

Speciation in *Daphnia*

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Abstract

The microcrustacean *Daphnia* is arguably one of the most studied zooplankton species, having a well understood ecology, life history, and a relatively well studied evolutionary history. Despite this wealth of knowledge, species boundaries within this genus often remain elusive and the major evolutionary forces driving the diversity of daphniids remain controversial. This genus contains more than 300 species with multiple cryptic species complexes, with many closely related species able to hybridize. Here we review speciation research in *Daphnia* within the framework of current speciation theory. We evaluate the role of geography, ecology, and biology in restricting gene flow and promoting diversification. Of the 253 speciation studies on *Daphnia*, the majority of studies examine geographic barriers (55%). While evidence shows that geographic barriers play a role in species divergence, ecological barriers are also likely prominent in *Daphnia* speciation. We assess the contribution of ecological and non-ecological reproductive isolating barriers between closely related species of *Daphnia* and found that none of the reproductive isolating barriers are capable of restricting gene flow completely. Research on reproductive isolating barriers has been disproportionately focused on two species complexes, *Daphnia pulex* and *Daphnia longispina*. Lastly, we identify areas of research that remain relatively unexplored and discuss future research directions that build our understanding of speciation in daphniids.

1. Introduction

Patterns and processes of speciation in freshwater environments are considered to be shaped by the relatively short persistence and high turnover rate of these habitats. Their ephemeral nature poses challenges related to the need to seek refuge during unfavourable conditions (e.g. drying or freezing habitats) often resulting in life history favouring stages of dormancy, high dispersal ability, rapid population establishment, and other r-selected traits. Moreover, the connectivity of freshwater systems across large spatial scales, which links ecologically distinct ecosystems (lentic and lotic), offers not only long corridors of dispersal but also distinct selection regimes and potential for habitat transitions.

Planktonic organisms such as *Daphnia* (Crustacea, Anomopoda) have offered important insights into the evolutionary forces promoting diversification in freshwater habitats. The biogeography of cladocerans has been investigated for more than a century (Lampert, 2011) with the genus *Daphnia* O. F. Müller, 1785 (Anomopoda: Daphniidae) receiving particular attention. Historically, daphniids, like many aquatic organisms, have been considered dispersalist *par excellence* (Mayr, 1963) with great ability to colonize new geographic locations and maintaining genetic cohesion across vast geographic ranges (Bilton, Freeland, & Okamura, 2001; Bohonak & Jenkins, 2003; Havel & Shurin, 2004). This view has been inspired by the massive production of resting eggs which offers passive dispersal ability in both time and space (Bilton et al., 2001). Daphniids' resting eggs are encapsulated in a hard structure known as an ephippium, which offers mechanical protection and resistance to desiccation and freezing along with great buoyancy. Ephippia enable movement between sites via vectors (e.g. water currents, wind, animals) as well as dispersal through time via deposition in sediments and subsequent hatching (Geerts et al., 2015; Frisch et al., 2020). The dormant embryos

encapsulated in the ephippia can remain dormant in undisturbed sediments for decades or centuries, forming rich ephippial banks that are considered equivalent to the seed banks of plants (Fryer, 1996; Cáceres, 1998).

Since direct methods of measuring dispersal rates are often difficult (Bilton et al., 2001), the high dispersal capability of daphniids (and cladocerans in general) was inferred from observations on the viability of ephippia after passing through the digestive tracts of animals (Proctor & Malone, 1965; Proctor, Malone, & DeVlaming, 1967; Figuerola, Green, & Michot, 2005), the high colonization rates of newly created habitats, and their broad geographic distribution. Such propensity for dispersal and long-distance colonization was assumed to fuel high levels of gene flow and provide genetic cohesion among populations not only at a regional scale, but also at continental and even intercontinental scale (Mayr, 1963). The early view that ‘everything is everywhere’ was reinforced by the observed morphological stasis (Frey, 1982; Frey, 1987) but remained untested for almost a century.

In contrast to the traditional view of cosmopolitanism, early genetic studies on *Daphnia* revealed unexpectedly high level of genetic structure across regional and local scales (Crease, Lynch, & Spitze, 1990; Colbourne & Hebert, 1996; Schwenk et al., 1998) and high level of cryptic endemism (Taylor, Finston, & Hebert, 1998). For example, phylogenetic analyses of the *Daphnia pulex* species complex show a polyphyletic origin of the group with European and North American *D. pulex* diverging over 5 Mya and having distinct evolutionary histories (Colbourne et al., 1998; Crease, Omilian, Costanzo, & Taylor, 2012; Markova, Dufresne, Manca, & Kotlik, 2013) as well as endemism within continents. Moreover, within North America, *Daphnia pulex* appears to be genetically highly subdivided (Lynch & Spitze, 1994; Crease et al., 1990). This low level of realized gene flow despite the high potential for dispersal suggested relatively low establishment success of new migrants. Rapid colonization, local adaptation, resting egg banks, along with resource exploitation are believed to reduce establishment success and gene flow among populations (De Meester, Gomez, Okamura, & Schwenk, 2002). These observations inspired a wave of molecular and experimental studies of the major species complexes of *Daphnia*. Despite the surge in molecular ecological research within this highly diverse genus, reproductive isolating barriers remain poorly understood. This highlights the need for this review, which integrates *Daphnia* in the framework of current speciation theory.

In this review, we explore patterns and processes of speciation in the genus *Daphnia*. We searched the literature using the Web of Science and ~30 combinations of keywords (Table 1; Supplementary Text; Supplementary Figure 1). We first evaluate the role of geographic barriers in restricting gene flow, and their effectiveness in maintaining species boundaries within the genus *Daphnia*. We then examine the role of ecological and nonecological isolating barriers in restricting gene flow between closely related species (Figure 1). We also estimate reproductive isolation metrics using methods from Sobel and Chen (2014) based on available studies that examine reproductive isolating barriers between closely related species of *Daphnia* (Table 2; Supplementary Table 1). We discuss the evolutionary forces that promote speciation within this genus and highlight the gaps in knowledge by exploring possible avenues of future research.

2. From the geography to the biology of speciation in *Daphnia*

2.1. Geographical isolation

The study of biogeography deeply shaped our understanding of speciation processes. It is of no surprise that the very broad pattern of geographic distribution of *Daphnia* appears to be influenced by vicariant processes such as the fragmentation of ancient continental landmasses or glaciation cycles. The genus *Daphnia* displays a geographic dichotomy, where species within the subgenus *Ctenodaphnia* occur in the southern hemisphere while the subgenus *Daphnia* contains species commonly found in the northern hemisphere and rarely in the tropics (Hebert, 1978; Benzie, 2005; Popova & Kotov, 2013). Fossils from the Jurassic-Cretaceous boundary indicate that daphniids originated more than 145 Mya ago (Kotov & Taylor, 2011), consistent with estimates of molecular dating (Lehman, Pfrender, Morin, Crease, & Lynch, 1995; Colbourne & Hebert, 1996; Adamowicz, Petrusek, Colbourne, Hebert, & Witt, 2009). This line of evidence suggests that the two subgenera (*Daphnia* and *Ctenodaphnia*) likely originated during the breakup of Pangea into Laurasia and Gondwana (Kotov & Taylor, 2011). Based on phylogenetic evidence, it was estimated that allopatric

speciation accounts for ~42% of the speciation processes in *Daphnia* (Adamowicz et al., 2009; Figure 2), of which the majority (30%) represent intercontinental splits, while 12% represent intracontinental isolation. Species counterparts of *D. pulex*, *D. pulicaria*, *D. obtusa*, *D. curvirostris*, and *D. magna* in European and North American displayed high sequence divergence indicating splits between 2–3 Mya (Colbourne et al., 1998; Cerny & Hebert, 1999; Hobæk & Weider, 1999; Weider et al., 1999a; De Gelas & De Meester, 2005; Markova, Dufresne, Rees, Cerny, & Kotlik, 2007). Intercontinental divergence between North and South America is also observed between daphniid species (Adamowicz, Hebert, & Marinone, 2004). As an example, South American and North American populations of the broadly distributed *Daphnia ambigua* show a split from a common ancestor of roughly 2 Mya (Hebert, Witt, & Adamowicz, 2003).

At the intracontinental level, lineages within species complexes often show disjointed distributions, suggestive of allopatric speciation. A phylogeographic survey of *D. ambigua* in North America showed regional divergence with distinct central and eastern lineages that coincide with the Appalachian mountain range barrier (Hebert et al., 2003). Genetic differentiation has also been found to occur between populations of *D. pulex* and *Daphnia arenata* on either side of the Rocky Mountains (Crease et al., 1997). The *Daphnia carinata* species complex, thought to have diversified roughly 70 Mya during the Mesozoic (Benzie, 1987), includes species that are endemic to various habitat-specific regions in southern Australia on either side of a montane barrier, with some of the more broadly distributed species showing regional divergence (Hebert & Wilson, 1994).

The repeated glacial cycles of the Pleistocene have been viewed as a ‘speciation pump’ (sensu Haffer, 1969) that has shaped current geographic distributions of *Daphnia*. Glaciation events have likely shaped the distribution of the *D. pulex* species complex in North America (Weider & Hobæk, 1994; Crease et al., 1997; Haileselassie et al., 2016), with many lineages originating during the Pleistocene (Colbourne et al., 1998; Crease et al., 2012). Arctic lineages in the *D. pulex* species complex display a biogeographic pattern consistent with a shift to a high-Arctic refuge during the last glaciation event, likely due to northward movement via passive dispersal. This dispersal colonized parts of Greenland, Iceland, Svalbard, and northern Europe (Van Raay & Crease, 1995; Weider, Hobæk, Crease, & Stibor 1996; Weider & Hobæk, 1997; Colbourne et al., 1998; Weider et al., 1999a; Weider & Hobæk, 2003). Populations from glaciated regions typically show decreased genetic divergence compared to populations from unglaciated regions (Ishida & Taylor, 2007a). Glaciation events have also shaped the distribution of closely related species *Daphnia parvula* and *Daphnia retrocurva*, with *D. retrocurva* distributed in northern regions of North America in large post-glacial regions (Costanzo & Taylor, 2010). Despite its broad distribution, *D. obtusa* shows cryptic allopatric lineages in North America (Hebert & Finston, 1996), which diverged roughly <1 Mya, suggesting recent range expansion from refugia following Pleistocene glaciation (Penton, Hebert, & Crease, 2004). In North America, molecular analyses revealed multiple cryptic lineages within the *Daphnia laevis* species complex, correlated with the emergence of glaciation events, followed by geographic dispersal along major migratory flyways (Taylor et al., 1998). In Europe, the *Daphnia longispina* species complex was found to originate roughly 5–7 Mya (Schwenk, 1993; Taylor, Hebert, & Colbourne, 1996), due to range expansion from multiple glacial refugia (Petrusek, Seda, Machacek, Ruthova, & Smilauer, 2008; Zuykova, Simonov, Bochkarev, Taylor, & Kotov, 2018a; Zuykova et al., 2018b). However, the majority of the lineages within this species complex are restricted to one continent, which distributions largely shaped by geographic barriers (Schwenk, Posada, & Hebert, 2000), although there are some exceptions (Ishida & Taylor, 2007a; Ishida & Taylor, 2007b). Recent phylogeographic surveys in Asia have uncovered a new cryptic species complex, *Daphnia mitsukuri*, with multiple lineages that span a wide altitude range due to multiple colonization events stemming from an eastern Palearctic refugia (Ma, Petrusek, Wolinska, Hu, & Yin, 2019). In the *Daphnia carinata* species complex, the restricted distribution of *Daphnia nivalis* in alpine glacial lakes in the Snowy Mountains of Australia was attributed to post-Pleistocene glaciation (Benzie, 1987).

Despite the overwhelming evidence that geography played an important role in driving speciation in *Daphnia*, particularly when looking at deep phylogenetic splits within daphniids, geographic processes cannot account for the great biodiversity of this genus. Recent studies on unglaciated regions show endemism, uncovering multiple cryptic lineages and relict groups (Benzie, 1986; Benzie & Bayly, 1996; Ishida & Taylor, 2007a;

Kotov & Taylor, 2019) and these regions are considered ‘hotspots’ for biodiversity. Thus, geographic barriers could not completely account for current biogeographic patterns in certain species complexes (Kotov & Taylor, 2010), suggesting that other speciation processes, such as ecological forces might have a strong influence. Unfortunately, delineation between geographic and ecological processes is notoriously difficult to make (Taylor et al., 1996; Weider et al., 1999b; Schwenk et al., 2000; Taylor, Sprenger, & Ishida, 2005), and it has been suggested that multiple processes often shape the current biodiversity of this genus.

2.2. On the biology of speciation: Nongeographical barriers to gene flow

Reproductive isolating barriers can restrict gene flow between species by preventing successful interbreeding among closely related species due to intrinsic or extrinsic factors (Coyne & Orr, 2004). These reproductive isolating barriers can act either early in an organism’s lifecycle (prezygotic, before zygote formation), or can be late-acting (postzygotic, after zygote formation) (Dobzhansky, 1937). Studies examining reproductive isolating barriers found that prezygotic isolating barriers typically exhibit a stronger influence than postzygotic barriers in restricting gene flow between closely related species (Ramsey, Bradshaw, & Schemske, 2003; Dopman, Robbins, & Seaman, 2009; Sanchez-Guillen, Cordoba-Aguilar, Cordero-Rivera, & Wellenreuther, 2014), and this is likely due to their early action in the organism’s lifecycle. However, examining how these reproductive isolating barriers emerge and restrict gene flow remains poorly understood. In this section, we review the most prevalent reproductive isolating barriers that occur between species of *Daphnia*, and the implications for advancing the field of speciation research.

2.2.1 Ecological modes of speciation: habitat and temporal isolation

Reproductive isolating barriers could arise as a byproduct of adaption to local ecological factors (e.g. habitat preference, resource use, predation pressure) that ultimately prevent locally adapted populations from interbreeding (Coyne & Orr, 2004). Ecology can play a central role in reproductive isolation, with ecological differentiation resulting in both prezygotic and/or postzygotic isolation, to the extreme where it promotes speciation (e.g. ecological speciation, Schluter, 1996). In the case of recently diverged species that occur in distinct habitats, ecological barriers are often considered important during the early stages of speciation (Orr & Smith, 1998; Ramsey et al., 2003; Sanchez-Guillen et al., 2014). In this section, we examine the role of ecology in prezygotic isolating barriers, specifically habitat and temporal isolation as it pertains to *Daphnia*.

Habitat isolation occurs when potentially interbreeding species are not encountering each other during mating season due to their inability to efficiently use each other’s habitat. In the case of *Daphnia*, many sister species appear to inhabit various types of freshwater habitats with distinct ecology (Taylor et al., 1996; Weider et al., 1999a), such as stratified lakes with fish or ephemeral ponds with invertebrate predators. Habitat shifts have been shown to accelerate rates of evolution in *Daphnia* (Colbourne, Wilson, & Hebert, 2006), shape life history traits (De Mott & Pape, 2005; Seidendorf et al., 2010), morphological traits (Zellmer, 1995; Miner et al., 2013; Brandon & Dudycha, 2014), biological functions such as energy metabolism (Simcic & Brancelj, 1997; Dolling et al., 2016), and behaviours (De Meester, 1993; Pijanowska & Kowalczewski, 1997). In the *D. pulex* complex, the North American *D. pulex* inhabits ephemeral ponds, while *D. pulicaria* occurs in permanent lakes. There are differences in life history between them (Dudycha & Tessier, 1999; Dudycha, 2004), such as distinct anti-predator behaviour, and there is strong genetic differentiation according to habitat (Pfrender, Spitze, & Lehman, 2000). The two closely related species, *D. parvula* and *D. retrocurva* also occur in different habitats and rarely co-occur (Costanzo & Taylor, 2010). While *D. parvula* occurs in small lakes with a lower risk of invertebrate predation, and displays no morphological defenses, *D. retrocurva* occurs in larger habitats with a higher risk of invertebrate predation and exhibits prominent helmets as an anti-predatory defense (Beaton & Hebert, 1997).

Coexistence of closely related species in lakes is also possible due to habitat segregation and partitioning, where closely related species can be found in distinct regions of the water column (Weider, 1984), and exhibit differences in body size depending on predation risk (Leibold & Tessier, 1991; Gonzalez & Tessier, 1997; Boersma, Spaak, & De Meester, 1998) and competition for resources (Leibold, 1991; Geedy, Tessier,

& Machledt, 1996). For example, although *D. mendotae* and *D. dentifera* frequently co-occur in large lakes, they segregate due to biotic factors. *D. mendotae* is often found in the upper water column and is better equipped to deal with invertebrate predators due to anti-predator defenses compared to *D. dentifera*, which inhabits the lower water column to avoid predation by fish (Taylor & Hebert, 1993; Duffy, Tessier, & Kosnik, 2004). Similarly, in the *Daphnia longispina* species complex, *D. galeata*, *D. longispina* (*hyalina* morph), and *D. cucullata* co-occur in the same lakes in Germany. *D. longispina* (*hyalina* morph) exhibits vertical diel migration during the year, while *D. galeata* remains in the upper 20m of the water column all year round (Weider & Stich, 1992). Coexistence between *D. galeata* and *D. cucullata* is possible due to niche segregation of resources due to differences in mesh size (Boersma, 1995). However, recent studies show *D. galeata* occurring south of the Alps at low altitudes prefer higher temperatures and higher phosphorus content (Yin, Giessler, Griebel, & Wolinska, 2014), while *D. longispina* (*hyalina* morph) and *D. cucullata* are distributed in the north, particularly with *D. longispina* (*hyalina* morph) occurring in large lakes with low phosphorus content (Keller, Wolinska, Manca, & Spaak, 2008). Despite habitat co-occurrence, the differential niche preferences of these two species could restrict gene flow between them. While collectively these examples suggest that habitat might play an important role in structuring species distribution in *Daphnia*, few experimental studies have investigated the role of ecological speciation in driving the diversification of daphniids. Furthermore, habitat choice and reciprocal transplant experiments have not been utilized to study directly the impact of habitat isolation in *Daphnia* speciation. However, indirect evidence for the role of habitat isolation in maintaining the integrity of species comes from studies that show how environmental stressors that impact the quality of the habitat (pollutants, metals, contaminants, temperature, etc.) can facilitate hybridization and introgression between closely related species and alter species distributions (Brede et al., 2009; Rogalski, Leavitt, & Skelly, 2017; Millette, Gonzalez, & Cristescu, 2020). Of particular interest are the genes that may be associated with habitat preference. For example, the ecological species *D. pulex* and *D. pulicaria* are fixed for different LDHA alleles, which could indicate adaptation to the different habitats due to differences in metabolic requirements in the environment (Hebert, Beaton, Schwartz, & Stanton, 1989; Crease, Floyd, Cristescu, & Innes, 2011; Cristescu, Demiri, Altshuler, & Crease, 2014).

Temporal (allochronic) isolation could also be an important barrier to gene flow in *Daphnia*. Closely related species often co-occur in the same habitats or region but breed (invest in sexual reproduction) at different times of the year. In the *D. longispina* species complex, *D. galeata*, *D. longispina* (*hyalina* morph) and *D. cucullata* are found to co-occur in lakes but sexual reproduction occurs in the spring and summer for *D. galeata* (Machacek, Vanickova, Seda, Cordellier, & Schwenk, 2013), whereas *D. longispina* (*hyalina* morph) and *D. cucullata* are found to invest in sexual reproduction during the fall season (Spaak, 1995; Spaak, 1996; Jankowski & Straile, 2004). Although strong seasonal dichotomy in sexual reproduction has not been observed between *D. longispina* (*hyalina* morph) and *D. cucullata*, differences in the annual occurrence of sexual reproduction between the two species has been reported (Vijverberg & Richter, 1982). In the *D. pulex* species complex, *D. pulex* and *D. pulicaria* show distinct responses to photoperiod. In laboratory conditions, the lake species *D. pulicaria* reproduces sexually during short days (Stross & Hill, 1965; Perez-Martinez, Barea-Arco, Conde-Porcuna, & Morales-Baquero, 2007) while the pond species *D. pulex* invests in sexual reproduction during long days (Deng, 1996; Deng, 1997). This finding reflects natural conditions, since ephemeral pond habitats are often subjected to complete evaporation by mid-summer while permanent lake habitats remain habitable until the beginning of winter (Threlkeld, 1987).

In daphniids, sex determination and sexual reproduction depend on environmental factors (Deng, 1996; Alekseev & Lampert, 2001; Tessier & Cáceres, 2004; Slusarczyk, Ochocka, & Cichocka, 2012; see Glossary). Induction of sexual reproduction of females and production of males under laboratory conditions is influenced primarily by photoperiod (Stross & Hill, 1965; Kleiven, Larsson, & Hobæk, 1992), and at times by a second stimulus such as population density (Stross & Hill, 1965; Hobæk & Larsson, 1990), temperature (Stross, 1969; Korpelainen, 1986; Camp, Haeba, & LeBlanc, 2019), chemical cues (Slusarczyk, 1995; Pijanowska & Stolpe, 1996; Navis, Waterkeyn, De Meester, & Brendonck, 2018), or a combination of these factors (Kleiven et al., 1992). Current research progress into the genetic and molecular basis of sexual reproduction revealed candidate genes that are likely to facilitate the switch from parthenogenetic reproduction to sexual

reproduction (Kato et al., 2008; Liu et al., 2014; Guo et al., 2015; Li et al., 2016), including the production of ephippial eggs and males (Kato, Kobayashi, Watanabe, & Iguchi, 2011; Xu et al., 2014; Guo et al., 2015). The use of juvenile hormones such as methyl farnesoate can stimulate the production of males. Methyl farnesoate receptors trigger a signalling cascade into the downstream expression of genes that are responsible for male production (LeBlanc & Medlock, 2015; Toyota et al., 2015; Toyota, Sato, Tatarazako, & Iguchi, 2017; Camp et al., 2019), and stimulated by photoperiod and environmental cues. Moreover, recent molecular studies show that in *D. magna*, the switch between parthenogenetic to sexual reproduction is associated with a photoreceptor gene, rhodopsin (Roulin, Bourgeois, Stiefel, Walser, & Ebert, 2016; Toyota et al., 2019), which could be a candidate gene associated with temporal isolation between closely related species. Other candidate genes such as the temporal clock genes (*per*), which have been found in the *D. pulex* genome (Bernatowicz et al., 2016) are likely influenced by photoperiod (Toyota et al., 2019). However, it is not clear whether there are differences in transcription activation of *per* across different species of *Daphnia*.

2.2.2. Behavioral and non-ecological isolation

Behavioural isolation can be a strong reproductive isolating barrier for species with complex mating signals and rituals. Also known as ethological isolation, this reproductive barrier can occur when closely related species do not mate due to differences in their complex courtship rituals. Behavioural isolation has been found to be a strong barrier between closely related species of rotifers (Schroder & Walsh, 2010). However, the role of behavioural isolation in the speciation of *Daphnia* received very little attention.

Fundamental aspects of the mating behaviour of daphniids remain largely unexplored. For example, it is unclear how males locate and recognize conspecific females. In copepods and rotifers, males use chemoreception, and it is suggested that males can discriminate the pheromones of conspecific females (Katona, 1973). In *Daphnia*, males are found to pursue sexually receptive females more often than unreceptive females (Winsor & Innes, 2002), suggesting some form of recognition of the reproductive stage of females. Additional evidence comes from swarming behaviour during sexual reproduction in *Daphnia* (Young, 1978). Furthermore, swimming patterns between males and females are distinct, specifically, males swim faster and orthogonally, a pattern known as ‘scanning’ behaviour (Gerritsen, 1980; Brewer, 1998) that can maximise encounter rate. Yet, Crease and Hebert (1983) were unable to replicate swarming behaviour in a laboratory setting and determine whether males were capable of detecting females through chemoreception. An assessment of the *D. pulex* reference genome revealed 58 gustatory chemoreceptor genes (Penalva-Arana, Lynch, & Robertson, 2009), which may be good subjects for research on mate recognition. Another proposed strategy for males to locate females is via mechanoreception of fluid disturbances generated by the specific swimming and filtering behaviour (Brewer, 1998). It is possible that glycoproteins located in the ovaries of females could provide a distinguishing signal for mate recognition once the male attaches to the female (Carmona & Snell, 1995). However, it has not been shown that either of these strategies are commonly used for mate recognition in daphniids.

Daphnia mating behaviours were first documented by Jurine (1820) and Weismann (1880) who concluded that *Daphnia* do not exhibit elaborate courtship rituals after males locate females. More recently, mating behaviours have been described in a few species of daphniids (Brewer, 1998; Winsor & Innes, 2002; La et al., 2014). Once the male attaches to the female, copulation occurs roughly 15 seconds before the male detaches (Brewer, 1998). While males appear to mate indiscriminately when they encounter females, females are found to exhibit behaviours to deter mating (e.g. escape response), suggesting female choice (Jurine, 1820). While Winsor and Innes (2002) have examined mate choice in conspecific *D. pulex*, mate choice experiments between closely related species have largely not been explored, and little is known about whether there are differences in mating behaviours across species of daphniids.

In the absence of ecological isolating barriers, hybridization between closely related species of daphniids is common (Schwenk & Spaak, 1995; Keller et al., 2008), suggesting that behavioural isolation may not be a strong reproductive barrier in this genus. However, not all sister species are found to hybridize indiscriminately when in contact, and it is not fully understood if daphniids can exhibit other subtle forms of mating recognition. Recently, no-choice mating experiments between *D. pulex* and *D. pulicaria* have found

lower mating-fertilization success in heterospecific than in conspecific crosses (Chin, Cáceres, & Cristescu, 2019). Mate choice experiments between closely related species are needed to determine the degree to which daphniids show preference for conspecifics in the presence of heterospecific mates.

2.2.3. Mechanical and gametic isolation

The degree to which mechanical and gametic isolation play a role in reproductive isolation between closely related species remain largely unexplored in *Daphnia*. While it appears that males exhibit little discrimination when approaching heterospecific females, it is uncertain if there are morphological differences in reproductive systems that could prevent successful mating and fertilization. Wuerz, Huebner, and Huebner (2017) described the male reproductive system in *D. magna*, but no morphological studies provide a contrast of morphological differences in the reproductive systems between species. When there is an excess of males in nature, unmated females are rare (Innes, 1997), and females may copulate with multiple males. While sperm storage appears unlikely (Huebner & Huebner, 2016), research into gamete viability (see Xu et al., 2015) and the process of sperm transmission towards eggs are direly needed. Thus, more studies are required to characterize the morphological differences in the anatomy of the reproductive organs as well as potential mechanisms of gametic isolation after successful heterospecific mating.

2.2.4. Postzygotic isolation

Postzygotic isolation occurs when hybridization between closely related species produces unfit hybrids due to intrinsic (developmental) or extrinsic (environmental) factors. In the *Daphnia* genus, interspecific hybridization is common, with closely related species in all species complexes producing hybrids with one potential exception, the *Daphnia longiremis* species complex. Interspecific hybridization was long suspected to occur due to the presence of intermediate morphological forms (Einsle, 1966; Lieder, 1983; Flossner & Kraus, 1986; Taylor & Hebert, 1992; Giessler, Mader, & Schwenk, 1999) and this observation was validated by molecular analyses (Wolf & Mort, 1986; Wolf, 1987; Taylor & Hebert, 1993; Spaak, 1996; Spaak, 1997; Giessler, 1997; Giessler & Englebrecht, 2009). Detailed studies on hybrids revealed intermediate life history attributes (Weider & Wolf, 1991; Spaak & Hoekstra, 1995; Dudycha & Tessier, 1999), differences in resource utilization (Boersma & Vijverberg, 1994a; Repka, 1996; Von Elert, 2004) and other ecological requirements (Taylor & Hebert, 1992; Duffy et al., 2004). Here, we summarize the potential of postzygotic isolating barriers in *Daphnia* based on intrinsic and extrinsic postzygotic isolation.

Intrinsic postzygotic isolation occurs as a result of genetic differences between closely related species that diminish the production and/or performance of hybrids and can occur either during the developmental process (hybrid inviability), or during sexual maturity (hybrid sterility). Three closely related species, *D. galeata*, *D. longispina* (*hyalina* morph), and *D. cucullata* are found to co-occur in the same area or habitats, and hybridization between these three species is often bidirectional (Giessler et al., 1999). Introgression of alleles from one species to another via hybridization and backcrossing has also been documented in many studies (Taylor & Hebert, 1992; Taylor & Hebert, 1993; Schierwater, Ender, Schwenk, Spaak, & Streit, 1994; Spaak, 1996; Spaak, 1997; Spaak, Denk, Boersma, & Weider, 2004; Yin, Wolinska, & Giessler, 2010). Field experiments found low hatching success and survivorship of hybrids compared to parental species (Carvalho & Wolf, 1989; Wolf & Carvalho, 1989; Keller & Spaak, 2004; Griebel, Giessler, Yin, & Wolinska, 2016). Laboratory hatching experiments between *D. galeata* and *D. cucullata*, and *D. galeata* and *D. longispina* (*hyalina* morph) corroborate these findings (Schwenk, Bijl, & Menken, 2001; Keller & Spaak, 2004; Brede, Straile, Streit, & Schwenk, 2007; Keller, Wolinska, Tellenbach, & Spaak, 2007). Asymmetric reproductive isolating barriers are also observed. For example, crosses between *D. cucullata* females and *D. galeata* males are more successful than the reciprocal crosses, consistent with observations of these particular hybrids commonly found in nature (Schwenk et al., 2001). While unidirectional crosses between *D. pulex* females with *D. pulicaria* males show higher hatching and survivorship than parentals (Heier & Dudycha, 2009), postzygotic isolating barriers were found to be symmetric between *D. pulex* and *D. pulicaria* (Chin et al., 2019).

Extrinsic postzygotic isolation occurs due to ecological or behavioural differences between closely related

species, which reduces the performance of hybrids that often have intermediate characteristics. In nature, hybrids are locally produced and occur in hybrid zones with environmentally favourable conditions (Taylor & Hebert, 1992; Muller & Seitz, 1995; Spaak, 1994; Spaak, 1997). Persistence of hybrids in the environment may be consistent with the hybrid inferiority model, where hybrids occur in ‘tension zones’ and experience the balancing forces of dispersal and selection against hybrids (Barton & Hewitt, 1985). However, since *Daphnia* hybrids can propagate by clonal reproduction, hybrid persistence and dominance can be observed in ‘tension zones’ (Weider, 1993; Spaak & Hoekstra, 1997; Schwenk, 1997), leading to the temporal hybrid superiority model (Spaak & Hoekstra, 1995). Examples of temporal hybrid superiority are relatively common in *Daphnia*, where hybrids are found to exhibit higher fitness than the parental species in certain environmental conditions and periods of the year, such as food quality (Seidendorf, Boersma, & Schwenk, 2007; Brzezinski & Von Elert, 2007; Weider, Jeyasingh, & Looper, 2008) and concentration (Boersma & Vijverberg, 1994b; Repka, Vesela, Weber, & Schwenk, 1999), predation (Declerck & De Meester, 2003), temperature (Weider & Wolf, 1991), parasitism (Wolinska, Bittner, Ebert, & Spaak, 2006) and a variety of other environmental factors (Griebel et al., 2015). However, hybrid fitness often varies in different environments (Löffler, Wolinska, Keeler, Rothhaupt, & Spaak, 2004). Ecological inviability of hybrids has been hypothesized to occur between hybrids of *D. cucullata* and *D. longispina* (*hyalina* morph), where hybrids often occur in intermediate habitats compared to parentals (Seda, Petrusek, Machacek, & Smilauer, 2007; Petrusek et al., 2008), exhibit intermediate traits for foraging (Machacek & Seda, 2016), and lower fitness in response to predation pressure (Spaak, Vanoverbeke, & Boersma, 2000). Hybrids of *D. cucullata* and *D. galeata* display intermediate traits linked to predator avoidance (Spaak, 1995). Moreover, overwintering strategies also differ between *D. galeata* and *D. longispina* (*hyalina* morph), where *D. galeata* overwinters, *D. longispina* (*hyalina* morph) produces resting eggs, and hybrids exhibit intermediate traits (Zeis, Horn, Gigengack, Koch, & Paul, 2010). *D. galeata* x *D. longispina* (*hyalina* morph) hybrids are infected by parasites more often than parental species, thereby reducing their fitness (Wolinska, Keller, Bittner, Lass, & Spaak, 2004). Additionally, low fitness was observed in these hybrids under low food quality (Brzezinski, 2015).

While life history experiments to determine the role of ecology in hybrids in *Daphnia* are common, the potential involvement of behavioural sterility in hybrids remains largely unexplored. Detailed observations of mating behaviour of hybrids compared with parental species would greatly benefit this line of research. Experimental case studies are particularly needed to determine the extent of postzygotic isolating barriers across different sister species of *Daphnia*. Such studies are particularly lacking in species from the southern USA and Mexico, where endemic daphniid species inferred from allozyme data (Hebert, Schwartz, Ward, & Finston, 1993; Hebert & Finston, 1996) produce hybrids detected in intermediate habitats compared to those occupied by the parental species.

3. On the genetics of speciation:

3.1 Hybridization and polyploidization

Hybridization is commonly found in nature (Arnold, 1997; Mallet, 2005), and yet the role of hybridization and gene flow on speciation remains contentious. On one hand, gene flow can be viewed as a detriment to the speciation process due to its homogenization effects on locally adapted alleles and the dismantling effect in emerging reproductive barriers (Mayr, 1963). And yet, gene flow can result in the production of new species (e.g. instantaneous speciation) by strengthening prezygotic reproductive barriers due to reinforcement (Slatkin, 1987; Rieseberg, 1997; reviewed in Abbott et al., 2013). Theoretical models have shown that under some scenarios, gene flow can aid the process of speciation (Kondrashov & Kondrashov, 1999; Pinho & Hey, 2010). These theoretical predictions are supported by increasing evidence of speciation-with-gene-flow occurring in nature (Niemiller, Fitzpatrick, & Miller, 2008; Via, 2009; Rougeux, Bernatchez, & Gagnaire, 2017). Hybrid persistence occurs in *Daphnia* due to continuous local production and clonal propagation under favourable conditions. In the *Daphnia* genus, a well documented instance of hybridization giving rise to a new species is the *Daphnia middendorffiana* case. *Daphnia middendorffiana* is primarily distributed in the Arctic regions and is believed to be the result of hybridization between *D. pulicaria* and *D. tenebrosa* or *D. melanica* sometime during the Pleistocene glaciations (Dufresne & Hebert, 1997). *D. middendorffiana*

has a high tolerance to lower temperatures (Yurista, 1999), and can show stronger pigmentation, which was hypothesized to be an adaptive trait against UV radiation (Luecke & O'Brien, 1983). While less explored, speciation has also been suggested to arise in North American *D. mendotae* from reticulate events between European populations of *D. galeata* and *D. longispina* (Taylor et al. 1996).

Interspecific hybridization in *Daphnia* can also result in polyploidy. Parthenogenesis has been found to be a prerequisite to polyploidy in plants (Stebbins, 1950), and this also appears to be the case for parthenogenic organisms such as *Daphnia*. Daphniid polyploids are generally triploids and tetraploids as a result of genome duplication (autopolyploidization), hybridization (allopolyploidization), or a combination of both. In crosses between *D. pulex* and *D. pulicaria*, the production of polyploids appears to depend on the direction of the cross. When *D. pulicaria* is the mother, polyploids are produced; yet diploids are formed when *D. pulex* is the maternal parent (Dufresne & Hebert, 1994; Dufresne & Hebert, 1997). These polyploids can often be found in arctic and subarctic regions, with increasing latitudes exhibiting an increase in the occurrence of polyploids (geographical parthenogenesis; Beaton & Hebert, 1988; Ward, Bickerton, Finston, & Hebert, 1994).

In the temperate regions of South America, asexual tetraploids are often identified based on molecular analyses (Adamowicz, Gregory, Marinone, & Hebert, 2002). Phylogenetic analyses showed that these temperate polyploids originated from a common ancestor that is likely related to North American *D. pulicaria*. It has been suggested that the common ancestor of these lineages was a hybrid form of *D. pulex* x *D. pulicaria*, which may have been introduced to South America (Mergeay et al., 2008). Asexual tetraploids are also found in high altitude lakes in the tropical Andes region (Aguilera, Mergeay, Wollebrants, Declerck, & De Meester, 2007). In contrast to the temperate polyploids in Argentina, these tropical polyploids are likely of local origin, as evident by a high degree of genetic variation, comparable to the Arctic polyploids.

It has been hypothesized that polyploidy is selected for extreme environments due to its high adaptive potential (Beaton & Hebert, 1988; Van de Peer, Mizrachi, & Marchal, 2017). In the case of Arctic polyploids, clonal diversity is higher than in the diploid counterparts, which can promote phenotypic diversity due to beneficial mutations, leading to an increase in fitness (Weider, Beaton, & Hebert, 1987). For example, some Arctic *Daphnia* polyploids exhibit melanism, which protects against UV radiation and are capable of inhabiting clear-water ponds unlike their non-melanic counterparts, which inhabit only ponds with high humic content (Hebert & McWalter, 1983; Weider & Hebert, 1987). Additionally, polyploids were found to have divergent physiological strategies in osmoregulation depending on their habitats (Weider & Hebert, 1987). Polyploids were also found to reach maturity at a later stage compared to diploids, producing larger body sizes at maturity and smaller clutch sizes with larger-sized offspring (Weider, 1987). Life-history comparisons between polyploid and their diploid counterparts found polyploids to be better adapted and have earlier maturation at lower temperatures and are therefore better suited for the short reproductive season in the Arctic (Dufresne & Hebert, 1998). Another advantage of polyploids is that the additional genetic material can reduce the effects of accumulating recessive deleterious mutations, as daphniid polyploids are typically obligately parthenogenic (OP). Unlike their sexual diploid counterparts, the obligately asexual polyploids cannot purge the mutational load and are theorized to represent evolutionary dead ends.

3.2. Transition to asexuality

While we discussed speciation of daphniids in the scope of reproductively isolated groups, we would be remiss to neglect the role of speciation in obligately asexual daphniids (see Glossary). Asexual species can be defined as distinct groups capable of adapting to different ecological niches due to divergent selection or geographic isolation (Barracough, Birky Jr., & Burt, 2003; Birky Jr., Wolf, Maughan, Herbertson, & Henry, 2005). The transition to obligate asexuality has been studied extensively within the *D. pulex* species complex, particularly in hybrids of *D. pulex* and *D. pulicaria*. Obligately parthenogenic (OP) populations of *Daphnia* often have a hybrid background (*D. pulex* x *D. pulicaria*) and are found in northeastern and southern North America in intermediate habitats such as permanent ponds (Pantel, Juenger, & Leibold, 2011) and can be also found in the central region of North America along with cyclically parthenogenic (CP) populations (Hebert et al., 1993; Hebert & Finston, 2001). The transition to OP has been traced back to

roughly 1-175 kya (Hebert et al., 1989; Crease, Stanton, & Hebert, 1989; Paland, Colbourne, & Lynch, 2005; Tucker, Ackerman, Eads, Xu, & Lynch, 2013), suggesting a relatively recent evolution of obligate asexuality.

The switch from CP to OP in *D. pulex* can be considered as a form of hybrid sterility, as a result of Dobzhansky-Muller incompatibilities. OP is caused by a cluster of meiosis suppressor genes that are located in at least four different genomic regions that interact epistatically (Lynch, Seyfert, Eads, & Williams, 2008; Tucker et al., 2013; Xu, Innes, Lynch, & Cristescu, 2013). Many of these alleles are found to be of *D. pulicaria* origin (Xu, et al., 2013). As OP populations have not been reported in *D. pulicaria* (but see Culver & Acosta, 2018; Millette et al., 2020), it is hypothesized that OP originated due to an ancient hybridization event between *D. pulex* and *D. pulicaria*, followed by introgression via multiple rounds of backcrossing (Tucker et al., 2013; Xu et al., 2013; Xu et al., 2015). Despite lower male production in OP populations (Innes, Fox, & Winsor, 2000), some OP females can produce males that can undergo spermatogenesis (Innes & Hebert, 1988; Hebert et al., 1989), as meiosis is not suppressed in males. These males can mate with sexual females in the population, thereby spreading obligate asexuality to sexual populations, a process termed ‘contagious asexuality’ (Innes & Hebert, 1988; Lynch et al., 2008). Another case of hybrid sterility due to Dobzhansky-Muller incompatibilities is the non-male producing clones observed within populations of *D. pulex* (Innes & Dunbrack, 1993). These non-male producers have a genetic basis which can be traced back to introgression with *D. pulicaria* (Ye et al., 2019).

While theory suggests that asexual lineages are considered evolutionary dead ends because they accumulate a high mutation load (e.g. Muller’s ratchet), high rates of loss of heterozygosity events (a form of ameiotic recombination) have been documented in obligate asexual lineages (Omilian, Cristescu, Dudycha, & Lynch, 2006; Xu, Omilian, & Cristescu, 2011). Moreover, OP populations that produce males can cross with CP populations and can account for the persistence of these lineages in nature (Paland et al., 2005). Other cases of asexuality have been documented in European populations of *D. pulex* (Lehto & Haag, 2010), *D. magna* (Svendsen et al., 2015) and *D. cephalata* (Hebert, 1981); however, little is known about the underlying mechanism involved in the transition to obligate asexuality in these species, and how these OP populations persist in nature.

4. Conclusions and Future Research Directions

Based on the literature search of 253 studies documenting speciation in *Daphnia* genus, we find that the majority of studies examine geographic barriers (55%; 139 studies). While geographic barriers clearly facilitate divergence between species of *Daphnia* (Hebert & Wilson, 1994; Ishida & Taylor, 2007b), ecological barriers are also likely to be prominent due to ecological opportunity and habitat differences shaped by the interaction of biotic and abiotic factors. Despite the presence of ecological barriers in many young species pairs of *Daphnia*, interspecific hybridization is frequent in species complexes within the genus, suggesting that reproductive isolating barriers between closely related species are permeable. Moreover, genetic studies suggest that in several instances, hybridization was the driver of speciation rather than the impediment to diversification.

Based on experimental studies (Table 2; Figure 3), we find that none of the reproductive isolating barriers are able to completely restrict gene flow completely between closely related species. However, when examining ecological and non-ecological isolating barriers, we find that the majority of studies examine ecological isolating barriers (68%), focusing mostly on two species complexes, *Daphnia pulex* and *Daphnia longispina*, especially when examining non-ecological isolating barriers (93%; Figure 1). There is a need for more experimental studies examining the relative strength of reproductive isolating barriers between closely related species of *Daphnia*, particularly to establish the importance of prezygotic and postzygotic isolating barriers. Specifically, there is a lack of studies that examine behavioural, mechanical, and gametic isolation between closely related species. Moreover, the increasing availability of genomic tools and resources, the identification of loci or regions that are associated with reproductive isolation between closely related species in *Daphnia*, as well as comparative studies of different sister species across the speciation continuum, make it increasingly possible to infer speciation processes.

Factors responsible for the maintenance of freshwater diversity are receiving increased attention. The rich biodiversity heritage of freshwater systems has been exploited by our civilization for millennia, perhaps more than any other natural systems and understanding the forces that shape and maintain this diversity continues to be of great interest (Dudgeon et al., 2006). With the increase of human activity in freshwater systems (Foley et al., 2005), identification of the major drivers of speciation in *Daphnia* provides an opportunity to identify the impact of human influence on the keystone species of freshwater ecosystems.

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Tables

Table 1. Summary of *Daphnia* speciation studies, grouped by experimental, genetic, and phylogenetic studies. Listed are the types of procedures and/or molecular markers used in the study. Numbers in parentheses

() indicate the number of studies associated.

Experimental (15)	Genetic (36)	Phylogenetic (47)
sampling/ surveys (3)	allozymes (21)	mitochondrial DNA (46)
cross experiment (2)	mitochondrial DNA (13)	nuclear DNA (13)
hatching assay (6)	microsatellites (7)	allozymes (3)
fitness assays (3)	nuclear DNA (7)	microsatellites (3)
survivorship (2)	RAD sequencing (1)	
photoperiod/timing of reproduction (3)		
tests for asexuality (1)		

Table 2. Mean estimates of the component of reproductive isolating barriers (RI_i) and estimated divergence time (Mya) of closely related species pairs in *Daphnia*. We omitted articles that only examine hybrid success, as these studies do not have a direct comparison with parental species. Estimates of RI_i for each species pair were obtained from data sources and were calculated based on methods from Sobel and Chen (2014). Sequence divergence estimates were based on Colbourne and Hebert 1996¹, Taylor et al. 1996², and Schwenk et al 2000³.

Species Pair	Divergence time (Mya)	Reproductive Isolating Barrier	Component of Reproductive Isolation
<i>D. galeata</i> x <i>D. longispina</i>	5.05 ²	Habitat	0.400
<i>D. cucullata</i> x <i>D. hyalina</i>	4-6 ²	Habitat	0.209
		Temporal	0.083
<i>D. hyalina</i> x <i>D. galeata</i>	3.73 ³	Habitat	-0.239
		Temporal	0.082
		Hybrid Inviability	0.652
<i>D. galeata</i> x <i>D. cucullata</i>	2.57 ³	Habitat	0.131
		Temporal	0.569
		Ecological Inviability	-0.048
<i>D. pulex</i> x <i>D. pulicaria</i>	2 ¹	Habitat	0.979
		Temporal	0.313
		Mating-Fertilization	0.174
		Hybrid Inviability	-0.104
		Hybrid Sterility	0.005

Sources:

1. Hebert et al. 1989. Patterns of genotypic diversity in Czechoslovakian *Daphnia*
2. Petrusek et al. 2008. *Daphnia* hybridization along ecological gradients in pelagic environments: the potential for the presence of hybrid zones in plankton.
3. Wolf and Mort 1986. Inter-specific hybridization underlies phenotypic variability in *Daphnia* populations
4. Wolf 1987. Inter-specific hybridization underlies phenotypic variability in *Daphnia* populations
5. Vijverberg and Richter 1982. Population dynamics and production of *Daphnia hyalina* Leydig and *Daphnia cucullata* Sars in Tjeukemeer
6. Jankowski and Straile 2004. Allochronic differentiation among *Daphnia* species, hybrids and backcrosses: the importance of sexual reproduction for population dynamics and genetic architecture
7. Spaak et al. 2004. Spatial and temporal patterns of sexual reproduction in a hybrid *Daphnia* species complex.
8. Carvalho and Wolf 1989. Resting eggs of lake *Daphnia* I. Distribution, abundance and hatching of eggs

- collected from various depth in lake sediments
9. Wolf and Carvalho 1989. Resting eggs of lake-*Daphnia* II. In situ observations on the hatching of eggs and their contribution to population and community structure
 10. Keller and Spaak 2004. Nonrandom sexual reproduction and diapausing egg production in a *Daphnia* hybrid species complex
 11. Keller et al. 2007. Reproductive isolation keeps hybridizing *Daphnia* species distinct.
 12. Brede et al. 2007. The contribution of differential hatching success to the fitness of species and interspecific hybrids.
 13. Zeis et al. 2010. A major shift in the *Daphnia* genetic structure after the first ice-free winter in a German reservoir.
 14. Bast, 1993. Population dynamik ausgewählter Cladocerenarten in Seen unterschiedlichen Trophiegrades. PhD thesis, Faculty of Biology, J-Gutenberg University, Mainz.
 15. Spaak et al. 2000. Predator-induced life-history changes and the coexistence of five taxa in a *Daphnia* species complex.
 16. Chin et al. 2019. The evolution of reproductive isolation in *Daphnia*.
 17. Heier and Dudycha 2009. Ecological speciation in a cyclic parthenogen: sexual capability of experimental hybrids between *Daphnia pulex* and *Daphnia pulicaria*

Figure captions:

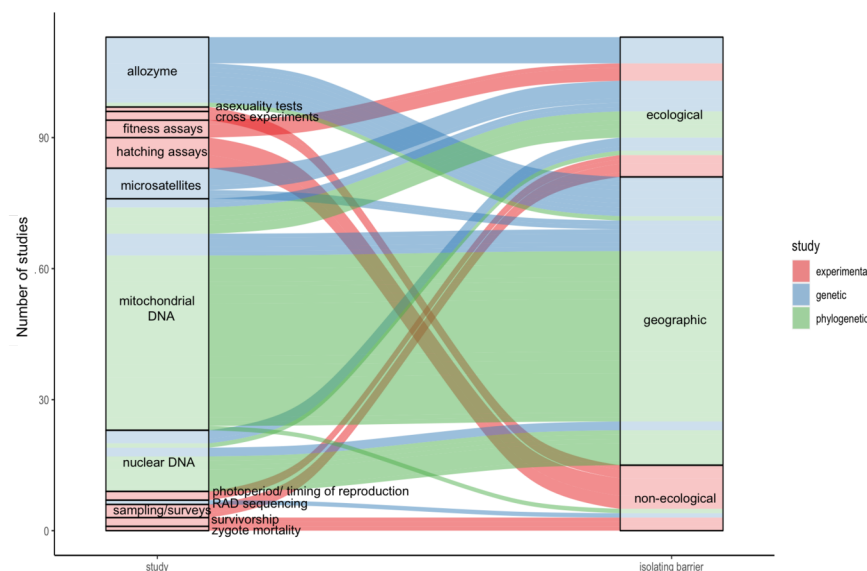
Figure 1. a) Number of *Daphnia* studies that examine geographic, ecological and non-ecological isolating barriers, associated with the type of method used in the study. The height of the bar indicates the total number of studies in the group, while the width of each line represents the number of studies corresponding to geographic, ecological or non-ecological isolating barriers. Each line is coloured by the type of study: experimental (red), genetic (blue), or phylogenetic (green) evidence. b) The number of geographic, ecological/ non-ecological studies that examine multiple species pairs in the subgenus *Ctenodaphnia*, *Daphnia*, or species pairs in the species complex level.

Figure 2. The maximum likelihood phylogeny of the genus *Daphnia* based on mitochondrial markers 12S rRNA, 16S rRNA, and cytochrome oxidase subunit I (COI) obtained from Adamowicz and colleagues (2009). The subgenera *Daphnia*, *Ctenodaphnia*, and *Australodaphnia* are shown in black bars on the right. Mitochondrial markers were individually aligned using CLUSTAL-W (Thompson, Higgins, & Gibson, 1994), trimmed, and concatenated into a 1737 nt alignment. A best fit GTR model and partitioning scheme was estimated using PartitionFinder2 (Lanfear, Calcott, Kainer, Mayer, & Stamatakis, 2014). Phylogeny reconstruction was based on RAxML-ng (Kozlov, Darriba, Flouri, Morel, & Stamatakis, 2019) with convergence at 500 bootstrap replicates. Bootstrap support is indicated at the nodes. Indicated in arrows at the nodes are the possible intracontinental splits, and labels in red show the species capable of intercontinental dispersal. Branch colours signify the geographic distribution of each species: North America (red), Eurasia (blue), South America (green), Australia (orange), Africa (purple), Tibet (pink), Antarctica (grey).

Figure 3. Strengths of the components of reproductive isolation (RI_i) plotted against divergence time (Mya) based on metrics from Sobel and Chen (2014) from 17 experimental studies. We show the relationship of reproductive isolation against divergence time for (a) prezygotic reproductive isolating barriers, and (b) postzygotic reproductive isolating barriers. Divergence time estimates were based on mitochondrial markers (Table 2).

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Glossary:

Allopolyploidy: a hybrid that inherits two or more sets of chromosomes from two different parental species.

Apomixis: asexual reproduction without fertilization. Suppression of meiosis I during normal meiosis, followed by a single maturation division emitting a polar body.

Cyclical parthenogenesis: asexual mode of reproduction with alternating periods of sexual reproduction (facultative).

Environmental sex determination: sex is determined based on environmental cue rather than by a genetic basis.

Ephippium (plural ephippia): a protective casing that envelops resting eggs (diapause at blastulation).

Genotype: genetic background that determines the phenotype of an organism.

Haplotype: set of genes that is inherited together from a single parent.

Inducible defense: defense response activated from a previous encounter from a competitor or predator to prevent or reduce competition or predation.

Local adaptation: population of organisms evolve to become better at coping with local conditions.

Parthenogenesis: asexual mode of reproduction without the need for fertilization of an ovum, where eggs are developed ameiotically, producing genetically identical offspring.

Obligate parthenogenesis: asexual mode of reproduction without fertilization by sperm, where sexual eggs are produced via modified meiosis.

Supplementary Information

Title: Speciation in *Daphnia*

Authors: Tiffany A. Chin, Melania E. Cristescu

Supplementary Text

We searched the Web of Science database using the following keywords:

Geographic barriers : *Daphnia* + allopatric; *Daphnia* + geography; *Daphnia* + geographic; *Daphnia* + phylogeography; *Daphnia* + biogeography/biogeographic; *Daphnia* + vicariance/vicariant; *Daphnia* + endemism; *Daphnia* + divergence; *Daphnia* + refugia

Ecological barriers : *Daphnia* + temporal isolation; *Daphnia* + allochronic; *Daphnia* + temporal; *Daphnia* + photoperiod; *Daphnia* + diapause; *Daphnia* + habitat isolation; *Daphnia* + ecological isolation; *Daphnia* + habitat; *Daphnia* + ecology

Non-ecological barriers : *Daphnia* + mating; *Daphnia* + mate; *Daphnia* + mate choice; *Daphnia* + sperm; *Daphnia* + testes

Postzygotic barriers: *Daphnia* + postzygotic isolation; *Daphnia* + postzygotic; *Daphnia* + hybrid vigor; *Daphnia* + heterosis; *Daphnia* + hybrid inviability; *Daphnia* + inviability; *Daphnia* + sterility; *Daphnia* + hybrid

Supplementary Table 1. Summary of *Daphnia* speciation studies that examines ecological, non-ecological, geographic barriers, and hybridization. Each study is listed by the type of isolating mechanism and barrier (if not applicable, 'NA' is listed), as well as the evidence and protocol used to detect the isolating mechanism for each pair of species in the subgenus/species complex.

Isolating mechanism	Isolating barrier	Isolating barrier	Evidence	Evidence protocol
ecological	prezygotic	habitat isolation	phylogenetic	mitochondrial DNA
ecological	prezygotic	habitat isolation	phylogenetic	mitochondrial DNA; r
ecological	prezygotic	habitat isolation	genetic	allozyme
ecological	prezygotic	habitat isolation	experimental	sampling/survey
ecological	prezygotic	habitat isolation	genetic	allozyme
ecological	prezygotic	habitat isolation	genetic	allozyme
ecological	prezygotic	habitat isolation	genetic	allozyme
ecological	prezygotic	habitat isolation	genetic	allozyme; microsatellit
ecological	prezygotic	habitat isolation	genetic	microsatellites
ecological	prezygotic	habitat isolation	genetic	microsatellites
ecological	prezygotic	habitat isolation	genetic	microsatellites; mitoch
ecological	prezygotic	habitat isolation	genetic	nuclear DNA
ecological	prezygotic	habitat isolation	phylogenetic	mitochondrial DNA
ecological	prezygotic	habitat isolation	genetic	mitochondrial DNA; r
ecological	prezygotic	habitat isolation	phylogenetic; genetic	microsatellites; mitoch
ecological	prezygotic	habitat isolation	phylogenetic	mitochondrial DNA
ecological	prezygotic	temporal isolation	genetic	NA
ecological	prezygotic	temporal isolation	genetic	allozyme
ecological	prezygotic	temporal isolation	experimental	photoperiod/timing of
ecological	prezygotic	temporal isolation	experimental	photoperiod/timing of
ecological	prezygotic	temporal isolation	experimental	photoperiod/timing of
ecological	prezygotic	mating-fertilization isolation	experimental	cross experiment
ecological	prezygotic	mating-fertilization isolation	experimental	cross experiment
non-ecological	postzygotic	hybrid inviability	experimental	zygote mortality

Isolating mechanism	Isolating barrier	Isolating barrier	Evidence	Evidence protocol
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	hatching assay
non-ecological	postzygotic	hybrid inviability	experimental	survivorship
non-ecological	postzygotic	hybrid inviability	experimental	survivorship
non-ecological	postzygotic	hybrid inviability	experimental	survivorship
non-ecological	postzygotic	hybrid sterility	experimental	asexuality tests
non-ecological	postzygotic	hybrid sterility	phylogenetic	mitochondrial DNA
non-ecological	postzygotic	hybrid sterility	genetic	RAD sequencing
ecological	postzygotic	ecological inviability	experimental	fitness assay
ecological	postzygotic	ecological inviability	experimental	fitness assay
ecological	postzygotic	ecological inviability	experimental	fitness assay
ecological	postzygotic	ecological inviability	experimental	fitness assay
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	microsatellites; mitoch
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	allozyme; mitochondri
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic/ hybridization	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	genetic	allozyme; mitochondri
geographic	NA	NA	genetic	allozyme; mitochondri
geographic	NA	NA	genetic	allozyme
geographic	NA	NA	genetic	mitochondrial DNA
geographic	NA	NA	genetic	nuclear DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA

Isolating mechanism	Isolating barrier	Isolating barrier	Evidence	Evidence protocol
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	microsatellites; mitoch
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA; r
geographic/ hybridization	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	mitochondrial DNA; r
geographic	NA	NA	phylogenetic	mitochondrial DNA
geographic	NA	NA	phylogenetic	allozyme; mitochondri
geographic	NA	NA	phylogenetic	mitochondrial DNA
hybridization	NA	NA	genetic	allozyme
hybridization	NA	NA	genetic	allozyme
hybridization	NA	NA	genetic	allozyme
hybridization	NA	NA	phylogenetic	mitochondrial DNA; r
hybridization	NA	NA	genetic	allozyme; nuclear DN
hybridization	NA	NA	genetic	mitochondrial DNA; r
hybridization	NA	NA	genetic	nuclear DNA
hybridization	NA	NA	genetic	microsatellites; mitoch

Figure captions:

Supplementary Figure 1. Number of studies based on the search terms from Web of Science (Supplementary Text 1), grouped by the type of isolating barrier. Black bars indicate the total number of studies, and grey bars are the studies relevant to *Daphnia* speciation. Pie chart indicating the number of relevant studies in *Daphnia* speciation, grouped by studies of geographic (dark grey), ecological (black), and non-ecological (light grey) isolation.

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