. Figuerola & Green, 2002; Green et al., 2008 and literature therein). Temporary ponds are often the preferred stopover for aquatic birds (Grillas et al., 2004), which thus may easily transport resting stages contained in the soil stuck in their feet and feathers (“epizoochory”). In addition, resting stages may pass undamaged through their digestive systems (“endozoochory”). It has been demonstrated that the dispersal operated by waterbirds can have an important historical role on the current phylogeography of crustacean species (see Muñoz et al., 2013 and literature therein). Seasonally migrating birds can in fact contribute to long-distance dispersal facilitating the colonization of aquatic environments as they become available along their migratory routes.

As shown in a series of papers by Brochet et al. (2009, 2010a, b, c), endozoochory can be more effective than epizoochory in favouring the dispersal of plant seeds, *Chara* spp. oogonia, as well as eggs of branchiopods and ostracods, and bryozoans’ statoblasts. Moreover, according to Rogers (2014), avian-mediated endozoochory might even enhance the fraction of resting stages which actually hatch once they are released in a new water body. Conversely, a study aimed at assessing the dispersal of freshwater taxa among Mediterranean temporary ponds through epizoochory and endozoochory on\in wild boars (Vanschoenwinkel et al., 2008c) showed that, since these environments are frequently used for mud bathing by these mammals, a larger number of hatching taxa was recorded in the mud coming from the skin rather than from the faeces, thus suggesting that over short distances epizoochory transport can be more effective than endozoochory. The potential role of large vertebrates as dispersal vectors was also investigated by Allen (2007) who studied adult zooplankton dispersal and found that it was more successful (and colonization occurred) in mesocosms which were open to large vertebrates like deer or raccoons. Short-distance dispersal can be favoured by several other vertebrates such as cattle, rats, rabbits, amphibians and fish (e.g. Zedler & Black, 1992; Bohonak & Whiteman, 1999; Beladjal et al., 2007; Van Leeuwen et al., 2013 and literature therein) as well as by invertebrates (Duthie, 1929); in particular, crayfish (Pérez-Bote et al., 2005) and flying insects (van de Meutter et al., 2008; Beladjal & Mertens, 2009) are documented vectors for the dispersal of resting stages and seeds among temporary waters, and water mites are known to be phoretic on insect larvae and adults (Di Sabatino et al., 2004; Bohonak et al., 2004).

Dispersal by human activities

The role exerted by human activities (i.e. “antropochory”) as dispersers of freshwater organisms cannot be neglected worldwide. As an example, the seasonal movements of livestock (transhumance) traditionally occurring since centuries in many Mediterranean countries may have played an important role in the dispersal of aquatic organism in this area even though few existing studies on this topic are dealing with terrestrial plants and animals (e.g. Fischer et al., 1996; Auffret et al., 2012). Moreover, pastoral activity all around the world is not the only human-driven activity which may enhance organism dispersal. As pointed out by Foissner (2006), species distribution changes due to human activities are largely ignored in the discussion of distribution of (micro)organisms. Since the “agriculture revolution”, which took place in the Middle East and along the eastern coast of the Mediterranean Sea (in the so-called “Fertile Crescent”—see Diamond, 1997) about 8,500 years BC, the construction of canals for agriculture and trading of goods and food have gradually moved millions of tons of soil and water and likely contributed to the actual distribution of several species inhabiting freshwater ecosystems in this area as well as in other part of the world. What Old Romans called "Mare Nostrum" was crossed by several trade routes and people living on its shores have been sailing across it since at least 5,000 years, founding settlements and actively transporting goods (and drinking water) all around the lands surrounding this sea (Abulafia, 2011). Further to historical reasons, other more recent human activities still contribute to freshwater organisms dispersal: construction of canals connecting separated watersheds (Dumont, 1995), recreational boating (Albrecht et al., 2009; Bruckerhoff et al., 2014), trade in ornamental species for aquaria (Padilla & Williams, 2004; Marrone & Naselli-Flores, 2011; Marrone et al., 2011; Havel et al., 2014), and ecotourism and/or scientific field-work (Waterkeyn et al., 2010) have been found to be responsible of dispersal and new species (even invasive) introductions. Trading of living fish for sport and professional fishing can be also responsible for the accidental introductions of (micro)organisms and a huge number of nonindigenous species are reported as "invaders" in freshwater ecosystems at a high frequency (Ruiz & Carlton, 2003; Alfonso & Belmonte, 2010; Havens & Beaver, 2014). Two calanoid copepods of Eastern origin, *Boeckella triarticulata* and *Neodiaptomus schmackeri*, were recently recorded in the Mediterranean area and their presence has been related to fish farming (Ferrari & Rossetti, 2006; Alfonso & Belmonte, 2008; Alfonso et al., 2014). Further examples of accidental introductions are those of *Pediastrum biwae*, an endemic microalga of Lake Biwa (Japan), now a well-established species in the phytoplankton assemblage of Lake Arancio, Sicily (Naselli-Flores & Barone, 2005), and *Isoëtes malinverniana,* a quillwort known from the Piedmont region of north-western Italy which is considered a species of Asian origin, transported along with rice seed to Italian rice fields (Hoot et al., 2006; but contrasting results can be found in Gentili et al., 2010). In addition to uncontrolled and accidental spread of species, as that of the anostracan *Artemia franciscana* commonly used as fish food in aquaculture (e.g. Lavens & Sorgeloos, 1996; Amat et al., 2007), deliberate introductions to support human activities may occur (e.g. Tackaert & Sorgeloos, 1993; Su & Mulla, 2002) and this may influence the natural biogeographical range of organisms (Muñoz et al., 2013). Moreover, it has been demonstrated that the introduction of exotic species reduces regional biodiversity by promoting pond assemblage homogenization and contributing to the extinction of indigenous, even endemic, species (e.g. Florencio et al., 2013).

Human-induced climate change has also been regarded as modifying the distribution ranges of several species, and the warmer climate may explain the colonization success of many tropical and subtropical species of microalgae as reported in the last decades in the continental waters of Europe (e.g. Cellamare et al., 2010 and literature therein).

What enhances or inhibits colonization processes?

Colonization of a new habitat by a propagule is a two-step process which includes the actual existence of a dispersal event, and the successful establishment in the new habitat of the dispersed propagules. Since quantifying dispersal can be a difficult task, colonization rates (i.e. the arrival and successful establishment of new species per time interval) are generally used as a proxy (e.g. Cáceres & Soluk, 2002; Bohonak & Jenkins, 2003; Cohen & Shurin, 2003). As pointed out by Riccardi & Rossetti (2007), colonization rates underestimate dispersal since several failed attempts may occur for every successful one colonization event (Williamson, 1996).

Several factors might influence each of these two steps of the colonization, both with inhibitory and facilitating effects on the process.

Resting stage characteristics, size, number and ornamentation

Freshwater organisms are generally considered more successful long-distance passive disperser than terrestrial ones (Kappes et al., 2014). Although the dispersal of adult snails and ostracods, or plant fragments (Karanovic, 2012; Havel et al., 2014; Bruckerhoff et al., 2014) can be related to their relatively high resistance to desiccation and UV radiation (e.g. Van den Broecke et al., 2012), or, as regard nematodes, to their ability to undergo anhydrobiosis (Ptatscheck & Traunspurger, 2014), resting stages are the main dispersal propagules for several organisms in temporary ponds (Rundle et al., 2002). Moreover, although several organisms inhabiting permanent waters produce resting stages and can be found in temporary waters, the opposite seldom occurs since ecological interactions (e.g. fish predation) can prevent many peculiar inhabitants of temporary ponds like large branchiopods from colonizing permanent waters (Dumont & Negrea, 2002).

Resting stages can be viable for years or decennia (e.g. Hairston et al., 1995; Straka, 2004), and able to survive pronounced environmental stresses (Wells et al., 1997; Dai et al., 2011). Along with viability, the number of resting stages (both considering the reproductive potential of single individuals and of populations) has been found to have a role in promoting a successful dispersal, since larger inocula have a higher probability to successfully colonize a new environment (e.g. Drake et al., 2005 and literature therein). In addition, their ability to sink, to float or to remain attached to plants or sediment particles (Brendonck & De Meester, 2003; Van Damme & Sinev, 2013) actually contribute to determine the dispersal vector(s) and thus the range of dispersal.

Even morphologies and ornamentations likely have a role in promoting resting stage dispersal. Protist cysts are supposed to lack morphological adaptations for air dispersal (Foissner, 2008). Conversely, the seeds of flowering plants show morphologies that have often been considered favouring dispersal, even though Higgins et al. (2003) found that the relationship between morphologically defined dispersal syndrome and long-distance dispersal is quite poor. Moreover, no information exists on the reasons underlying the striking morphological convergence, both as regard ornamentation and size, which can be observed in the eggs and megaspores produced by phylogenetically unrelated inland water organisms such as anostracan crustaceans and quillworts (Fig. 5), and which could have a role in the passive dispersal of these organisms (e.g. Thiéry & Gasc, 1991; Mura, 2001; Samchyshyna & Santer, 2010; Bagella et al., 2011). Conversely, some information is available in the marine realm, e.g. Belmonte et al. (1997) suggest that the widespread spiny covering of resting stages in the marine zooplankton might be the result of a convergent evolution aimed at favouring flotation and at granting a passive defence against predators and abiotic adversities.

To date, factors shaping the external layer of resting stages and their ornamentation in inland water crustaceans are largely unknown (Frey, 1982a; Thiéry et al., 2007; Bruner et al., 2013) even though Dumont et al. (2002) tentatively explained it as a possible mechanism to decrease predation.

Environmental filters

The analysis of colonization rates may offer useful insights to investigate what can hamper the dispersal potential. Once a new potential colonizer reaches a new habitat, it has to pass through sequential “filters” in the colonization sequence (e.g. Williamson & Fitter, 1996; Muirhead & MacIsaac, 2005) before becoming successfully established. The strength of these filters encompasses local factors depending on the (i) biological features of the species that is colonizing the habitat; (ii) its tolerance range to local physical and chemical conditions (Soininen et al., 2013; Florencio et al., 2014); (iii) the morphological features of the water body (e.g. water surface, depth) to be colonized and its hydroperiod length, and (iv) the structure of the receiving community (see next subchapter). However, also regional factors related to altitude distribution of water bodies (Catalán et al., 2009; Wang et al., 2012), as well as the spatial distance among water bodies, and thus their isolation and density in a given territory, may act as important filters (Soininen et al., 2007; Ripley & Simovich, 2009 and literature therein) influencing colonization success.

By studying zooplankton colonization rates and spatial patterns in a large-scale experimental system of ponds in the Doñana National Park (Southern Spain), Frisch et al. (2012) found that, in accordance to the theory of island biogeography (MacArthur & Wilson, 1967), connectivity, spatial distance among ponds and surface area of the studied water bodies (target-area effect: larger surfaces are better receivers of inocula, see Lomolino, 1990) were key determinants of colonization rates for crustacean zooplankton. Conversely, in a study carried out in a network of temporary ponds, Eitam et al. (2004) found that crustacean species richness was positively related to hydroperiod length but not to surface area. This result could be explained by the assumption that increased isolation of ponds due to the progressive disappearing of the aquatic habitat during the dry phase, as it may occur in a network of temporary ponds with different hydroperiods, can limit local immigration and unbalance the immigration/extinction patterns generating nested patterns of ponds with species-poor sites containing a subset of species-rich sites (Florencio

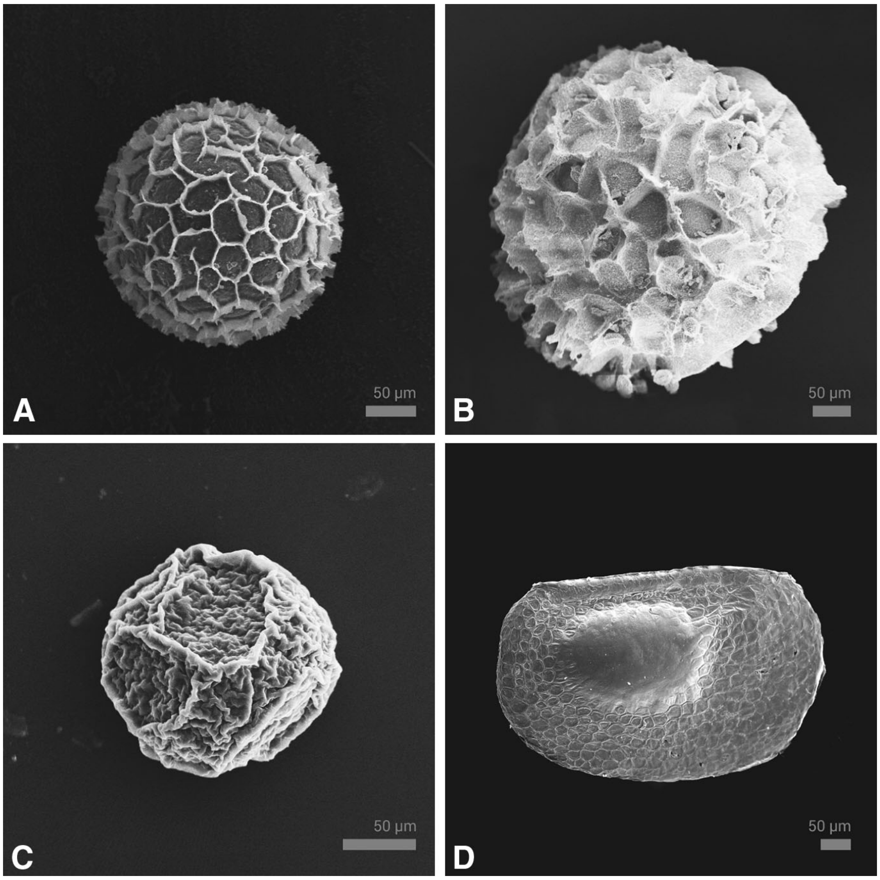


Fig. 5 Resting stages morphological convergence. Resting egg of the anostracan branchiopod *Chirocephalus* cf. *diaphanus*. (**A**); megaspore of the quillwort *Isoëtes* sp. (**B**); resting egg of the calanoid copepod *Hemidiaptomus gurneyi* (**C**) and ephippium of the anomopod branchiopod *Moina diksamensis* (modified from Van Damme & Dumont, 2008) (**D**)

et al., 2011). The degree of nestedness thus quantifies the overlap in species composition between high and low diversity areas (McAbendroth et al., 2005). Conversely, Frisch et al. (2006) suggest that ponds with a hydroperiod of intermediate length host a higher species richness than those characterized by longer or shorter hydroperiods.

As observed by Ebert & Balko (1987) and Florencio et al. (2011), isolation in time, as resulting from the different length of hydroperiod among the ponds of a network, can give similar patterns to those observed when it occurs in space, further confirming that both pond density and hydroperiod length in a given area are important in determining the colonization chances (Ruhí et al., 2013).

Species dispersal on short distance minimizes the fragmentation of metacommunities as caused by the reduction in geographical pond density (Florencio et al., 2014). As suggested by Allen (2007), this reduction might lead to stronger priority effects (see next subchapter), higher levels of inbreeding and selection against traits favouring high dispersability. Miracle (1982) and Sahuquillo & Miracle (2013), in order to explain the distribution of some peculiar crustacean assemblages in the ponds of the Iberian Peninsula, hypothesized the existence of a former and ancient network of wetlands which allowed the presence of highly diversified crustaceans assemblages. Climate changes and human activities occurring during the Holocene may have caused a reduction in the number of suitable habitats for these assemblages, which nowadays represent a relic remnant surviving in a few isolated ponds.

In recent years, anthropogenic impacts (including global change) have reduced the number of ponds worldwide (Williams, 2002). In the Mediterranean area, as an example, temporary ponds are presently disappearing at a very fast rate (Cancela da Fonseca et al., 2008; Naselli-Flores & Barone, 2012). Their deliberate destruction, along with the loss of pastoral activities, contributes to a growing isolation of the relic ponds which hinders dispersal among sites,

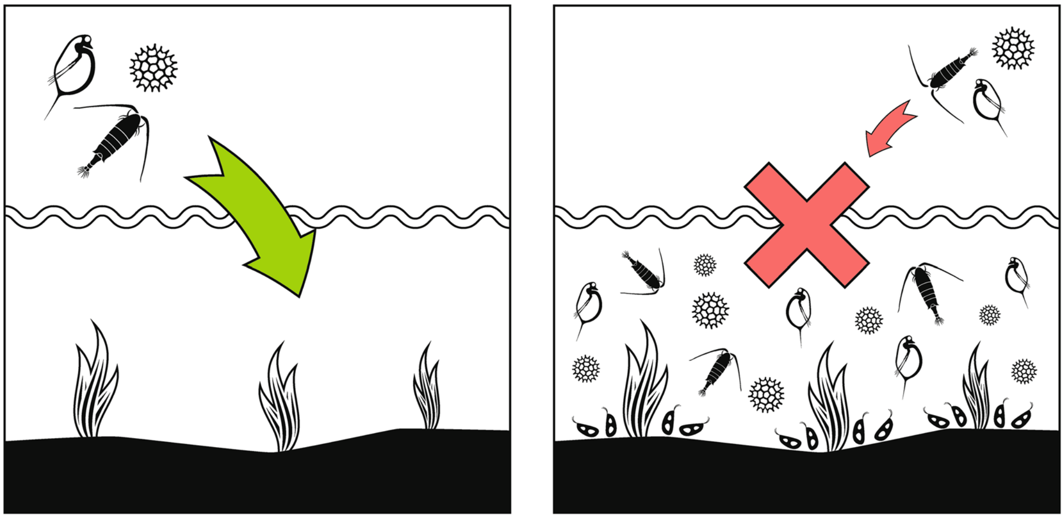


Fig. 6 Sketch illustrating the effectiveness of biological filters in the colonization processes (priority effects). Disperser reaching a newly created habitat without an already established community (*left panel*) can more easily colonize it compared to those reaching an "old" one with an already well-structured community (*right panel*)

increases metacommunity fragmentation and leads to a higher risk of local (and global) extinctions (Miyazono & Taylor, 2013).

Biological filters and reproductive strategies

The diversity and composition of the resident species pool has been generally recognized as an important factor determining the colonization success of later immigrants (e.g. Case, 1990; Tilman, 1997; Levine, 2000; Louette et al., 2006). Species-poor communities are generally linked to recently formed water bodies (see Alfonso et al., 2010), or to particular environmental conditions selecting for a reduced pool of "stress-adapted" species (Naselli-Flores et al., 2003). Species-rich communities show stronger and more complex biotic interactions that can impair the colonization success of new immigrants (Shurin, 2000; Cadotte et al., 2006). Moreover, immigrants can undergo Allee effects (Sarnelle & Knapp, 2004) which would further slow down their population growth rates.

Biological interactions, e.g. predation, competition and allelopathy, are frequently reported as strong filters contributing to make difficult the establishment of new immigrants (e.g. Eitam et al., 2004; Uronen et al., 2007; Yawata et al., 2014); these interactions historically determine the composition of a community and strengthen the relationships existing among its members during time. Altogether they are named as "priority effects" (i.e. species or lineages already present in a community affect the establishment of later arriving immigrants) (Fig. 6) and are often considered as powerful inhibitors of colonization success (Shurin, 2000; Allen, 2007; Louette & De Meester, 2007; Symons & Arnott, 2014). In some conditions, however, as those occurring in autogenic succession, priority effects may have a facilitative role when a species arriving earlier at a site alters the biotic and abiotic characteristics in a way that enhance the colonization chances of a species arriving later (Connell & Slatyer, 1977).

As suggested by Hoverman & Relyea (2008), the phenotypic plasticity frequently observed in freshwater organisms can be an important driver behind priority effects. Phenotypic plasticity can be due to historical exposure to predators, as in the case of the potential for inducible defence expressed when predators are present (e.g. Petrusek et al., 2009). The seasonal cyclomorphosis in rotifers and cladocerans (Dodson, 1989) or the production of spines in phytoplankton (Van Donk et al., 2011) is commonly observed effect of inducible defences. Predators thus (i) select those organisms which have defensive phenotypes and (ii) alter their traits in different environments (Werner & Peacor, 2003), therefore decreasing the colonization success of those organisms with phenotypes more susceptible to predation

(Covich, 2010). Phenotypic plasticity is also an adaptive response to resource limitation in highly variable environments as temporary ponds (Naselli-Flores & Barone, 2011) and thus the degree of morphological plasticity of the species historically present in a given environment can be regarded as an adaptive tool, which improves species fitness and enhances priority effects against new colonizers with different phenotypes.

Competition (or its absence) can determine the presence and distribution of organisms in a given area. As an example, the calanoid copepod *Copidodiaptomus numidicus* is commonly found in temporary waters in Tunisia (Turki & El Abed, 1999), while in Sicily it only occurs in permanent, recently built reservoirs (Calvo et al., 1993). The lack of this taxon in Sicilian temporary waters has been attributed to the presence of already existing species-rich and well-structured calanoid copepod assemblages which effectively hinder its settling in these environments (Marrone et al., 2006a, b). Similarly, Alfonso et al. (2010) suggested that the differences observed between the zooplankton assemblages of lakes and reservoirs in Southern Italy and Sicily are to be ascribed to the absence of pure lacustrine taxa in Sicily. This absence, due to the lacking of natural lakes in the island which might serve as source habitats for the colonization of man-made reservoirs, allows typical littoral or pond crustacean species to colonize a sub-optimal habitat (i.e. the pelagic zone of large reservoirs), where they are usually outcompeted by the more specialized lacustrine taxa.

Reproductive strategies used by different taxa might influence their dispersal and colonization rates. The first, more evident, effect is related to the actual chance of a given propagule which reaches a new habitat to establish a vital population. A taxon which is able to reproduce asexually or parthenogenetically can successfully establish a population even when a single specimen reaches a new water body. Conversely, for those organisms with obligate sexual reproduction, colonization requires the dispersal of a mated female or, less realistically, the synchronic dispersal of one male and one female which have to reach the sexual maturity contemporarily, and to meet in the new environment. Furthermore, non-gonochoric populations have a higher intrinsic potential for demographic growth when compared to the sexual ones as each member of the population is able to produce offspring versus the "female" individual only in the sexual populations.

The combination of (i) the costs (and uncertainties) related with the search of the partner and (ii) the slower demographic increase in the sexual organisms, which is known as the "twofold cost of sex" (Maynard Smith, 1978; Schön et al., 2009), gives an advantage to non-gonochoric taxa or strains over gonochoric ones, which present lower dispersal and colonization abilities. The higher colonizing abilities of non-gonochoric taxa or lineages is empirically confirmed by two independent lines of evidences: (i) artificial (thus recently built) habitats do much more often host asexual taxa or lineages than sexual ones, and (ii) the asexual/parthenogenetic lineages coming from southern refugia proved to be much more efficient than their sexual counterparts in colonizing the newly available waterbodies in deglaciated Europe (e.g. Korn et al., 2006; Muñoz et al., 2008; Schmit et al., 2013), leading to a scenario of "geographical parthenogenesis" (see Horne & Martens, 1998; Haag & Ebert, 2004). On the other hand, there are some evidences that sexual populations are competitively superior to the asexual\parthenogenetic ones in the more ecologically variable habitats, thus allowing them not to be completely outcompeted by the non-gonochoric strains (e.g. Schmit et al., 2013; Park et al., 2014).

Genetic evidences about dispersal and colonization

The "EiE" hypothesis and the "Cosmopolitanism paradigm" were based on the finding of apparently identical organisms in different continents, e.g. the vast majority of Cladocera were till recently considered cosmopolitan or subcosmopolitan taxa (e.g. Smirnov & Timms, 1983; Margaritora, 1985; Araya & Zuñiga, 1985; Seaman et al., 1999; Flössner, 2000), so that investigating their biogeography was considered impossible or worthless (Fontaneto & Brodie, 2011). However, upon more detailed morphological studies, some evidences began to pop up about the presence of overlooked morphological characters which in fact allow to distinguish among complexes of closely related and allopatric taxa (e.g. Frey, 1982b, 1986, 1995; Reid, 1997). Afterwards, with the advent and spreading of molecular techniques, an ever increasing amount of evidences showed that as a rule, in clear antithesis with the "Cosmopolitan paradigm", inland water organisms belong to a high number of different species, and that these are characterized by a noteworthy degree of endemism (e.g. Korn et al., 2006; Belyaeva & Taylor, 2009; Bode et al., 2010; Komárek & Mareš, 2012; Krienitz & Bock, 2012; Marrone et al., 2013, and references therein). The taxa belonging to these species complex are sometimes hard or impossible to be told apart based on morphology (e.g. Fontaneto et al., 2007; Packer et al., 2009), while sometimes they prove to be in fact distinguishable based on morphological micro-characters which were previously neglected (e.g. Korn et al., 2010). Nowadays, a large consensus is achieved on the fact that the cosmopolitanism paradigm has to give way to the evidences of pronounced "regionalism" or "provincialism" which emerged in almost all the investigated taxa (e.g. De Gelas & De Meester, 2005; Xu et al., 2009; Crease et al., 2012).

At a within-species level, quite a low ongoing gene flow between conspecific populations is usually observed (Boileau et al., 1992), which contributes to the presence of marked phylogeographic structures in the vast majority of inland water taxa (e.g. Gómez et al., 2000; De Gelas & De Meester, 2005; Muñoz et al., 2008; Marrone et al., 2013). Actual genetic connectivity seems to be, as a rule, scarce to absent even among nearby conspecific populations (De Meester, 1996; Meglécz & Thiéry, 2005, Ketmaier et al., 2003, 2012, but see also Aguilar, 2011), or it is not possible to single out a coherent geographic pattern in the distribution of the genetic lineages (e.g. McCafferty et al., 2010), although a few exceptions are known (Schwentner et al., 2012).

The evidences of a sharp regionalism and of a noteworthy molecular structuring of even proximate populations suggest the absence of a dispersal-mediated extensive gene flow among them: when this issue was explicitly tested, it resulted that no measurable gene flow occurred among populations of a temporary-pond-dwelling anostracan for distance greater than a few tens of kilometres (Ketmaier et al., 2012). The apparent conflict based on the empirical evidences of the absence of a significant gene flow among geographically close and conspecific populations of organisms which have the potential for long-range passive dispersal is known as the "dispersal – gene flow paradox" (De Meester et al., 2002).

Boileau et al. (1992) were among the first authors who stressed the importance of the "persistent founder effect" in shaping the distribution patterns of molecular diversity in pond-dwelling organisms; according to them, the first lineages which colonize a newly available habitat rapidly constitute very large populations and egg banks in the sediments, that might require an extremely long time to be interested by genetic erosion. The rapid establishment of very large populations saturates the habitat to its carrying capacity in few generations and actually prevents other conspecific lineages to successfully establish in the site through diluting the contribute of invading haplotypes in the resident population. Furthermore, due to wallowing activities of large animals, pond substrate where resting stages are laid might be turned over, allowing the hatching of the viable resting stages produced long time before (even decennia or centuries, cf. Hairston & Kearns, 2002, and literature therein) and until then buried in the sediments. This buffering phenomenon stabilizes the genetic structure of local populations, and hinders the successful establishment of new immigrant genotypes (Rogers, 2014).

Such a neutral "dilution" effect on the invading lineages is a priority effect and it is further reinforced by the rapid establishment of local adaptations in the resident populations. This selective process gives to the residents a competitive advantage on the newcomers, which reduces the impact of the new migrant lineages. Although local adaptations might have a primary role in shaping the geographical pattern of genetic diversity in pond-dwelling organisms, this aspect was overlooked for a long time. Only recently the importance of the "isolation by adaptation" in shaping the geographical distribution of genetic diversity has been adequately stressed, when approaches to the detection of the relative importance of "isolation by adaptation" and "isolation by dispersal limitation" were described (Orsini et al., 2013).

The combination of the two processes (i.e. a neutral dilution effect due to the priority effects and a selective effect due to the establishment of local adaptations in the resident lineages) was described as the "Monopolization Hypothesis" (De Meester et al., 2002), and it currently constitutes a cornerstone in the interpretation of the distribution of the genetic diversity in freshwater organisms.

This way, due to the additive effects of "priority effects" and "local adaptations", in spite of the actual existence of an ongoing and effective short- and long-range dispersal of freshwater organisms, the current pattern of genetic diversity for these organisms does much more mirror the historical events of colonization rather than the actual existence of a contemporary gene flow (cfr. Orsini et al., 2013; Ventura et al., 2014). In fact, during the very first years after the first colonization of a new habitat, it is actually still possible for immigrant conspecific specimens to establish themselves, possibly taking advantage of the "outbreeding vigour", however, priority effects become soon fully operational, thus hindering or halting the establishment of alien lineages and sustaining the genetic differentiation of the local population from those inhabiting nearby water bodies (Ortells et al., 2014 and references therein).

The accumulation of largely consistent genetic evidences shows that in spite of the existence of a significant realized short- to long-range dispersal for organisms producing resting eggs, their dispersal is actually followed by a local establishment of migrating genetic lineages only when they reach sites where no conspecific lineages are already established (cfr. De Meester et al., 2002; Orsini et al., 2013; Ventura et al., 2014) or during the very first few years after the first colonization of the site, i.e. before the combination of priority effect and local adaptations grants the local population an insurmountable resistance and resilience against newcomers (Ortells et al., 2014).

Final remarks

Although a general consensus on the relative importance of different physical and biological vectors has not to date been achieved, sound evidences are available on the actual ability of inland water organisms for long- and short-range passive dispersal, with obvious idiosyncrasies linked to each taxon, habitat typology, and landscape characteristics of the different case studies. In good accordance with the early observations carried out in the XVIII and XIX centuries, it is now demonstrated that the combination of both physical and biological vectors is actively influencing dispersal of freshwater taxa from an "aquatic island" to another across unfavourable habitats like both "terrestrial" and "marine" oceans. However, the progresses achieved in the last decades in taxonomy and genetic studies, and their careful integration, have first highlighted the existence of an apparent "dispersal – gene flow paradox". A clearer distinction between the "dispersal" and the "actual establishment" steps in the processes of colonization by organisms producing resting stages allowed to overcome the paradox. This distinction was achieved through the identification of the effects and processes which might condition the realization of a significant gene flow among conspecific populations.

In spite of the high potential for passive dispersal, current inland water communities are now considered outcomes of both ancient historical processes and ongoing local adaptations. Furthermore, they host well-diversified (and often private) taxa and lineages even at a small geographical scale. This highlights the need for a careful protection and management of the relic habitats and biota, which are the result of an extremely long history of independent evolution.

In the light of the current status of knowledge, the theoretical scenario depicted by the EiE hypothesis, and its implications in conservation and biogeography, has thus to be definitively forsaken. Moreover, the development of modern and effective conservation management strategies needs further in-depth investigations on the geographical distribution of genetic diversity and on the historical and current relationships among different populations and biota.

Acknowledgements Cristiano Liuzzi (R.N.S. "Le Cesine", Italy) and Kay Van Damme (University of Birmingham, UK) are gratefully acknowledged for having provided some pictures. We are also grateful to three anonymous reviewers who provided valuable suggestions to an early draft of this paper. This review has been assembled with the contribution of a grant (2012-ATE-0148) from the University of Palermo.

References

Abulafia, D., 2011. The Great Sea: A Human History of the Mediterranean. Oxford University Press, Oxford.

Aguilar, A., 2011. Weak phylogeographic structure in the western North American fairy shrimp *Branchinecta lynchi* (Eng, Belk, & Erickson 1996). Aquatic Sciences 73: 15–20.

Akasaka, M. & N. Takamura, 2012. Hydrologic connection between ponds positively affects macrophyte α and γ diversity but negatively affects β diversity. Ecology 93: 967–973.

Albrecht, C., O. Kroll, E. Terrazas & T. Wilke, 2009. Invasion of ancient Lake Titicaca by the globally invasive *Physa acuta* (Gastropoda: Pulmonata: Hygrophila). Biological Invasions 11: 1821–1826.

Alfonso, G. & G. Belmonte, 2008. Expanding distribution of *Boeckella triarticulata* (Thomson, 1883) (Copepoda: Calanoida: Centropagidae) in Southern Italy. Aquatic Invasions 3: 247–251.

Alfonso, G. & G. Belmonte, 2010. *Neoergasilus japonicus* (Harada, 1930): a new non-indigenous copepod for the Italian fauna. Italian Journal of Zoology 77: 172–178.

Alfonso, G. & G. Belmonte, 2013. *Neolovenula alluaudi* (Guerne & Richard, 1890) (Calanoida: Diaptomidae: Paradiaptominae): first record in Italy and review of geographical distribution. Journal of Limnology 72: 251–261.

Alfonso, G., G. Belmonte, F. Marrone & L. Naselli-Flores, 2010. Does lake age affect zooplankton diversity in Mediterranean lakes and reservoirs? A case study from southern Italy. Hydrobiologia 653: 149–164.

Alfonso, G., R. Russo & G. Belmonte, 2014. First record of the Asian diaptomid *Neodiaptomus schmackeri* (Poppe & Richard, 1892) (Crustacea: Copepoda: Calanoida) in Europe. Journal of Limnology 73: 584–592.

Allen, M. R., 2007. Measuring and modelling dispersal of adult zooplankton. Oecologia 153: 135–143.

Amat, F., F. Hontoria, J. C. Navarro, N. Vieira & G. Mura, 2007. Biodiversity loss in the genus *Artemia* in the Western Mediterranean Region. Limnetica 26: 387–404.

Araya, J. M. & L. R. Zuňiga, 1985. Manual taxonomico del zooplankton lacustre de Chile. Boletin Informativo Limnologico 8: 1–110.

Audet, C., S. MacPhee & W. Keller, 2013. Constructed ponds colonized by crustacean zooplankton: local and regional influences. Journal of Limnology 72: 524–530.

Auffret, A. G., R. Schmucki, J. Reimark & S. A. O. Cousins, 2012. Grazing networks provide useful functional connectivity for plants in fragmented systems. Journal of Vegetation Science 23: 970–977.

Avise, J. C., J. Arnold, R. M. Ball, E. Bermingham, T. Lamb, J. E. Neigel, C. A. Reeb & N. C. Saunders, 1987. Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Annual Review of Ecology and Systematics 18: 489–522.

Bagella, S., M. C. Caria, A. Molins & J. A. Rosselló, 2011. Different spore structures in sympatric *Isoetes hystrix* populations and their relationship with gross morphology, chromosome number, and ribosomal nuclear ITS sequences. Flora 206: 451–457.

Baujard, P. & B. Martiny, 1994. Transport of nematodes by wind in the peanut cropping area of Senegal, West Africa. Fundamental and Applied Nematology 17: 543–550.

Beladjal, L. & J. Mertens, 2009. Diaspore dispersal of Anostraca by flying insects. Journal of Crustacean Biology 29: 266–268.

Beladjal, L., K. Dierckens & J. Mertens, 2007. Dispersal of fairy shrimp *Chirocephalus diaphanus* (Branchiopoda: Anostraca) by the trout (*Salmo trutta*). Journal of Crustacean Biology 27: 71–73.

Belmonte, G., A. Miglietta, F. Rubino & F. Boero, 1997. Morphological convergence of resting stages of planktonic organisms: a review. Hydrobiologia 355: 159–165.

Belyaeva, M. & D. J. Taylor, 2009. Cryptic species within the *Chydorus sphaericus* species complex (Crustacea: Cladocera) revealed by molecular markers and sexual stage morphology. Molecular Phylogenetics and Evolution 50: 534–546.

Bilton, D. T., J. R. Freeland & B. Okamura, 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology, Evolution and Systematics 32: 159–181.

Bode, S. N. S., S. Adolfsson, D. K. Lamatsch, M. J. F. Martins, O. Schmit, J. Vandekerkhove, F. Mezquita, T. Namiotko, G. Rossetti, I. Schön, R. K. Butlin & K. Martens, 2010. Exceptional cryptic diversity and multiple origins of parthenogenesis in a freshwater ostracod. Molecular Phylogenetics and Evolution 54: 542–552.

Bohonak, A. J. & H. H. Whiteman, 1999. Dispersal of the fairy shrimp *Branchinecta coloradensis* (Anostraca): effects of hydroperiod and salamanders. Limnology and Oceanography 44: 487–493.

Bohonak, A. J. & D. G. Jenkins, 2003. Ecological and evolutionary significance of dispersal by freshwater invertebrates. Ecology Letters 6: 783–796.

Bohonak, A. J., B. P. Smith & M. Thornton, 2004. Distributional, morphological and genetic consequences of dispersal for temporary pond water mites. Freshwater Biology 49: 170–180.

Boileau, M. G., P. D. N. Hebert & S. S. Schwartz, 1992. Non-equilibrium gene frequency divergence: founder effects in natural populations. Journal of Evolutionary Biology 5: 25–39.

Brendonck, L. & L. De Meester, 2003. Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediments. Hydrobiologia 491: 65–84.

Brendonck, L., B. Riddoch, V. Van de Weghe & T. Van Dooren, 1998. The maintenance of egg banks in very short-lived pools—a case study with anostracans (Branchiopoda). In Brendonck, L., L. de Meester & N. Hairstonjr (eds), Evolutionary and Ecological Aspects of Crustacean Diapause, Vol. 52., Archiv für Hydrobiologie-Advances in Limnology: 141–161.

Brochet, A.-L., M. Guillemain, H. Fritz, M. Gauthier-Clerc & A. J. Green, 2009. The role of migratory ducks in the long-distance dispersal of native plants and the spread of exotic plants in Europe. Ecography 32: 919–938.

Brochet, A.-L., M. Guillemain, H. Fritz, M. Gauthier-Clerc & A. J. Green, 2010a. Endozoochory of Mediterranean aquatic plant seeds by teal after a period of desiccation: determinants of seed survival and influence of retention time on germinability and viability. Aquatic Botany 93: 99–106.

Brochet, A.-L., M. Gauthier-Clerc, M. Guillemain, H. Fritz, A. Waterkeyn, Á. Baltanás & A. J. Green, 2010b. Field evidence of dispersal of branchiopods, ostracods and bryozoans by teal (*Anas crecca*) in the Camargue (southern France). Hydrobiologia 637: 231–255.

Brochet, A.-L., M. Guillemain, H. Fritz, M. Gauthier-Clerc & A. J. Green, 2010c. Plant dispersal by teal (Anas crecca) in the Camargue: duck guts are more important than their feet. Freshwater Biology 55: 1262–1273.

Bruckerhoff, L., J. Havel & S. Knight, 2014. Survival of invasive aquatic plants after air exposure and implications for dispersal by recreational boats. Hydrobiologia. doi:10.1007/s10750-014-1947-9.

Bruner, E., D. Costantini & G. Mura, 2013. Fractal analysis of the egg shell ornamentation in anostracans cysts: a quantitative approach to the morphological variations in *Chirocephalus ruffoi*. Hydrobiologia 705: 1–8.

Cáceres, C. E. & D. A. Soluk, 2002. Blowing in the wind: a field test of overland dispersal and colonization by aquatic invertebrates. Oecologia 131: 402–408.

Cadotte, M. W., D. V. Mai, S. Jantz, M. D. Collins, M. Keele & J. A. Drake, 2006. On testing the competition-colonization trade-off in a multispecies assemblage. American Naturalist 168: 704–709.

Calvo, S., R. Barone, L. Naselli-Flores, C. Fradà-Orestano, G. Dongarrà, A. Lugaro & G. Genchi, 1993. Limnological studies on lakes and reservoirs of sicily. Naturalista siciliano 17(Suppl.).

Cancela da Fonseca, L., M. Cristo, M. Machado, J. Sala, J. Reis, R. Alcazar & P. Beja, 2008. Mediterranean temporary ponds in Southern Portugal: key faunal groups as management tools? Pan-American Journal of Aquatic Sciences 3: 304–320.

Case, T. J., 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences 87: 9610–9614.

Catalán, J., M. G. Barbieri, F. Bartumeus, P. Bitusík, I. Botev, A. Brancelj, D. Cogălniceanu, M. Manca, A. Marchetto, N. Ognjanova-Rumenova, S. Pla, M. Rieradevall, S. Sorvari, E. Štefková & E. Stuchlík, 2009. Ecological thresholds in European alpine lakes. Freshwater Biology 54: 2494–2517.

Cellamare, M., M. Leitão, M. Coste, A. Dutartre & J. Haury, 2010. Tropical phytoplankton taxa in Aquitaine lakes (France). Hydrobiologia 639: 129–145.

Céréghino, R., D. Boix, H.-M. Cauchie, K. Martens & B. Oertli, 2014. The ecological role of ponds in a changing world. Hydrobiologia 723: 1–6.

Champeau, A. & A. Thiery, 1990. Les Crustacés Entomostracés des eaux stagnantes de Corse. Importance particulière des espèces monovoltines méditerranéennes de Copépodes Calanoïdes et d'Anostracés dans le Sud-Est de l'île. Bulletin de la Société zoologique de France 115: 55–75.

Chrisostomou, A., M. Moustaka-Gouni, S. Sgardelis & T. Lanaras, 2009. Air-dispersed phytoplankton in a Mediterranean river-reservoir system (Aliakmon-Polyphytos, Greece). Journal of Plankton Research 31: 877–884.

Cohen, G. M. & J. B. Shurin, 2003. Scale-dependence and mechanisms of dispersal in freshwater zooplankton. Oikos 103: 603–617.

Collins, P. M., J. O. Kaplan & B. A. S. Davis, 2010. Could anthropogenic soil erosion have influenced Mediterranean vegetation distribution over the Holocene? IOP Conference Series: Earth and Environmental Sciences 9: 012011.

Connell, J. H. & R. O. Slatyer, 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119–1144.

Covich, A. P., 2010. Winning the biodiversity arms race among freshwater gastropods: competition and coexistence through shell variability and predator avoidance. Hydrobiologia 653: 191–215.

Crease, T. J., A. R. Omilian, K. S. Costanzo & D. J. Taylor, 2012. Transcontinental phylogeography of the *Daphnia pulex* species complex. PLoS One 7: e46620.

Dahms, H. U., 1995. Dormancy in the Copepoda: an overview. Hydrobiologia 306: 199–211.

Dai, L., D. F. Chen, Y. L. Liu, Y. Zhao, F. Yang, J. S. Yang & W. J. Yang, 2011. Extracellular matrix peptides of *Artemia* cyst shell participate in protecting encysted embryos from extreme environments. PLoS One 6: e20187.

Darwin, C. R., 1859. On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

De Bie, T., L. De Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, K. Van der Gucht, J. Van Wichelen, W. Vyverman & S. A. J. Declerck, 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15: 740–747.

De Gelas, K. & L. De Meester, 2005. Phylogeography of *Daphnia magna* in Europe. Molecular Ecology 14: 753–764.

De Meester, L., 1996. Local genetic differentiation and adaptation in freshwater zooplankton populations: patterns and processes. Ecoscience 3: 385–399.

De Meester, L., A. Gómez, B. Okamura & K. Schwenk, 2002. The monopolization hypothesis and the dispersal-gene flow paradox in aquatic organisms. Acta Oecologica 23: 121–135.

Di Sabatino, A., A. Boggero, F. P. Miccoli & B. Cicolani, 2004. Diversity, distribution and ecology of water mites (Acari: Hydrachnidia and Halacaridae) in high Alpine lakes (Central Alps, Italy). Experimental and Applied Acarology 34: 199–210.

Diamond, J., 1997. Guns, Germs, and Steel: The Fates of Human Societies. W.W. Norton & Company, New York.

Dodson, S., 1989. Predator-induced reaction norms. BioScience 39: 447–452.

Drake, J. M., P. Baggenstos & D. M. Lodge, 2005. Propagule pressure and persistence in experimental populations. Biology Letters 22: 480–483.

Dumont, H., 1995. Ecocide in the Caspian Sea. Nature 377: 673–674.

Dumont, H. J. & S. V. Negrea, 2002. Introduction to the Class Branchiopoda. Backhuys Publishers, Leiden.

Dumont, H., J. Mertens & A. M. Maeda-Martinez, 1995. Historical biogeography and morphological differentiation of *Streptocephalus torvicornis* (Waga) since the Würm III-glaciation. Hydrobiologia 298: 281–286.

Dumont, H., S. Nandini & S. S. S. Sarma, 2002. Cyst ornamentation in aquatic invertebrates: a defence against egg-predation. Hydrobiologia 486: 161–167.

Duthie, A. V., 1929. The method of spore dispersal of three south African species of *Isoëtes*. Annals of Botany 43: 411–412.

Ebert, T. A. & M. L. Balko, 1987. Vernal pools as islands in space and time. In Jain, S. & P. Moyle (eds), Vernal Pools and Intermittent Streams. Institute of Ecology Publication, University of California, Davis: 90–101.

Eitam, A., L. Blaustein, K. Van Damme, H. J. Dumont & K. Martens, 2004. Crustacean species richness in temporary pools: relationships with habitat traits. Hydrobiologia 525: 125–130.

Ferrari, I. & G. Rossetti, 2006. New records of the centropagid *Boeckella triarticulata* (Thomson, 1883) (Copepoda:

Calanoida) in Northern Italy: evidence of a successful invasion? Aquatic Invasions 1: 219–222.

Fierer, N., 2008. Microbial biogeography: patterns in microbial diversity across space and time. In Zengler, K. (ed.), Accessing Uncultivated Microorganisms: From the Environment to Organisms and Genomes and Back. ASM Press, Washington DC: 95–115.

Figuerola, J. & A. J. Green, 2002. Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. Freshwater Biology 47: 483–494.

Finlay, B. J., 2002. Global dispersal of free-living microbial eukaryote species. Science 296: 1061–1063.

Fischer, S. F., P. Poschold & B. Beinlich, 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology 33: 1206–1222.

Florencio, M., C. Díaz-Paniagua, L. Serrano & T. Bilton, 2011. Spatio-temporal nested patterns in macroinvertebrate assemblages across a pond network with a wide hydroperiod range. Oecologia 166: 469–483.

Florencio, M., P. Cardoso, J. M. Lobo, E. Brito de Azevedo & P. A. V. Borges, 2013. Arthropod assemblage homogenization in oceanic islands: the role of indigenous and exotic species under landscape disturbance. Diversity and Distributions 19: 1450–1460.

Florencio, M., C. Díaz-Paniagua, C. Gómez-Rodríguez & L. Serrano, 2014. Biodiversity patterns in a macroinvertebrate community of a temporary pond network. Insect Conservation and Diversity 7: 4–21.

Flössner, D., 2000. Die Haplopoda und Cladocera Mitteleuropas. Backhuys Publishers, Leiden.

Foissner, W., 2006. Biogeography and dispersal of microorganisms: a review emphasizing protists. Acta Protozoologica 45: 111–136.

Foissner, W., 2008. Protist diversity and distribution: some basic considerations. Biodiversity and Conservation 17: 235–242.

Foissner, W. & D. L. Hawksworth (eds), 2009. Protist Diversity and Geographical Distribution. Springer Science, Heidelberg.

Fontaneto, D. & J. Brodie, 2011. Why biogeography of microorganisms? In Fontaneto, D. (ed.), Biogeography of Microscopic Organisms. Is Everything Small Everywhere?. Cambridge University Press, Cambridge.

Fontaneto, D., I. Giordani, G. Melone & M. Serra, 2007. Disentangling the morphological stasis in two rotifer species of the *Brachionus plicatilis* species complex. Hydrobiologia 583: 297–307.

Frey, D. G., 1982a. The honeycombed species of *Chydorus* (Cladocera, Chydoridae): comparison of *C. bicornutus* and *C. bicollaris* n. sp. with some preliminary comments on *C. faviformis*. Canadian Journal of Zoology 60: 1892–1916.

Frey, D. G., 1982b. Questions concerning cosmopolitanism in Cladocera. Archiv für Hydrobiologie 93: 484–502.

Frey, D. G., 1986. The non-cosmopolitanism of chydorid Cladocera: implications for biogeography and evolution. In Gore, R. H. & K. L. Heck (eds), Crustacean Biogeography (Crustacean Issues 4). Balkema, Rotterdam: 237–256.

Frey, D. G., 1995. Changing attitudes toward chydorid anomopods since 1796. Hydrobiologia 307: 43–55.

Frisch, D. & A. J. Green, 2007. Copepods come in first: rapid colonization of new temporary ponds. Fundamental and Applied Limnology 168: 289–297.

Frisch, D., B. S. Libman, S. J. D'Surney & S. T. Threlkeld, 2005. Diversity of floodplain copepods (Crustacea) modified by flooding: species richness, diapause strategies and population genetics. Archiv für Hydrobiologie 162: 1–17.

Frisch, D., E. Moreno-Ostos & A. J. Green, 2006. Species richness and distribution of copepods and cladocerans and their relation to hydroperiod and other environmental variables in Doñana, south-west Spain. Hydrobiologia 556: 327–340.

Frisch, D., K. Cottenie, A. Badosa & A. J. Green, 2012. Strong spatial influence on colonization rates in a pioneer zooplankton metacommunity. PLoS One 7: e40205.

Genitsaris, S., K. A. Kormas & M. Moustaka-Gouni, 2011a. Airborne algae and cyanobacteria: occurrence and related health effects. Frontiers in Biosciences 3: 772–787.

Genitsaris, S., M. Moustaka-Gouni & K. A. Kormas, 2011b. Airborne microeukaryote colonists in experimental water containers: diversity, succession, life histories and established food webs. Aquatic Microbial Ecology 62: 139–152.

Gentili, R., T. Abeli, G. Rossi, M. Li, C. Varotto & S. Sgorbati, 2010. Population structure and genetic diversity of the threatened quillwort *Isoëtes malinverniana* and implication for conservation. Aquatic Botany 93: 147–152.

Gómez, A., G. R. Carvalho & D. H. Lunt, 2000. Phylogeography and regional endemism of a passively dispersing zooplankter: mitochondrial DNA variation in rotifer resting egg banks. Proceedings of the Royal Society B: Biological Sciences 267: 2189–2197.

Graham, T. B. & D. Wirth, 2008. Dispersal of large branchiopod cysts: potential movement by wind from potholes on the Colorado plateau. Hydrobiologia 600: 17–27.

Green, A. J., K. M. Jenkins, D. Bell, P. J. Morris & R. T. Kingsford, 2008. The potential role of waterbirds in dispersing invertebrates and plants in arid Australia. Freshwater Biology 53: 380–392.

Green, J. & B. J. M. Bohannan, 2006. Spatial scaling of microbial diversity. Trends in Ecology and Evolution 21: 501–507.

Grillas, P., P. Gauthier, N. Yavercovski & C. Perennou, 2004. Mediterranean Temporary Pools, Vol. 1. Issue relating to conservation, functioning and management. Station biologique de la Tour du Valat, Arles.

Haag, C. R. & D. Ebert, 2004. A new hypothesis to explain geographic parthenogenesis. Annales Zoologici Fennici 41: 539–544.

Hairston, N. G. & C. M. Kearns, 2002. Temporal dispersal: ecological and evolutionary aspects of zooplankton egg banks and the role of sediment mixing. Integrative and Comparative Biology 42: 481–491.

Hairston Jr, N., R. A. Van Brunt, C. M. Kearns & D. R. Engstrom, 1995. Age and survivorship of diapausing eggs in a sediment egg bank. Ecology 76: 1706–1711.

Hamilton, W. D. & T. M. Lenton, 1998. Spora and Gaia: how microbes fly with their clouds. Ethology, Ecology and Evolution 10: 1–16.

Havel, J., L. A. Bruckerhoff, M. A. Funkhouser & A. R. Gemberling, 2014. Resistance to desiccation in aquatic invasive snails and implications for their overland dispersal. Hydrobiologia 741: 89–100.

Havens, K. & J. R. Beaver, 2014. Predicting impacts of an invading copepod by ecological assessment in the animal's native range. Inland Waters 4: 49–56.

Heino, J., 2013. Does dispersal ability affect the relative importance of environmental control and spatial structuring of littoral macroinvertebrate communities? Oecologia 171: 971–980.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405: 907–913.

Hickerson, M. J., B. C. Carstens, J. Cavender-Bares, K. A. Crandall, C. H. Graham, J. B. Johnson, L. Rissler, P. F. Victoriano & A. D. Yoder, 2010. Phylogeography's past, present, and future: 10 years after Avise, 2000. Molecular Phylogenetics and Evolution 54: 291–301.

Higgins, S. I., R. Nathan & M. L. Cain, 2003. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84: 1945–1956.

Hill, J., W. Mehl & M. Altherr, 1994. Land degradation and soil erosion mapping in a Mediterranean Ecosystem. Eurocourses Remote Sensing 4: 237–260.

Hoot, S. B., W. C. Taylor & N. S. Napier, 2006. Phylogeny and biogeography of *Isoëtes* (Isoëtaceae) based on nuclear and chloroplast DNA sequence data. Systematic Botany 31: 449–460.

Horne, D. J. & K. Martens, 1998. Geographical parthenogenesis in European non-marine ostracods: post-glacial invasion or Holocene stability? Hydrobiologia 391: 1–7.

Hoverman, J. T. & R. A. Relyea, 2008. Temporal environmental variation and phenotypic plasticity: a mechanism underlying priority effects. Oikos 117: 23–32.

Jenkins, D. G. & A. L. Buikema, 1998. Do similar communities develop in similar sites? Ecological Monographs 68: 421–443.

Jenkins, D. G. & M. O. Underwood, 1998. Zooplankton may not disperse readily in wind, rain, or waterfowl. Hydrobiologia 387(388): 15–21.

Jenkins, D. G., C. R. Brescacin, C. V. Duxbury, J. A. Elliott, J. A. Evans, K. R. Grablow, M. Hillegass, B. N. Lyon, G. A. Metzger, M. L. Olandese, D. Pepe, G. A. Silvers, H. N. Suresch, T. N. Thompson, C. M. Trexler, G. E. Williams, N. C. Williams & S. E. Williams, 2007. Does size matter for dispersal distance? Global Ecology and Biogeography 16: 415–425.

Kappes, H., O. Tackenberg & P. Haase, 2014. Differences in dispersal- and colonization-related traits between taxa from the freshwater and terrestrial realm. Aquatic Ecology 48: 73–83.

Karanovic, I., 2012. Recent Freshwater Ostracods of the World: Crustacea, Ostracoda, Podocopida. Springer, Heidelberg.

Ketmaier, V., P. Zarattini, E. De Matthaeis, M. Cobolli & G. Mura, 2003. Intra- and inter-specific relationships in the six Italian species of the fairy shrimp genus *Chirocephalus*: combing allozymes and mtDNA data. Journal of Zoological Systematics and Evolutionary Research 41: 276–285.

Ketmaier, V., F. Marrone, G. Alfonso, K. Paulus, A. Wiemann, R. Tiedemann & G. Mura, 2012. Mitochondrial DNA regionalism and historical demography in the extant populations of *Chirocephalus kerkyrensis* (Branchiopoda: Anostraca). PLoS One 7: e30082.

Komárek, J. & J. Mareš, 2012. An update to modern taxonomy (2011) of freshwater planktic heterocytous cyanobacteria. Hydrobiologia 698: 327–351.

Korn, M., F. Marrone, J. L. Pérez-Bote, M. Machado, M. Cristo, L. Cancela da Fonseca & A. K. Hundsdoerfer, 2006. Sister species within the *Triops cancriformis* lineage (Crustacea, Notostraca). Zoologica Scripta 35: 301–322.

Korn, M., A. J. Green, M. Machado, J. García-de-Lomas, M. Cristo, L. Cancela da Fonseca, D. Frisch, J. L. Pérez-Bote & A. K. Hundsdoerfer, 2010. Phylogeny, molecular ecology and taxonomy of southern Iberian lineages of *Triops mauritanicus* (Crustacea: Notostraca). Organisms Diversity & Evolution 10: 409–440.

Korn, M., N. Rabet, H. V. Ghate & F. Marrone, 2013. Molecular phylogeny of the Notostraca. Molecular Phylogenetics and Evolution 69: 1159–1171.

Krienitz, L. & C. Bock, 2012. Present state of the systematic of planktonic coccoid green algae of inland waters. Hydrobiologia 698: 295–326.

Kristiansen, J., 1996. Dispersal of freshwater algae – a review. Hydrobiologia 336: 151–157.

Kristiansen, J., 2008. Dispersal and biogeography of silicascaled chrysophytes. Biodiversity and Conservation 17: 419–426.

Lavens, P. & P. Sorgeloos, 1996. Manual on the Production and Use of Live Food in Aquaculture. FAO Fisheries Technical Papers 361.

Levine, J. M., 2000. Species diversity and biological invasions: relating local process to community patterns. Science 288: 852–854.

Lomolino, M. V., 1990. The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. Oikos 57: 297–300.

Louette, G. & L. De Meester, 2005. High dispersal capacity of cladoceran zooplankton in newly founded communities. Ecology 86: 353–359.

Louette, G. & L. De Meester, 2007. Predation and priority effects in experimental zooplankton communities. Oikos 116: 419–426.

Louette, G., M. Vander Elst & L. De Meester, 2006. Establishment success in young cladoceran communities: an experimental test. Limnology and Oceanography 51: 1021–1030.

MacArthur, R. H. & E. O. Wilson, 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Maguire, B., 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecological Monographs 33: 161–185.

Margaritora, F. G., 1985. Cladocera Fauna d'Italia 23. Edizioni Calderini, Bologna.

Marrone, F. & L. Naselli-Flores, 2011. Primo reperto di una lenticchia d'acqua alloctona in Sicilia: *Lemna minuta* Kunth (Araceae Lemnoideae). Naturalista Siciliano 35: 179–185.

Marrone, F., G. Castelli, R. Barone & L. Naselli-Flores, 2006a. Ecology and distribution of calanoid copepods in Sicilian inland waters. Verhandlungen des Internationalen Verein Limnologie 29: 2150–2156.

Marrone, F., R. Barone & L. Naselli-Flores, 2006b. Ecological characterization and cladocerans, calanoid copepods and large branchiopods of temporary ponds in a Mediterranean island (Sicily, southern Italy). Chemistry and Ecology 22: 181–190.

Marrone, F., G. Castelli & L. Naselli-Flores, 2009. Sicilian temporary ponds: an overview of the composition and affinities of their crustacean biota. In Fraga i Arguimbau, P. (ed), International Conference on Mediterranean Temporary Ponds. Proceedings & Abstracts. Consell Insular de Menorca. Recerca, 14. Maó, Menorca: 189–202.

Marrone, F., S. Lo Brutto & M. Arculeo, 2010. Molecular evidence for the presence of cryptic evolutionary lineages in the freshwater copepod genus *Hemidiaptomus* G.O. Sars, 1903 (Calanoida, Diaptomidae). Hydrobiologia 644: 115–125.

Marrone, F., S. Lo Brutto & M. Arculeo, 2011. Cryptic invasion in Southern Europe: the case of *Ferrissia fragilis* (Pulmonata: Ancylidae) Mediterranean populations. Biologia 66: 484–490.

Marrone, F., S. Lo Brutto, A. K. Hundsdoerfer & M. Arculeo, 2013. Overlooked cryptic endemism in copepods: Systematics and natural history of the calanoid subgenus *Occidodiaptomus* Borutzky 1991 (Copepoda, Calanoida, Diaptomidae). Molecular Phylogenetics and Evolution 66: 190–202.

Martiny, J. B. H., B. J. M. Bohannan, J. H. Brown, R. K. Colwell, J. A. Fuhrman, J. L. Green, M. C. Horner-Devine, M. Kane, J. Adams Krumins, C. R. Kuske, P. J. Morin, S. Naeem, L. Øvreås, A.-L. Reysenbach, V. H. Smith & J. T. Staley, 2006. Microbial biogeography: putting microorganisms on the map. Nature Reviews Microbiology 4: 102–112.

Maynard Smith, J., 1978. The Evolution of Sex. Cambridge University Press Archive, Cambridge.

McAbendroth, L., A. Foggo, S. D. Rundle & D. T. Bilton, 2005. Unravelling nestedness and spatial pattern in pond assemblages. Journal of Animal Ecology 74: 41–49.

McCafferty, S., N. Warren, C. Wilbur & S. Shumway, 2010. Genetic divergence among Massachusetts populations of the vernal pool fairy shrimp *Eubranchipus vernalis* (Crustacea: Anostraca). Northeastern Naturalist 17: 258–304.

Meglécz, E. & A. Thiéry, 2005. Genetic structure of a rare, temporary pond dwelling fairy shrimp *Linderiella massaliensis* (Crustacea: Anostraca). Archiv für Hydrobiologie 164: 277–286.

Meier, S. & J. Soininen, 2014. Phytoplankton metacommunity structure in subarctic rock pools. Aquatic Microbial Ecology 73: 81–91.

Miracle, M. R., 1982. Biogeography of the freshwater zooplanktonic communities of Spain. Journal of Biogeography 9: 455–467.

Miyazono, S. & C. M. Taylor, 2013. Effects of habitat size and isolation on species immigration–extinction dynamics and community nestedness in a desert river system. Freshwater Biology 58: 1303–1312.

Moustaka-Gouni, M., E. MIchaloudi, K. A. Kormas, M. Katsiapi, E. Vardaka & S. Genitsaris, 2012. Plankton changes as critical processes for restoration plans of lakes Kastoria and Koronia. European Water 40: 43–51.

Muirhead, J. R. & H. J. MacIsaac, 2005. Development of inland lakes as hubs in an invasion network. Journal of Applied Ecology 42: 80–90.

Muñoz, J., A. Gómez, A. J. Green, J. Figuerola, F. Amat & C. Rico, 2008. Phylogeography and local endemism of the native Mediterranean brine shrimp *Artemia salina* (Branchiopoda: Anostraca). Molecular Ecology 17: 3160–3177.

Muñoz, J., F. Amat, A. J. Green, J. Figuerola & A. Gómez, 2013. Bird migratory flyways influence the phylogeography of the invasive brine shrimp *Artemia franciscana* in its native American range. PeerJ 1: e200.

Mura, G., 2001. Morphological diversity of the resting eggs in the anostracan genus *Chirocephalus* (Crustacea, Branchiopoda). Hydrobiologia 450: 173–185.

Mura, G., 2004. Structure and functioning of the ''egg bank'' of a fairy shrimp in a temporary pool: *Chirocephalus ruffoi* from Pollino national park (Southern Italy) as a case study. International Review of Hydrobiology 89: 35–50.

Mura, G., 2005. Cyst distribution and hatching pattern of *Chirocephalus ruffoi* (Crustacea, Anostraca) in an experimental undisturbed pool. International Review of Hydrobiology 90: 277–291.

Naselli-Flores, L. & R. Barone, 2005. Water-level fluctuations in Mediterranean reservoirs: setting a dewatering threshold as a management tool to improve water quality. Hydrobiologia 548: 85–99.

Naselli-Flores, L. & R. Barone, 2011. Fight on plankton! Or, phytoplankton shape and size as adaptive tools to get ahead in the struggle for life. Cryptogamie, Algologie 32: 157–204.

Naselli-Flores, L. & R. Barone, 2012. Phytoplankton dynamics in permanent and temporary Mediterranean waters: is the game hard to play because of hydrological disturbance? Hydrobiologia 698: 147–159.

Naselli-Flores, L., J. Padisák, M. Dokulil & I. Chorus, 2003. Equilibrium/steady state concept in phytoplankton ecology. Hydrobiologia 502: 395–403.

O'Malley, M. A., 2007. The nineteenth century roots of 'everything is everywhere'. Nature Reviews Microbiology 5: 647–651.

Orsini, L., J. Vanoverbeke, I. Swillen, J. Mergeay & L. De Meester, 2013. Drivers of population genetic differentiation in the wild: isolation by dispersal limitation, isolation by adaptation and isolation by colonization. Molecular Ecology 22: 5983–5999.

Ortells, R., J. Vanoverbeke, G. Louette & L. De Meester, 2014. Colonization of *Daphnia magna* in a newly created pond: founder effects and secondary immigrants. Hydrobiologia 723: 167–179.

Packer, L., J. Gibbs, C. Sheffield & R. Hanner, 2009. DNA barcoding and the mediocrity of morphology. Molecular Ecology Resources 9(s1): 42–50.

Padilla, D. K. & S. L. Williams, 2004. Beyond ballast water: aquarium and ornamental trades as sources of invasive species in aquatic ecosystems. Frontiers in Ecology and the Environment 2: 131–138.

Padisák, J., L. Crossetti & L. Naselli-Flores, 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. Hydrobiologia 621: 1–19.

Park, A. W., J. Vandekerkhove & Y. Michalakis, 2014. Sex in an uncertain world: environmental stochasticity helps restore competitive balance between sexually and asexually reproducing populations. Journal of Evolutionary Biology 27(8): 1650–1661.

Pérez-Bote, J. L., A. Muñoz del Viejo, J. M. García & S. P. Rodríguez, 2005. Evidence of dissemination of *Triops cancriformis mauritanicus* Ghigi, 1921 (Branchiopoda, Notostraca) cysts by the red swamp crayfish, *Procambarus clarkii* (Girard, 1852) (Decapoda, Cambaridae). Crustaceana 78: 481–485.

Petrusek, A., R. Tollrian, K. Schwenk, A. Haas & C. Laforsch, 2009. A "crown of thorns" is an inducible defense that protects Daphnia against an ancient predator. Proceedings of the National Academy of Sciences (PNAS) 106: 2248–2252.

Pfenninger, M. & K. Schwenk, 2007. Cryptic animal species are homogeneously distributed among taxa and biogeographical regions. BMC Evolutionary Biology 7: 121.

Pretus, J. L., 1990. A commented check-list of the Balearic Branchiopoda (Crustacea). Limnetica 6: 157–164.

Ptatscheck, C. & W. Traunspurger, 2014. The meiofauna of artificial water-filled tree holes: colonization and bottom-up effects. Aquatic Ecology 48: 285–295.

Reid, J. W., 1997. How "cosmopolitan" are the continental cyclopoid copepods? Comparison of the North American and Eurasian faunas, with description of *Acanthocyclops parasensitivus* sp. n. (Copepoda: Cyclopoida) from the U.S.A. Zoologischer Anzeiger 236: 109–188.

Reynolds, C. S., 2007. Variability in the provision and function of mucilage in phytoplankton: facultative responses to the environment. Hydrobiologia 578: 37–45.

Riccardi, N. & G. Rossetti, 2007. *Eudiaptomus gracilis* in Italy: how, where and why. Journal of Limnology 66: 64–69.

Ripley, B. J. & M. A. Simovich, 2009. Species richness on islands in time: variation in ephemeral pond crustacean communities in relation to habitat duration and size. Hydrobiologia 617: 181–196.

Roberts, M. S. & F. M. Cohan, 1995. Recombination and migration rates in natural populations of *Bacillus subtilis* and *Bacillus mojavensis*. Evolution 49: 1081–1094.

Rogers, D. C., 2014. Larger hatching fractions in avian dispersed anostracan eggs (Branchiopoda). Journal of Crustacean Biology 34: 135–143.

Ruhí, A., D. Boix, S. Gascón, J. Sala & X. D. Quintana, 2013. Nestedness and successional trajectories of macroinvertebrate assemblages in man-made wetlands. Oecologia 171: 545–556.

Ruiz, G. M. & J. T. Carlton, 2003. Invasive Species. Island Press, Washington (DC).

Rundle, S. D., A. Foggo, V. Choiseul & D. T. Bilton, 2002. Are distribution patterns linked to dispersal mechanisms? An investigation using pond invertebrate assemblages. Freshwater Biology 47: 1571–1581.

Sahuquillo, M. & M. R. Miracle, 2013. The role of historic and climatic factors in the distribution of crustacean communities in Iberian Mediterranean ponds. Freshwater Biology 58: 1251–1266.

Samchyshyna, L. & B. Santer, 2010. Chorion structure of diapause and subitaneous eggs of four diaptomid copepods (Calanoida, Diaptomidae): SEM observations. Vestnik zoologii 44: 26–32.

Sarnelle, O. & R. A. Knapp, 2004. Zooplankton recovery after fish removal: limitations of the egg bank. Limnology and Oceanography 49: 1382–1392.

Schmit, O., S. N. S. Bode, A. Camacho, D. J. Horne, D. K. Lamatsch, K. Martens, M. J. F. Martins, T. Namiotko, G. Rossetti, J. Rueda-Sevilla, I. Schön, J. Vandekerkhove & F. Mesquita-Joanes, 2013. Linking present environment and the segregation of reproductive modes (geographical parthenogenesis) in *Eucypris virens* (Crustacea: Ostracoda). Journal of Biogeography 40: 2396–2408.

Schön, I., K. Martens & P. van Dijk (eds), 2009. Lost Sex. The Evolutionary Biology of Parthenogenesis. Springer, Dordrecht.

Schulz, G., T. Siqueira, G. Stefan & F. de Oliveira Roque, 2012. Passive and active dispersers respond similarly to environmental and spatial processes: an example from metacommunity dynamics of tree hole invertebrates. Fundamental and Applied Limnology 181: 315–326.

Schwentner, M., B. V. Timms & S. Richter, 2012. Flying with the birds? Recent large-area dispersal of four Australian *Limnadopsis* species (Crustacea: Branchiopoda: Spinicaudata). Ecology and Evolution 2: 1605–1626.

Seaman, M. T., D. J. Kok & M. Watson, 1999. Chapter 4: Cladocera. In: J. A. Day, B. A. Stewart, I. J. de Moor, & A. E. Louw, (eds), Guides to the Freshwater Invertebrates of Southern Africa, Vol. 2: Crustacea I (Notostraca, Anostraca, Conchostraca and Cladocera). South African Water Research Commission, Pretoria. Report TT121/00: 1–123.

Sharma, N. K., S. Singh & A. K. Rai, 2006. Diversity and seasonal variation of viable algal particles in the atmosphere of a subtropical city in India. Environmental Research 102: 252–259.

Sharma, N. K., A. K. Rai, S. Singh & R. M. Brown Jr., 2007. Airborne algae: their present status and relevance. Journal of Phycology 43: 615–627.

Shurin, J. B., 2000. Dispersal limitation, invasion resistance, and the structure of pond zooplankton communities. Ecology 81: 3074–3086.

Shurin, J. B., K. Cottenie & H. Hillebrand, 2009. Spatial autocorrelation and dispersal limitation in freshwater organism. Oecologia 159: 151–159.

Smirnov, N. N. & B. V. Timms, 1983. A revision of the Australian Cladocera (Crustacea). Records of the Australian Museum, suppl. 1: 1–132.

Soininen, J., R. McDonald & H. Hillebrand, 2007. The distance decay similarity in ecological community. Ecography 30: 3–12.

Soininen, J., J. Korhonen & M. Luoto, 2013. Stochastic species distributions are driven by organism sizes. Ecology 94: 660–670.

Stoch, F. & L. Naselli-Flores, 2014. Acque temporanee: biodiversità, funzioni ecosistemiche, vulnerabilità e sensibilità ai cambiamenti climatici. Biologia Ambientale 28: 188–194.

Straka, U., 2004. Aktuelle Vorkommen von Groß-Branchiopoden (Crustacea: Anostraca, Notostraca, Conchostraca) im Tullner Feld (Niederösterreich). Annalen des Naturhistorischen Museums in Wien 105B: 35–45.

Su, T. & M. S. Mulla, 2002. Introduction and establishment of tadpole shrimp *Triops newberryi* (Notostraca: Triopsidae) in a date garden for biological control of mosquitoes in the Coachella Valley, Southern California. Journal of Vector Ecology 27: 138–148.

Symons, C. C. & S. E. Arnott, 2014. Timing is everything: priority effects alter community invasibility after disturbance. Ecology and Evolution 4: 397–407.

Tackaert, W. & P. Sorgeloos, 1993. Use of brine shrimp to increase salt production, Vol. 1. In Seventh Symposium on Salt: 617–622.

Thiéry, A., 1997. Horizontal distribution and abundance of cysts of several large branchiopods in temporary pool and ditch sediments. Hydrobiologia 359: 177–189.

Thiéry, A. & C. Gasc, 1991. Resting eggs of Anostraca, Notostraca and Spinicaudata (Crustacea, Branchiopoda) occurring in France: identification and taxonomical value. Hydrobiologia 212: 245–259.

Thiéry, A., N. Rabet & G. Nève, 2007. Modelling intraspecific resting egg shape variation in a freshwater fairy shrimp *Tanymastix stagnalis* (L., 1758) (Crustacea, Branchiopoda). Biological Journal of the Linnean Society 90: 55–60.

Tilman, D., 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology 78: 81–92.

Turki, S. & A. El Abed, 1999. Nouvelles informations sur les copépodes calanoïdes et cyclopoïdes des eaux continentales tunisiennes. Crustaceana 72: 157–169.

Uronen, P., P. Kuuppo, C. Legrand & T. Tamminen, 2007. Allelopathic effects of toxic haptophyte *Prymnesium parvum* lead to release of dissolved organic carbon and increase in bacterial biomass. Microbial Ecology 54: 183–193.

Van Damme, K. & A. Y. Sinev, 2013. Tropical Amphi-Pacific disjunctions in the Cladocera (Crustacea: Branchiopoda). Journal of Limnology 72(s2): 209–244.

van de Meutter, F., R. Stoks & L. de Meester, 2008. Size-selective dispersal of *Daphnia* resting eggs by backswimmers (*Notonecta maculata*). Biology Letters 4: 494–496.

Van den Broecke, L., K. Martens, V. Pieri & I. Schön, 2012. Ostracod valves as efficient UV protection. Journal of Limnology 71: 119–124.

Van Damme, K. & H. Dumont, 2008. A new species of *Moina* Baird, 1850 (Crustacea: Anomopoda) from Socotra Island, Yemen. Zootaxa 1721: 24–34.

Van Donk, E., A. Ianora & M. Vos, 2011. Induced defences in marine and freshwater phytoplankton: a review. Hydrobiologia 668: 3–19.

Van Leeuwen, C. H. A., N. Huig, G. Van Der Velde, T. A. Van Alen, C. A. M. Wagemaker, C. D. H. Sherman, M. Klaassen & J. Figuerola, 2013. How did this snail get here? Several dispersal vectors inferred for an aquatic invasive species. Freshwater Biology 58: 88–99.

Vanschoenwinkel, B., S. Gielen, H. Vandewaerde, M. Seaman & L. Brendonck, 2008a. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. Ecography 31: 567–577.

Vanschoenwinkel, B., S. Gielen, M. Seaman & L. Brendonck, 2008b. Any way the wind blows – frequent wind dispersal drives species sorting in ephemeral aquatic communities. Oikos 117: 125–134.

Vanschoenwinkel, B., A. Waterkeyn, T. Vandecaetsbeek, O. Pineau, P. Grillas & L. Brendonck, 2008c. Dispersal of freshwater invertebrates by large terrestrial mammals: a case study with wild boar (*Sus scrofa*) in Mediterranean wetlands. Freshwater Biology 53: 2264–2273.

Ventura, M., A. Petrusek, A. Miró, E. Hamrová, D. Buňay, L. De Meester & J. Mergeay, 2014. Local and regional founder effects in lake zooplankton persist after thousands of years despite high dispersal potential. Molecular Ecology 23: 1014–1027.

Vernadsky, V. I., 1998. The Biosphere. Complete Annotated Edition. Copernicus, Springer, New York.

Wang, J., J. Soininen, Y. Zhang, B. Wang, X. Jiang & J. Shen, 2012. Patterns of elevational beta diversity in micro- and macroorganisms. Global Ecology and Biogeography 21: 743–750.

Waterkeyn, A., B. Vanschoenwinkel, S. Elsen, M. Anton-Pardo, P. Grillas & L. Brendonck, 2010. Unintentional dispersal of aquatic invertebrates via footwear and motor vehicles in a Mediterranean wetland area. Aquatic Conservation 20: 580–587.

Wells, M. L., S. A. Hathaway & M. A. Simovich, 1997. Resilience of anostracan cysts to fire. Hydrobiologia 359: 199–202.

Werner, E. E. & S. D. Peacor, 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology 84: 1083–1100.

Whittaker, R. J. & J. M. Fernández-Palacios, 2007. Island Biogeography. Ecology, Evolution and Conservation, 2nd ed. Oxford University Press, Oxford.

Williams, D. D., 2002. Temporary water crustaceans: biodiversity and habitat loss. In Escobar-Briones, E. & F. Alvarez (eds), Modern Approaches to the Study of Crustacea. Kluwer Academic Publishers, Dordrecht: 223–233.

Williams, D. M., 2011. Historical biogeography, microbial endemism and the role of classification: everything is endemic. In Fontaneto, D. (ed.), Biogeography of Microscopic Organisms. Is Everything Small Everywhere?. Cambridge University Press, Cambridge.

Williams, P., J. Biggs, G. Fox, P. Nicolet & M. Whitfield, 2001. History, origins and importance of temporary ponds. Freshwater Forum 17: 7–15.

Williamson, M., 1996. Biological Invasions. Chapman and Hall, London.

Williamson, M. & A. Fitter, 1996. The varying success of invaders. Ecology 77: 1661–1666.

Xu, S., P. D. N. Hebert, A. A. Kotov & M. E. Cristescu, 2009. The noncosmopolitanism paradigm of freshwater zooplankton: insights from the global phylogeography of the predatory cladoceran *Polyphemus pediculus* (Linnaeus, 1761) (Crustacea, Onychopoda). Molecular Ecology 18: 5161–5179.

Yawata, Y., O. X. Cordero, F. Menolascina, J.-H. Hehemann, M. F. Polz & R. Stocker, 2014. Competition-dispersal tradeoff ecologically differentiates recently speciated marine bacterioplankton populations. Proceedings of the National Academy of Sciences (PNAS) 111: 5622–5627.

Zacharias, I., E. Dimitriou, A. Dekker & E. Dorsman, 2007. Overview of temporary ponds in the Mediterranean region: threats, management and conservation issues. Journal of Environmental Biology 28: 1–9.

Zedler, P. H. & C. Black, 1992. Seed dispersal by a generalised herbivore: rabbits as dispersal vectors in semi-arid California vernal pools landscape. The American Midland Naturalist 128: 1–10.