Synthesis and scope of the role of postmating prezygotic isolation in speciation

Short title: Postmating prezygotic isolation in speciation

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ABSTRACT

How barriers to gene flow arise and are maintained are key questions in evolutionary biology. Speciation research has mainly focussed on barriers that occur either before mating or after zygote formation. In comparison, postmating prezygotic (PMPZ) isolation – a barrier that acts after gamete release but before zygote formation – is less frequently investigated but may hold a unique role in generating biodiversity. Here we discuss the distinctive features of PMPZ isolation, including the primary drivers and molecular mechanisms underpinning PMPZ isolation. We then present the first comprehensive survey of PMPZ isolation research, revealing that it is a widespread form of prezygotic isolation across eukaryotes. The survey also exposes obstacles in studying PMPZ isolation, in part attributable to the challenges involved in directly measuring PMPZ isolation and uncovering its causal mechanisms. Finally, we identify outstanding knowledge gaps and provide recommendations for improving future research on PMPZ isolation. This will allow us to better understand the nature of this often-neglected reproductive barrier and its contribution to speciation.

1. Introduction

Understanding the origin of species requires identifying barriers to gene flow between lineages and quantifying how different barriers contribute to total reproductive isolation (Marie Curie SPECIATION Network *et al.*, 2012; Sobel & Chen, 2014). There has been a tendency to categorise such barriers as either: i) **pre- mating/pollination** vs. **post-mating/pollination** (herein collectively called pre- or post- mating **isolation** (see Table 1: Glossary)) or ii) **prezygotic** vs. **postzygotic isolation** (Coyne & Orr, 2004) (Fig. 1). As a result, the terms premating and prezygotic, and postmating and postzygotic are often used interchangeably and speciation research tends to focus either on premating or postzygotic isolation (Coyne & Orr, 2004; Merrill et al., Reifova et al., Shaw et al., this volume). This framing has led to a dearth of research investigating the barriers to gene flow that act after **gamete release**, but before **karyogamy**, termed **postmating prezygotic (PMPZ) isolation** (Darwin, 1859; Lillie, 1921; Dobzhansky, 1937) (Fig. 1). Overlooking or confounding PMPZ isolation with other barriers to gene flow is more than a semantic problem. Neglecting or misidentifying the contribution of PMPZ isolation may lead to misinterpretation of the mode and tempo of reproductive isolation, skewing our understanding of the speciation process.

PMPZ isolation emerges from interactions between female and male gametes, and/or reproductive tract tissues and their secretions (e.g., pollen interacting with the stigma, or sperm traversing the female reproductive tract), that result in the reduced frequency of successfully fertilised eggs in crosses between taxa. Reduced fertilisation can occur via the interruption of the transport, storage, contact and/or fusion of gametes. The ubiquity of reproductive interactions leading to fertilisation means that PMPZ isolation can act in any taxa where sexual interactions are a necessary step in reproduction (i.e., most eukaryotes, outside of fungi which have a dikaryotic stage that does not neatly fit PMPZ categorisation; Giraud & Goubiere, 2012). This fact makes PMPZ isolation perhaps the most widespread potential form of prezygotic isolation to be found in eukaryotes. Consequently, studying PMPZ isolation offers a unique opportunity to make direct comparisons about the accumulation, strength, and types of prezygotic barriers across the eukaryotic tree of life.

PMPZ isolation was recognised early in the history of speciation research as a potential barrier to gene flow (Darwin, 1859; Lillie, 1921; Dobzhansky, 1937) but has been understudied compared to premating and postzygotic isolation (Howard *et al.*, 2009). Akin to the late realisation that sexual selection may continue after mating (Parker, 1970; Thornhill, 1983), the cryptic nature of **postmating interactions** has likely hindered progress in the field. The most recent reviews of PMPZ isolation in animals or plants were conducted over a decade ago (Howard, 1999; Howard *et al.*, 2009), and there have been no reviews examining **PMPZ mechanisms** and **PMPZ barriers** across eukaryotes. A contemporary review is timely since there have been significant advances in molecular techniques in the last 15 years enabling new insights into the prevalence, mechanisms, and evolution of PMPZ isolation (Manier *et al.*, 2013; Higashiyama & Takeuchi, 2015; Carlisle & Swanson, 2021; Cheung *et al.*, 2022).

Here, we provide a synthesis of the unique role of PMPZ isolation in generating biodiversity and, by summarising the current state of the field, we outline the scope for future research. First, we discuss the evolutionary processes involved in the evolution and maintenance of PMPZ isolation and detail the underlying physiological and genetic mechanisms. Second, we conduct the first comprehensive survey of the speciation literature concerning PMPZ isolation to identify similarities and differences in the mechanisms and measures of PMPZ isolation across eukaryotes. Third, we identify gaps in the speciation literature and suggest avenues for future research. We conclude by suggesting where efforts could provide new insights into this often-neglected stage of reproductive isolation.

2. The unique role of PMPZ isolation in speciation

2.1 The role of sexual selection and sexual conflict in promoting the evolution of PMPZ isolation

Traits that influence mating and fertilisation success within populations are frequently under strong sexual selection and sexual conflict. Most theoretical models connecting sexual selection to reproductive isolation are agnostic to the traits underlying divergence (Kirkpatrick & Ravigné, 2002). However, premating and postmating sexual selection place different emphasis on the traits that mediate reproductive success (Parker *et al.*, 2013; Lüpold *et al.*, 2014; Evans & Garcia-Gonzalez, 2016). The evolution of premating sexually selected traits can (in principle) involve both male and female intra- and inter-sexual selection, and competition is often temporally separated from choice (Rosenthal, 2017). Targets of premating sexual selection may be spread across many traits (e.g. behavioural, morphological and physiological; e.g., Andersson, 1994; Rosenthal, 2017) and given that many premating traits are condition dependent (Rowe & Houle, 1997), individual loci may be under weak selection. In contrast, sexual selection operating after mating is restricted to sperm competition and cryptic female choice and thus the traits involved are localised. In particular, selection necessarily operates directly on the gametes and surrounding fluid/tissue within the female reproductive tract in internally fertilising animals, or within the carpel in land plants (Birkhead & Pizzari, 2002; Tonnabel *et al.*, 2021). As a consequence, a dynamic unique to PMPZ interactions occurs when the outcome of male-male competition might vary across females, creating an emergent three-way female × male × male interaction, where competition is always concurrent with choice (Lüpold *et al.*, 2020).

Another distinct feature of postcopulatory interactions is the tightly coordinated molecular interplay between the sexes (McCullough *et al.*, 2022; Misra *et al.*, 2022). For instance, sperm proteins are replaced by female proteins during sperm transport and storage after mating (McCullough *et al.*, 2022). As such, mismatches between mating partners that disrupt this tight coordination may rapidly cause incompatibilities underlying PMPZ isolation. Together, selection acting on a potentially reduced subset of tightly associated interacting traits may subject traits associated with PMPZ isolation to a more restricted set of selection pressures, and reduce the number of loci under divergent selection, compared

to selection influencing premating traits. Disruptive selection might therefore be more effective in generating rapid divergence in postmating traits (Orr, 1998; Yeaman & Whitlock, 2011). Alternatively, fewer loci under divergent selection may slow barrier formation compared to polygenic divergence involved in premating isolation (Westram et al., 2018; Martin et al., 2019). Regardless, the restricted physiological targets of selection and potentially simple genetic basis suggest that the study of PMPZ isolation provides a highly tractable opportunity to study sexual interactions and prezygotic isolation in a relatively simple model.

Postmating traits have profound effects on fitness and such conditions may favour the rapid coevolution of postmating interactions between the sexes. For example, in internally fertilising animals, coevolution between female reproductive tract dimensions and sperm length have been found widely across taxa (Pitnick *et al.*, 2009). Additionally, experimental evolution studies have shown that traits involved in fertilisation respond to the strength of sexual selection, or to correlated selection between the sexes, over short evolutionary timeframes (Holland & Rice, 1999; Miller & Pitnick, 2002; Crudgington *et al.*, 2009; Wigby *et al.*, 2009; Godwin *et al.*, 2017). Combined, these findings at both the macroevolutionary and microevolutionary level suggest that PMPZ isolation may be a critical early contributor to population divergence (Devigili *et al.*, 2018; Turissini *et al.*, 2018; Garlovsky *et al.*, 2020). Indeed, PMPZ isolation is the only known barrier to gene flow in some taxa (Palumbi & Metz, 1991; Fricke & Arnqvist, 2004; Marshall *et al.*, 2011). Thus, if traits acting after mating, which are under strong sexual selection, play such a critical role in reproductive isolation, then we should expect a strong signature of sexual selection on patterns of biodiversity. However, the role of sexual selection as a driver of speciation has long been contested (Ritchie, 2007; Servedio & Boughman, 2017), and recent evidence remains mixed (Kraaijeveld *et al.*, 2011; Janicke *et al.*, 2018). If PMPZ isolation is especially important in the early stages of speciation, then its signature may be overwritten as other barriers evolve. A comparative study in animals found that the signal of speciation via sexual selection might weaken over time (i.e., deeper nodes showed a smaller effect size than shallower phylogenetic distances; Kraaijeveld et al. (2011)). Moreover, if strong premating barriers have evolved, then detecting the role of PMPZ isolation in early divergence may be difficult. Thus, despite the unique selection pressures acting on postmating traits that may promote

the early evolution of PMPZ isolation, its detectable effect may be transient. As such, we are likely underestimating the number of cases where PMPZ isolation may occur and the importance it may have had at an earlier stage of speciation.

2.2 Extrinsic PMPZ isolation and the role of natural selection

Although PMPZ isolation is most often thought to be shaped by sexual selection or sexual conflict, certain forms of PMPZ isolation could also be affected by natural selection. External environmental conditions (e.g., temperature, salinity, or pH) can directly influence the function of reproductive traits (Reinhardt *et al.*, 2015) and populations may vary in reproductive function under certain conditions (e.g., temperature extremes). Thus, environmental conditions could select against immigrant gametes as a form of **extrinsic PMPZ isolation** (see Thompson et al., this volume). The environment may also indirectly shape the reproductive environment in which PMPZ interactions take place. Resources incorporated into reproductive traits, such as gamete cell membranes or reproductive tissues, can affect their quality or function (Cardozo & Pilastro, 2018). For instance, nutritional status can impact the number of gametes produced or the composition of reproductive fluids (Macartney *et al.*, 2019). In this way, the expression of PMPZ barriers may be context dependent, resulting from an emergent genotype (e.g., female) × genotype (e.g., male) × environment (e.g., temperature) interaction.

In plants, there is clear evidence of external environmental conditions contributing to PMPZ isolation. For instance, in spiral gingers (*Costus spp.*), pollinator-driven selection on floral traits has led to differences in style length between species such that pollen grains from short-styled species do not have the appropriate energy reserves needed to reach the ovule of long-styled species ("pollen attrition") (Yost & Kay, 2009). Similarly, in the yellow monkey flower (*Mimulus guttatus*), pollen from copper-sensitive populations performed poorly when crossed to copper-resistant individuals grown in copper-heavy soil (Searcy & Macnair, 1990). In animals, environmental effects on the expression of PMPZ barriers are likely to be especially important for **spermcasters** and external fertilisers where gametes are directly exposed to the external environment. For example, in the sand goby (*Pomatoschistus minutus*), differences in salinity between populations inhabiting brackish and marine environments reduces immigrant male sperm viability and fertilisation success (Svensson *et*

al., 2017). Similarly, on the Island of São Tomé the sister species *Drosophila santomea and D. yakuba* inhabit high and low elevations, respectively, where *D. santomea* become sterile at lower temperatures than *D. yakuba* (Matute *et al.*, 2009). Indeed, evidence suggests that species ranges are better predicted by fertility- rather than lethal- thermal limits (Parratt *et al.*, 2021), suggesting that environmental selection on fertility traits might pleiotropically influence the performance of these traits in heterospecific crosses.

2.3 Opportunity costs and reinforcement as drivers of PMPZ isolation

Postmating reproductive traits might be uniquely positioned to mitigate costs involved in mating decisions, indirectly or directly leading to PMPZ isolation (i.e., as the result of **reinforcement**). For instance, PMPZ isolation could evolve via indirect selection to reduce the costs of going unmated while minimising the production of hybrid offspring. Theory predicts that females may alleviate the costs of going unmated by relaxing mate preferences and mating with the first male encountered, even if this male is of low quality, rather than wasting time and resources searching for a suitable mate and risking going unmated before death (Kokko & Mappes, 2005; but see Richardson & Zuk, 2022). In polyandrous species, the benefit to females of mating with the first available male can be strong if they can later "trade-up" to a better quality male (Kokko & Mappes, 2005; Kokko & Jennions, 2008). In the context of speciation, a similar process could operate if females encounter heterospecifics at a high enough frequency for mating to occur, but then are able to bias paternity towards "higher quality" conspecific males via **conspecific gamete precedence** (Larson *et al.*, 2019). In this case, conspecific gamete precedence could decrease short-term costs of going un- (or under-) mated while restricting any potential long-term hybridization costs (Marshall *et al.*, 2002).

Mating with heterospecific males might even come with advantages for females, for example, through receipt of **fecundity** boosting resources such as nuptial gifts or proteins that stimulate oviposition (Peterson *et al.*, 2011), or access to higher quality territories or resources (Cramer et al. 2016); although this requires that the short term benefit to females outweighs the costs of heterospecific mating. Heterospecific mating costs can themselves be expressed as PMPZ isolation in the form of **non-competitive gametic isolation (NCGI).** NCGI arises if interactions between the male gametes or seminal fluid and female

reproductive tract are disrupted after a single heterospecific mating. NCGI can be expressed in the form of reduced fertilisation success after a single heterospecific mating (Kay, 2006; Jennings *et al.*, 2014; Garlovsky & Snook, 2018), reduced female lifespan (Ting *et al.*, 2014; Kao *et al.*, 2015) reduced fecundity (Matute, 2010; Marshall & Dirienzo, 2012; Turissini *et al.*, 2018), or temporary or permanent blocking of mating opportunities (e.g. satyrization, copulatory plugs, and stigma clogging) (Patterson, 1946; Knowles & Markow, 2001; Holland & Chamberlain, 2007; Matute, 2010). Notably, some forms of NCGI may be more costly than others. For instance, reduced fertilisation success may impose elevated costs compared to reduced fecundity, if females lay similar numbers of eggs as in a conspecific cross (Garlovsky & Snook, 2018). The costs to females of reduced fertilisation success are therefore equivalent to producing inviable (hybrid) embryos and NCGI could itself act as the source, rather than outcome, of reinforcing selection (Lorch & Servedio, 2007).

Regardless of whether selection is imposed by postzygotic incompatibilities or NCGI, PMPZ barriers could be a particularly responsive target of reinforcement (Lorch & Servedio, 2007). For example, conspecific gamete precedence can provide a reliable mechanism to ensure conspecific paternity that does not depend on external signals/stimuli-based mate discrimination, therefore it can be selected where premating barriers are not reliable (Matute, 2015; Cramer *et al.*, 2016). Reinforcement of PMPZ barriers has been suggested in various taxa, including flowering plants (Kay & Schemske, 2008), insects (Matute, 2010; Castillo & Moyle, 2019), birds (Cramer *et al.*, 2016; Albrecht *et al.*, 2019) and sea urchins (Geyer & Palumbi, 2003; Zigler *et al.*, 2003). Given the relatively few cases in which any specific mechanism of reinforcement is known (Servedio & Noor, 2003; Ortiz-Barrientos *et al.*, 2009), PMPZ barriers appear to be uniquely and intriguingly responsive to reinforcing selection (Slaughter *et al.*, 2008; but see Geyer & Lessios, 2009; Popovic *et al.*, 2014).

2.4 Molecular mechanisms and targets of PMPZ isolation

Several features of the function and rate of evolution of genes involved in postmating interactions might promote the evolution of PMPZ isolation. Many genes tightly associated with fertilisation are highly conserved (Dean *et al.*, 2009; Finseth *et al.*, 2014; Kasimatis & Phillips, 2018; Wassarman & Litscher, 2021; Garlovsky *et al.*, 2022), such that relatively little divergence between taxa might disrupt interacting reproductive traits resulting in PMPZ

barriers. Postmating reproductive traits primarily have an effect on fertilisation success, while premating traits often have additional functions outside of reproduction. Therefore, the number of mutations necessary to generate PMPZ barriers may be fewer than for premating isolation as they are likely to be less pleiotropic, facilitating the more rapid emergence of PMPZ isolation. For instance, molecular divergence within a single gene acting as an egg receptor or a sperm cell surface protein (e.g., EBR1 and bindin in sea urchin; reviewed in Vacquier & Swanson, 2011), or divergence in pollen tube guidance genes (e.g. AtLURE1 and PRK6; Liu *et al.*, 2021), may be the only step necessary to prevent interspecific fertilisation (Vacquier, 1998; Swanson & Vacquier, 2002).

Reproductive genes are expected to be highly conserved and experience relatively strong purifying selection. However, specific regions of these genes can evolve quickly (Vacquier & Swanson, 2011). Thus, while some reproductive genes are highly conserved, genes specifically expressed in tissues relevant to PMPZ isolation (e.g., gonads) often include genes with elevated rates of non-synonymous evolution (Swanson & Vacquier, 2002; Arunkumar *et al.*, 2013; Gossmann *et al.*, 2014; Dapper & Wade, 2020; Moyle *et al.*, 2021). These rapidly evolving loci include classes of mutations such as deletions and novel chimeric loci, consistent with relaxed selection (Walters & Harrison, 2011; Gossmann *et al.*, 2016; Harrison *et al.*, 2019; Dapper & Wade, 2020; Patlar *et al.*, 2021). These data suggest that some genes expressed in males involved in PMPZ isolation (e.g., seminal fluid proteins) might evolve via unusual evolutionary mechanisms, including arising *de novo* with no initial function, and therefore under limited constraint, until they are co-opted for reproductive function (Hurtado *et al.*, 2022).

More data are needed to assess whether evolution via these kinds of mechanisms is broadly true for loci underlying PMPZ isolation. If true, it would suggest a clear instance in which variation fuelling the novel evolution of traits involved in PMPZ isolation is distinct from other reproductive traits. With the exception of some well-described egg membrane receptor proteins (Grayson, 2015) and pollen tube guidance molecules (Kanaoka *et al.*, 2011; Zhong *et al.*, 2019), most studies investigating the genetic architecture of PMPZ isolation have focussed on male traits (Britch *et al.*, 2007; Ahmed-Braimah, 2016). As PMPZ isolation necessarily involves an interaction between interacting mating partners more

306 research is needed to understand the molecular nature of female traits involved in PMPZ
307 isolation (Sweigart, 2010; Yeates *et al.*, 2013; Cramer *et al.*, 2016; McCullough *et al.*, 2020;
308 Ahmed-Braimah *et al.*, 2021).
309
310 There is accumulating evidence to suggest that intraspecific mechanisms ensuring high
311 fertility are directly associated with PMPZ isolation, via either the same phenotypes or the
312 same genes. For example, in *Drosophila* the same genes conferring advantages in sperm
313 competition within species influence conspecific sperm precedence (Castillo & Moyle, 2014;
314 Civetta & Finn, 2014). In the house mouse (*Mus spp.*) species complex, species experiencing
315 stronger intraspecific sperm competition have greater interspecific fertilisation success,
316 possibly as a result of differences in the strength of sexual conflict and selection against
317 polyspermy (Martín-Coello et al., 2009). In the nightshade family (Solanaceae), loci
318 underlying the mechanism of genetic self-incompatibility also directly affect the expression
319 of pollen-pistil barriers between species (e.g., Jewell *et al.*, 2020; Tovar-Méndez *et al.*,
320 2014). In the guppy (*Poecilia reticulata*), the ovarian fluid both favours sperm from
321 unrelated males in the context of inbreeding avoidance (Gasparini & Pilastro, 2011) and
322 favours sperm from males of the same, versus different drainages (Devigili *et al.*, 2018).
323 Similarly, major histocompatibility complex genotype at gamete surfaces influences
324 fertilisation success in birds (e.g., *Gallus gallus*) and mice (*Mus musculus*) as a mechanism
325 for inbreeding avoidance (Rülicke *et al.*, 1998; Løvlie *et al.*, 2013; Firman & Simmons, 2015)
326 and could contribute to outbreeding avoidance (i.e., against heterospecifics) (Mays & Hill,
327 2004; Kopp *et al.*, 2018). Selection for immune compatibility at CMAH/Neu5Gc egg cell-
328 surface antigens may even have contributed to PMPZ isolation early in human evolutionary
329 history (Ghaderi *et al.*, 2011).
330
331 In summary, PMPZ isolation may play a unique role in speciation because it: 1) is expected
332 to have more restricted targets of selection compared to premating isolation; 2) is expected
333 to emerge early due to rapid coevolution between the sexes; 3) may be particularly
334 important early during divergence, but be hard to detect; 4) may be environmentally
335 dependent; 4) potentially evolves via indirect selection and reinforcement; and 5) may
336 involve evolutionary mechanisms including *de novo* functions and co-option of intra-specific

337 mechanisms promoting fertilisation success (e.g., sperm competition or inbreeding
338 avoidance).

3. Survey of PMPZ isolation in speciation

We performed the first comprehensive literature survey on PMPZ isolation across the tree of life to evaluate similarities and differences in the types of barriers and mechanisms reported. We identified 462 relevant studies on PMPZ isolation using the Web Of Science (accessed May 26th, 2022, see Supplemental Material) including both inter- and intra-specific crosses, and analyses of sequence and expression divergence of reproductive traits. From these, we identified the number of studies that reported various pieces of information to determine: 1) the diversity of taxa in which PMPZ isolation has been documented, 2) the types of barriers that have been measured, and 3) where compelling evidence of PMPZ isolation has been demonstrated.

3.1 PMPZ isolation is widespread across the eukaryotic tree of life

Our survey highlights the ubiquity of PMPZ isolation across eukaryotes consistent with fertilisation being a universal aspect of sexual reproduction (Fig. 2). We found PMPZ isolation in taxa with various reproductive systems (e.g., **gonochoric/dioecious**, hermaphroditic, facultative sexual) and different modes of fertilisation (internal, external, spermcasters). The majority of studies focused on animals and land plants (290 and 160 studies, respectively) with only 12 studies outside of these two groups (six on brown algae, one on diatoms, three on green algae, one on red algae, and one on the apicomplexan *Plasmodium*; Fig. S1). Fungi were not included in the survey as mapping the reproductive barriers from plant and animal taxa on to what the fungal community uses is currently difficult, with some fungal researchers using equivalent terms (Ament-Velasquez et al., 2022; Turner et al., 2010) and others not. Reviews of reproductive isolation in fungi only use the terms premating and postmating where postmating really is postzygotic (Giraud et al., 2008) or alternatives (Giraud & Goubiere, 2012). Moreover, variation in life cycles of fungal taxa has been suggested to make direct comparisons between the animal and plant literature and fungal studies problematic (Giraud & Goubiere, 2012). Future collaboration between speciation researchers crossing this taxonomic divide may help to better map terminology which could extend the number of taxa exhibiting PMPZ isolation.

Studies of land plants were almost exclusively conducted on angiosperms, with only a single study each on gymnosperms and ferns (Fig. 2). Among animals, internal fertilisers accounted for the majority of studies (61.7%; 179/290). The majority of studies on internally fertilising animals were conducted on insects (43.4%; 126/290), of which over half used *Drosophila* species (50.8%; 64/126). Externally fertilising animals such as echinoderms and some fishes were also well represented (Fig. 2). However, while echinoderms are one of the earliest and best studied groups regarding PMPZ isolation, studies to date are limited to only a few groups within the clade and confirmed instances of PMPZ isolation are restricted to taxa in just two Orders (Fig. 2). Aside from fishes, studies of vertebrates were very limited (Fig. 2). Overall, over half of studies performed interspecific crosses (53.5%; 247/462), while 21.9% of studies examined intraspecific crosses and 12.1% compared both inter- and intra-specific crosses (Fig. 2). The remaining 58 studies (12.6%) did not perform experimental crosses (e.g., were based exclusively on analyses of sequence or expression divergence of genes involved in reproduction). Thus, studies of PMPZ isolation span a range of divergence, with studies of intraspecific pairs highlighting the potential role of PMPZ isolation at the earliest stages of speciation.

3.2 Diversity of PMPZ measures across eukaryotic taxa

Plant studies are unified in the ways in which PMPZ isolation is measured, with nearly all studies using one or more of four common measures (Fig. 3; Table S1): 1) pollen performance, 2) fruit set, 3) seed set, and 4) the proportion of hybrid seeds produced from a competitive pollination experiment (Fig. S2). In contrast, animal studies used a wider range of measures (Table S2), some of which differed in terminology and methodology between taxa. For instance, “fertilisation success” included both direct measures: i.e., observations of the proportions of successfully fertilised eggs using direct assessment of fertilisation status, or offspring sex ratio (in systems with haplodiploidy); and indirect measures, such as assessing the proportions of successfully developing embryos at various stages of early development, or the proportions of successfully hatched eggs. To consolidate information across studies, we grouped measures of PMPZ isolation in animals into 9 categories (Fig. 3; Table S2).

Many measures of PMPZ isolation are analogous in plants and animals. For example, seed set and fruit set are analogous to indirect measures of fertilisation success in animals; pollen tube growth and sperm motility measure male gamete performance; and some PMPZ barriers such as conspecific gamete precedence are described in both plants and animals (Fig. 3). However, important differences in PMPZ mechanisms exist between taxa. Differences between species in reproductive trait morphology have clearly been demonstrated as mechanisms underlying PMPZ isolation in plants (i.e., style length; Brothers & Delph, 2017), but have only been used as indirect measures in animals in the absence of direct evidence for a role in PMPZ isolation. Similarly, chemotaxis is key to PMPZ isolation in externally fertilising taxa (Riffell *et al.*, 2004; Yeates *et al.*, 2013; Weber *et al.*, 2017), but its significance in mediating PMPZ isolation in internally fertilising animals remains largely unknown (Sun *et al.*, 2003). Inconsistencies in what is considered evidence of PMPZ isolation across taxa and how PMPZ mechanisms operate limit our ability to make broader conclusions.

3.3 Limitations of current PMPZ isolation research

3.3.1 Indirect measures infer but do not demonstrate PMPZ isolation

Many studies reported PMPZ isolation using indirect measures such as divergence in reproductive gene sequences or trait morphologies. For example, some studies alluded to PMPZ isolation from elevated rates of sequence evolution or divergence in the molecular composition of reproductive tissues, but most cases lack direct evidence connecting divergence of reproductive genes and proteins with a PMPZ mechanism. Likewise, divergent postmating traits such as sperm morphology are often used as indirect evidence for PMPZ isolation, particularly in systems where it is more difficult to study postmating interactions directly (e.g., birds and mammals). Reduced female survival after heterospecific mating has also been reported as a PMPZ barrier, presumably due to reductions in lifetime fecundity (Ting *et al.*, 2014; Kao *et al.*, 2015). Conclusively demonstrating PMPZ isolation requires the often difficult task of measuring the outcome of cryptic sexual interactions and showing that these interactions result in a potential reduction of gene flow (Zigler *et al.*, 2008; Palumbi, 2009; Manier *et al.*, 2013; Moyle *et al.*, 2014; Cramer *et al.*, 2016). Experiments adequately demonstrating conspecific gamete precedence are alone sufficient evidence of PMPZ

isolation. For other barriers, care must be taken to ensure the barrier observed is acting at the PMPZ stage (Fig. 1).

3.3.2 Proxy measures may conflate PMPZ and postzygotic isolation

A difficulty in establishing the presence of PMPZ isolation is the use of proxy measures that may conflate PMPZ isolation with other isolating barriers – an issue that few studies acknowledge (e.g., Pernet, 1999). Measuring fertilisation success via proxies such as hatching success, embryonic cleavage, seed set, or fruit set could conflate failed **syngamy** or karyogamy (i.e., PMPZ isolation) with early embryonic inviability (i.e., postzygotic isolation). Of the four predominant measures of PMPZ isolation used in plants, only pollen performance is not a proxy measure. However, what constitutes a proxy measure can be subtle and depend on the taxa in question. For instance, in orchids (Orchidaceae), fruit set may be a true measure of PMPZ isolation, when only compatible pollination triggers fruit development, prior to fertilisation (Zhang & O'Neill, 1993; Scopece *et al.*, 2007). Likewise, in animals, reduced female fecundity can be considered a true measure of PMPZ isolation in taxa where ovulation can be separated from fertilisation success. For example, reduced female fecundity after heterospecific mating may arise from either overstimulation (i.e., prolonged **insemination reaction** mass preventing ovulation in *Drosophila*; Patterson, 1946) or understimulation (i.e., an ejaculate does not promote stimulation of the normal postmating female response preceding egg-laying; Marshall *et al.*, 2009).

3.3.3 Pericopulatory processes are not measures of PMPZ isolation

In animals, several potential barriers occurring immediately before PMPZ interactions have been considered PMPZ isolation in previous studies (e.g. copulation duration or **mechanical isolation**), or their position during the reproductive timeline remains ambiguous (Sánchez-Guillén *et al.*, 2012; Oxford & Croucher, 2014). Such **pericopulatory processes** have posed difficulties when defining PMPZ isolation as they can influence which **gamete × gamete interactions** take place (Fig. 1; Table 2). For example, the mechanism of **male gamete priming** in some fishes allows males to modulate the numbers of sperm ejaculated after first assessing female quality (or species identity), which can lead to lower interspecific fertility (Aspbury & Gabor, 2004). Furthermore, female remating rate is a pericopulatory barrier as it can bias representation of 'preferred' (i.e. conspecific) male sperm in the **fertilisation set**

(Chang, 2004) and similarly, reduced copulation duration resulting from genitalic mismatch could decrease the number of sperm or other ejaculate components transferred to females. Indeed, reduced sperm transfer is thought to be one of the primary mechanisms underlying conspecific gamete precedence between *Drosophila simulans* and *D. mauritania* (Manier *et al.*, 2013). However, as PMPZ isolation necessarily requires the opportunity for gametes and/or reproductive tissues to interact, we do not consider these barriers as components of PMPZ isolation *sensu stricto*. Mechanical isolation as described in plants can be considered as a PMPZ barrier, as this barrier involves pollen interacting with the female reproductive tract (e.g., pollen attrition). In animals, however, mechanical isolation is not a PMPZ barrier, as genitalic mismatch precludes the transfer of sperm to the female reproductive tract, thus preventing sperm from interacting with the female or ova (see Table 2) (Wojcieszek & Simmons, 2013).

4. Scope of future PMPZ research

Having assessed the potentially unique contribution of PMPZ isolation as a barrier to gene flow and summarising the current state of PMPZ isolation research, we now set out recommendations we hope will help to advance the field. These suggestions generally mirror the challenges discussed in section 3.3 and fall under three categories. First, issues related to measuring PMPZ isolation; second, addressing taxonomic biases in research efforts; and finally, resolving the physiological and genetic mechanisms underpinning PMPZ isolation. We conclude by outlining a set of open questions to encourage avenues of future research.

4.1 Recommendations for PMPZ isolation research

4.1.1 Use unified and direct measures of PMPZ isolation

Our survey reveals a lack of consistency in how PMPZ isolation is measured and defined across animals. When combined with the variable inclusion of pericopulatory processes in PMPZ isolation (see section 3.3.3), this makes broader conclusions difficult. However, this may not be the case for plant studies, which use a comparatively reduced and consistent set of four measures, albeit only one of which is a direct measure of PMPZ isolation.

Accurately assessing the relative contribution of different barriers (i.e., premating vs. PMPZ vs. postzygotic) to total reproductive isolation at various stages of divergence provides critical information about the speciation process (Sobel & Chen, 2014). When focusing on PMPZ isolation, two problems may arise in addressing this question. First, the signature of PMPZ isolation may be overwritten by premating or postzygotic barriers that evolve later during divergence, making its effect difficult to detect, tending to decrease the observed contribution of PMPZ isolation towards total reproductive isolation. Second, ambiguities about which barriers are acting, and when, can lead to over- or under-estimating the strength and occurrence of PMPZ isolation and weaken the ability to assess the contribution of PMPZ isolation to total reproductive isolation (see section 3.3). Current estimates of total reproductive isolation, while sparse, provide mixed evidence of the strength of PMPZ isolation relative to other barriers (Ramsey *et al.*, 2003; Dopman *et al.*, 2010; Peterson *et al.*, 2011; Jewell *et al.*, 2012; Sánchez-Guillén *et al.*, 2012; Jennings *et al.*, 2014; Rose *et al.*,

2014; Martin & Mendelson, 2016; Kostyun & Moyle, 2017; Lackey & Boughman, 2017; Turissini *et al.*, 2018). In *Drosophila*, PMPZ isolation evolves at a similar rate to premating isolation (Turissini *et al.*, 2018). In fishes, there is little evidence of PMPZ isolation (Martin & Mendelson, 2016; Lackey & Boughman, 2017). In plants, on average, PMPZ barriers appear to be weaker than premating barriers, but stronger than any individual postzygotic barrier (Christie et al., 2022).

To avoid conflating PMPZ isolation with other barriers, we suggest using experiments that enable the separation of fertilisation success and embryo mortality by confirming the fertilisation status of unhatched eggs or ungerminated seeds. Reliable cell staining protocols exist for insects, birds, and plants, but are rarely used in studies of PMPZ isolation. Further, complementary experiments can be used to confirm the presence of PMPZ isolation, such as performing both a heterospecific cross and conspecific gamete precedence experiment in tandem (Fig. S2). Few studies do this and there are likely many instances in the literature that attribute reduced numbers of hybrid offspring produced to postzygotic barriers that may rather be the result of PMPZ isolation.

4.1.2 Diversify the taxonomic range of systems used to study PMPZ isolation

Our survey highlighted taxonomic biases in the study of PMPZ isolation towards insects, externally fertilising animals, and angiosperms. These biases may reflect differences in the relative ease of studying different groups in the laboratory and directly observing fertilisation kinetics (e.g., in externally fertilising aquatic taxa) (Howard, 1999; Howard *et al.*, 2009). We note a distinct lack of studies in tetrapod vertebrates (mammals, birds, amphibians, and reptiles), non-flowering plants, and insects outside the Diptera, Coleoptera, and Orthoptera. Without focussed research effort outside of well-studied groups, it is difficult to assess whether the lack of documented evidence of PMPZ isolation reflects real biological differences in its prevalence. Some currently understudied taxa show promise to improve understanding of PMPZ isolation. For example, in haplodiploid organisms only fertilised eggs develop into female offspring and thus fertilisation success can easily be disentangled from hybrid inviability. Further, researchers do not currently take full advantage of gamete mixing experiments or artificial insemination, in which con- and

hetero- specific gametes are mixed in known quantities to directly test for PMPZ barriers (Ludlow & Magurran, 2006; Perez-Velazquez *et al.*, 2010).

4.1.3 Uncover the causal mechanisms underlying PMPZ isolation

Identifying the types of PMPZ barriers present between taxa provides only the first step towards understanding the role of PMPZ isolation as a barrier to gene flow. With recent advances in molecular techniques, it should be a priority in the field to identify the physiological and molecular mechanisms and underlying genetic architecture of PMPZ barriers. In this respect, PMPZ isolation research lags behind other areas of speciation research where the genetic and developmental bases of isolation are beginning to be resolved (e.g., Presgraves, 2010; Streisfeld *et al.*, 2013; Bradley *et al.*, 2017; Rossi *et al.*, 2020; Liang et al., 2023, Merrill et al., Reifova et al., this volume). To this end, we suggest using complementary approaches to link observed phenotypes to the underlying barrier loci, for instance by genetically modifying gamete recognition proteins. Similarly, evidence of PMPZ isolation from indirect measures (e.g., molecular and morphological divergence) should be confirmed by laboratory or field experiments that estimate the strength of reproductive isolation.

Box 1: **Open questions for future research**

In surveying the PMPZ isolation literature and the current state of the field, we highlight a number of open questions and potentially fruitful avenues of future research.

1. When does PMPZ isolation emerge during speciation?
2. What are the evolutionary forces that promote the evolution of PMPZ isolation (i.e., natural selection, sexual selection, genetic conflict, genetic drift)?
3. Does the intensity of sexual selection (i.e., monandrous vs polyandrous; selfing vs outcrossing) impact the rate of evolution of PMPZ isolation?
4. What are the physiological and molecular mechanisms underlying PMPZ isolation?
5. How often do PMPZ barriers use the same mechanisms as intraspecific sperm/pollen choice?
6. Is there direct evidence for a role of divergence in gamete/reproductive tract morphology as a mechanism underlying PMPZ isolation in animals?

7. What role does chemotaxis play in determining fertilisation outcomes influencing PMPZ isolation?
8. What is the genetic architecture underlying PMPZ isolation and is it simpler than that of premating isolation?

[end of box]

5. Concluding remarks

Understanding the process of speciation requires understanding reproductive isolation and quantifying the contribution of different barriers to gene flow. Although PMPZ isolation has been historically understudied in speciation research compared to premating and postzygotic isolation, PMPZ isolation holds a unique role in generating biodiversity. Indeed, PMPZ barriers appear ubiquitous across eukaryotes, and a number of shared barriers have evolved convergently in animals and plants. Our survey highlighted some challenges inherent to PMPZ isolation research, such as a lack of consistency in how PMPZ isolation is measured, the use of indirect measures of PMPZ isolation and the lack of knowledge about the physiological and genetic mechanisms of PMPZ isolation. Overcoming these challenges is essential to better understand how PMPZ barriers are formed and to further progress speciation research. Despite these challenges, these are exciting times to work on PMPZ isolation research thanks to recent developments in 'omics' technologies (e.g., genomics, metabolomics, proteomics) and genome editing which will allow us to make important discoveries on the role of PMPZ isolation in generating and maintaining biodiversity.

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Figures

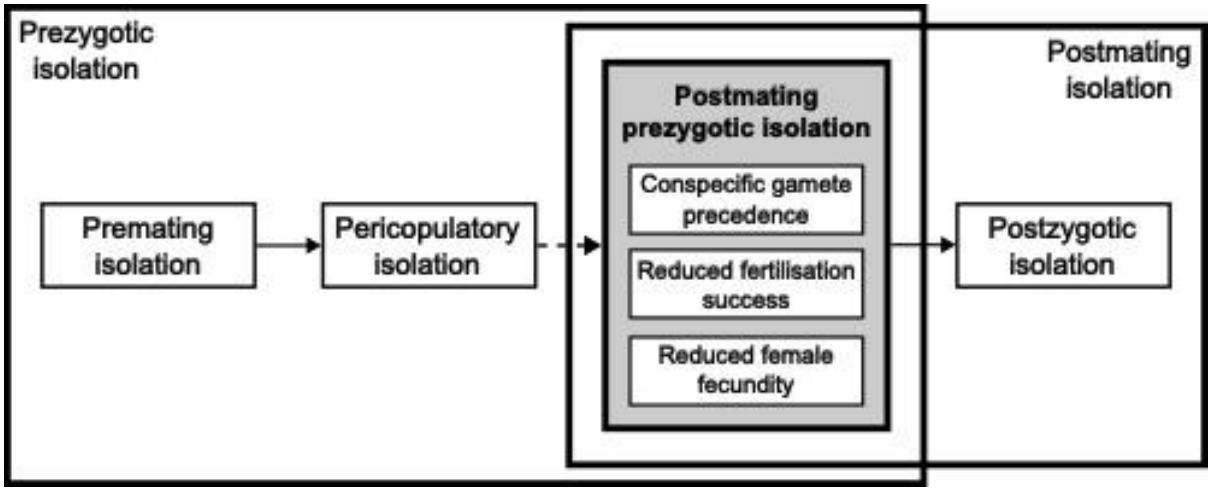

Figure 1. Position of PMPZ isolation along sequential stages of reproductive isolation. Pericopulatory isolation involves reproductive processes that occur immediately before or during mating and that may impact PMPZ isolation. See Table 2 for examples of pericopulatory and PMPZ barriers. The dashed arrow between pericopulatory and PMPZ isolation represents the time at which gamete release takes place. Fertilisation (karyogamy) occurs within the grey box.

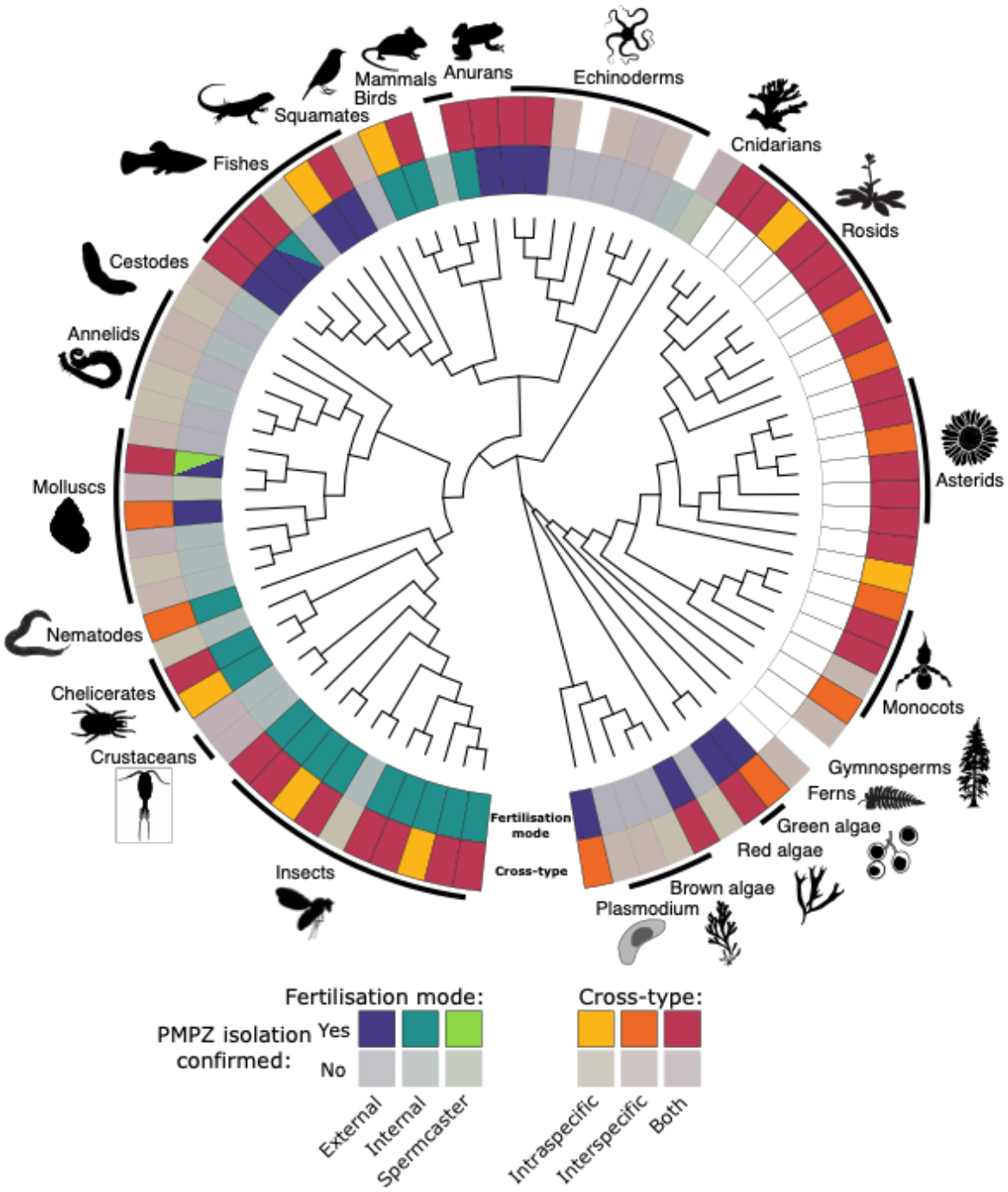

Figure 2. Summary of PMPZ isolation across the eukaryotic tree of life.
Each tip represents a taxonomic Order in which PMPZ isolation has been studied. Inner ring shows fertilisation mode (internal fertilisers/external fertilisers/spermcasters). Fertilisation mode is variable within plant Orders and not shown. Outer ring indicates whether PMPZ isolation has been studied between populations within species only (yellow), between species only (orange), or both between populations and between species (red). Ring shading indicates where PMPZ isolation has been measured directly (confirmed = yes, full) or only inferred via indirect methods or proxies (confirmed = no, transparent; see section 3.3). Tips with no colour indicate taxa where there is no available data. Branch lengths do not reflect divergence time.

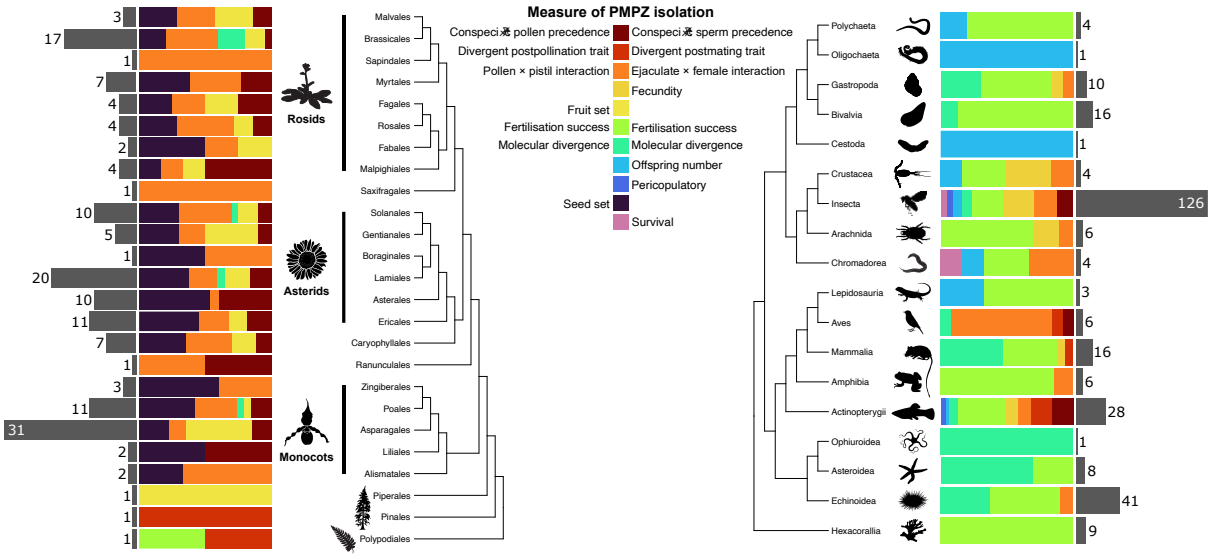

Figure 3. Distribution of measures of PMPZ isolation across plants and animals. Each tip represents a taxonomic Order (land plants) or Class (animals) in which PMPZ isolation has been studied. Stacked bar charts show the proportion of studies within each taxa reporting the grouped measures of PMPZ isolation. We classified measures of PMPZ used into 11 categories. The 7 categories in plants are noted on the left and the 9 animal categories are noted on the right (see Tables S1 and S2). The total number of studies in each taxon are indicated by the height of the outer grey bars and numbers. Branch lengths do not reflect divergence time.

Tables

Table 1. Glossary.

Conspecific gamete precedence	Paternity bias towards conspecific males over heterospecific males, regardless of the normal patterns of within-species competitive gamete precedence. Also called conspecific sperm precedence and conspecific pollen precedence.
Dioecious	Male and female reproductive organs occurring in separate individuals. Term mainly used in plants.
Extrinsic postmating prezygotic isolation	External factors that differentially impact fertility, e.g., differences in thermal fertility limits between species.
Fecundity	The number of eggs laid, or seeds produced within a given timeframe.
Fertilisation set	The population of gametes that are able to compete to fertilise a given ovum.
Gamete release	Also called ejaculation; insemination; mating; sperm transfer; spawning; masting; pollen deposition; pollination.
Gonochoric	Male and female reproductive organs in separate individuals. Term mainly used in animals.
Karyogamy	Fusion of parental pronuclei inside the ovum preceding the formation of the zygote.
Male gamete priming	Adjustment of male gamete production and/or expenditure according to the fitness return associated with a specific mating/in response to stimuli from con- vs. hetero- specific potential mates.
Gamete × gamete interactions	Interactions between the male gametes (sperm, pollen) and female gametes (egg, ovule) either in the environment (external fertilisation) or in the female reproductive tract (internal fertilisation).
Insemination reaction	Opaque mass secreted by the female reproductive tract into the bursa after mating in some *Drosophila* species. Females generally do not lay eggs until the reaction mass subsides.

Postmating interactions	Also called ejaculate-female reproductive tract interactions; pollen-pistil interactions.
Non-competitive gametic isolation (NCGI)	Forms of PMPZ isolation that result after a single heterospecific mating, i.e., in the absence of competition between gametes (e.g. sperm or pollen competition). For example, reduced fertilisation success or fecundity.
Mechanical isolation	Mismatch in the morphology of reproductive structures (e.g., external genitalia in animals and style length in plants).
Pericopulatory isolation	Any barrier to gene flow that acts immediately before or at copulation.
Postmating isolation	Any barrier to gene flow that acts after gametes are released. Includes postmating prezygotic isolation and postzygotic isolation.
Postmating prezygotic (PMPZ) isolation	Any barrier to gene flow that acts after gamete release and before fertilisation (karyogamy). Also called gametic isolation.
PMPZ barrier	The interaction between reproductive traits leading to a potential reduction of gene flow between taxa, e.g., conspecific gamete precedence, reduced fertilisation success, reduced fecundity.
PMPZ mechanism	The causal physiological or molecular mechanism that manifests as a barrier, e.g., reduced sperm chemotaxis, sperm-egg misrecognition, reduced pollen-tube growth.
Postzygotic isolation	Any barrier to gene flow that acts after fertilisation (karyogamy) resulting in inviable, sterile, or reduced fitness hybrid offspring.
Premating isolation/pre-pollination isolation	Any barrier to gene flow that reduces the frequency of interspecific matings. In this chapter, we limit our discussion to sexual forms of premating isolation including behavioural isolation, pollinator isolation, and mechanical isolation (in animals).
Prezygotic isolation	Any barrier to gene flow that acts before karyogamy. Includes premating and postmating prezygotic isolation.

Reinforcement	The strengthening of prezygotic isolation resulting from selection against costly hybridisation.
Spermcaster	Reproductive mode found in aquatic organisms where sperm are released into the external environment but fertilisation takes place internally.
Syngamy	Fusion of gamete cell surfaces.

Table 2: Pericopulatory and PMPZ barriers and underlying mechanisms.

A non-exhaustive list of the physiological or cellular mechanisms underlying postmating prezygotic barriers to gene flow with example taxa. Many mechanisms underlying reduced fertilisation success after a single heterospecific cross (NCGI) may also underlie patterns of conspecific gamete precedence where there is opportunity for con- and hetero- specific gametes to compete for fertilisation. Abbreviations: CGP, conspecific gamete precedence; NCGI, non-competitive gametic isolation.

Barrier	Mechanism
Pericopulatory barriers	
Sperm priming	Modulation of sperm number - males increase or decrease the numbers of sperm available for ejaculation following an assessment of female quality or species identity. *E.g., male sailfin mollies (*Poecilia latipinna*) produce more sperm in the presence of con- vs. hetero- specific (*Poecilia formosa*) females (Aspbury & Gabor, 2004).*
Mechanical isolation in animals	Mismatch in genital morphology - copulation fails or is suboptimal due to mismatch between male and female genitalia. *E.g., intromission is not completed due to mismatch in genital morphology or position in crosses between sympatric millipede (*Parafontaria spp.*) populations (Tanabe & Sota, 2008).*
Copulation duration	Reduced ejaculate transfer - truncated heterospecific copulation reduces ejaculate transfer. *E.g., most copulations end before sperm transfer in crosses between* Drosophila simulans *females and* D. mauritania *males (Price et al., 2001).*
Remating rate	Biased representation in the fertilisation set - females increase the relative number of conspecific sperm in the fertilisation set by preferentially remating with conspecifics. *E.g., female whiteflies (*Bemisia tabaci*) ameliorate reproductive interference by increasing acceptance of copulation attempts by homotypic males (Crowder et al., 2010).*
Postmating prezygotic barriers	
Extrinsic factors	Species-specific abiotic fertility limits - species differ in gamete tolerance to abiotic factors (e.g., temperature, pH, salinity). *E.g., germination of pollen from copper-sensitive populations of*

	*yellow monkeyflowers (*Mimulus guttatus*) is reduced in the pistils of copper resistant individuals grown under high copper concentrations (Searcy & Macnair, 1990).* *E.g.,* Drosophila santomea *become sterile at lower temperatures than* D. yakuba *(Matute et al., 2009).*
Mechanical isolation in plants	Pollen grain size × style length - mismatch between species in pollen reserves and style length results in pollen tubes not reaching the ovule. *E.g., small-flowered populations of* Silene latifolia *produce small pollen grains that are not capable of growing pollen tubes long enough to reach the ovules of females from large-flowered populations which have longer styles (Brothers & Delph, 2017).*
Conspecific gamete precedence	Ejaculate × female reproductive fluid interactions - female reproductive fluid favours conspecific sperm or impedes heterospecific sperm. *E.g., collared flycatcher (*Ficedula albicollis*) sperm swimming speed decreases more rapidly in heterospecific pied flycatcher (*F. hypoleuca*) female cloacal fluid (Cramer et al., 2016).* *E.g., ovarian fluid increases conspecific sperm motility and attraction in Salmonids (Yeates et al., 2013).*
	Sperm storage dynamics - sperm entry into, retention, or exit from, sperm storage organs is biased towards conspecifics. *E.g., females bias sperm use towards the sperm storage organ containing conspecific sperm, rather than last male sperm, in crosses between* Drosophila mauritiana *and* D. simulans *(Manier et al., 2013).*
	Pollen tube growth - pollen tube growth is impaired or arrested (pollen attrition) in a heterospecific style. *E.g., pollen tubes of self-compatible species are actively rejected in the pistils of self-incompatible species, and pollen-tube growth rate is reduced in some heterospecific crosses of wild tomato (*Solanum spp.*) (Baek et al., 2016).*
	Pollen tube guidance - incompatibilities between pollen tube receptors and heterospecific female attractant molecules result in abnormal pollen tube growth. *E.g., wild-type* Arabidopsis thaliana *ovules are mainly targeted by conspecific pollen tubes.* A. thaliana *mutant ovules that do not*

	express the female attractant AtLURE1 are also fertilised by heterospecific A. lyrata *pollen tubes (e.g. AtLURE1 and PRK6; Liu et al., 2021).*
Reduced fertilisation success (NCGI)	Sperm chemotaxis - incompatibilities between sperm receptors and female attractant molecules result in impaired sperm orientation and motility towards the egg. *E.g., exposure to heterospecific eggs did not induce sperm motility and orientation in crosses between three coral species (genus* Acropora*) (Morita et al., 2006).*
	Differential pollen germination - germination of pollen grains is impaired on heterospecific stigma. *E.g., germination of* Costus pulverulentus *pollen on* C. scaber *stigmas is reduced (Yost & Kay, 2009).*
	Failed syngamy - incompatibilities between gamete recognition proteins lead to failed syngamy. *E.g., sperm-egg attachment and fusion of gamete cell membranes mediated by species-specific gamete recognition proteins (EBR1 and bindin) in sea urchins (*Strongylocentrotus spp.*) (Vacquier & Swanson, 2011).*
Reduced female fecundity (NCGI)	Disrupted female postmating response - mismatched ejaculate × female interactions that do not elicit the stereotypical female postmating response preceding ovulation (e.g., physiological or conformational changes in the female reproductive tract). *E.g., perturbation of the postmating transcriptional response in the lower female reproductive tract results in a prolonged insemination reaction mass that blocks female egg laying after* Drosophila mojavensis *females mate with heterospecific* D. arizonae *males (Knowles & Markow, 2001; Bono et al., 2011).*
	Reduced female survival - heterospecific mating reduces female lifespan resulting in lower overall lifetime fecundity. *E.g., ectopic sperm migration breaching the reproductive tract and entering non-gonadal tissue causes increased mortality, indirectly decreasing reproductive output, and directly blocks ovulation in heterospecific crosses between* Caenorhabditis spp. *(Ting et al. 2014).*

Supplementary Material

Supplementary methods

We performed a literature search using the Web Of Science conducted on 26/05/2022 (for search terms used see Table S4) which resulted in 2730 unique publications. We randomly assigned publications among co-authors for screening of titles and abstracts to refine our list of publications to include only empirical studies of the primary literature investigating PMPZ isolation. After screening we added other relevant publications that were not identified in our initial search and redistributed the final list of 461 publications among co-authors based on field of expertise for data collection.

We performed all analyses in R v.4.2.2 (R Core Team, 2020) using the following packages: tidyverse v.1.3.2 (Wickham *et al.*, 2019), ggtree v.3.6.2 (Yu *et al.*, 2017), ggstance v.0.3.6, treedata.table v.0.1.0, treeio v.1.22.0 (Wang *et al.*, 2020). All code and analyses are available on GitHub: (https://martingarlovsky.github.io/CSH_PMPZ/). Silhouettes were downloaded from Phylopic (https://www.phylopic.org/). Picture credits: *Phoenicurus*: Martin Bulla, based on François Desbordes' illustration; Cestoda to Maxime Dahirel both under a CC licence 4.0 (https://creativecommons.org/licenses/by/4.0/), *Mytilus* and *Strongylocentrotus*: Harold N Eyster; Gastropod: Armelle Ansart (photograph), Maxime Dahirel (digitisation); Peromyscus: Nina Skinner; Gymnosperm (Tsuga): Ian Burt (original) and T. Michael Keesey (vectorization), all under a CC licence 3.0 (https://creativecommons.org/licenses/by/3.0/); all other images are used under a public domain licence CC 1.0 (https://creativecommons.org/publicdomain/zero/1.0/).

Table S1. Measures of PMPZ isolation in land plants were combined into 7 categories. Numbers in parentheses are counts of studies using each measure.

Measure	Includes
Molecular divergence	Molecular divergence (8)
Pollen-pistil interaction	Pollen tube growth (63); pollen germination (26); pollen adhesion (4); pollen hydration (1); *in vitro* pollen tube attraction assay (2); *semi-in vivo* pollen tube attraction assay (1); style length and varying pollen placement along the style (1)
Divergent postpollination traits	Sperm swimming speed† (1), sperm longevity† (1), gamete size (1), pollen wall anatomy (1)
Seed set	Seed set (88), fruit size (proxy for seed set) (1), seed yield (proxy for seed set) (1)
Fruit set	Fruit set (56)
Conspecific gamete precedence	Conspecific pollen precedence (44)
Fertilisation success	Sporophyte formation (1)

†Divergent postmating traits when measured between species only (without demonstrating an incompatibility).

Table S2. We combined the various measures of PMPZ isolation in animals into 9 categories. Some measures are considered "ejaculate × female interactions" when measured in a con- vs. heterospecific cross, or as "divergent postmating traits" when measured between taxa only (without demonstrating a direct role in PMPZ isolation). Numbers in parentheses are counts of studies using each measure.

Measure	Includes
Molecular divergence	Expression divergence (10), intron retention (1), alternative splicing (1), postmating female response divergence (transcript abundance) (3), population genetics (genome scans) (1), molecular evolution of reproductive proteins (45)
Ejaculate × female interaction	Sperm transfer (17), sperm storage (17), sperm depletion (1), sperm swimming speed* (8), sperm motility (12), sperm viability* (3), acrosome reaction (3), syngamy (1), karyogamy (1), fertilisation (1), insemination reaction (3)
Divergent postmating traits	Sperm morphology (2), sperm number (4), sperm swimming speed† (3), ovarian fluid composition (i.e., physiological differences including pH, Ca^{2+} concentration, total protein concentration and osmolality) (1)
Fertilisation success**	Fertilisation success (106), hatching success (49), offspring sex ratio (haplodiploidy) (1)
Offspring number	Egg-to-adult viability (3), progeny number (20)
Pericopulatory traits	Copulation duration (8), remating rate (5), sperm priming (2)
Conspecific gamete precedence	Conspecific sperm precedence (36)
Fecundity	Number of eggs laid (68)
Survival	Female survival (11)

*Traits that are considered as a mechanism when measured in a con- vs. heterospecific context;

†Divergent postmating traits when measured between species only (without demonstrating an incompatibility);

**We included both direct measures and proxy measures (e.g., hatching success) to reflect the authors intended, albeit indirect, measurement of PMPZ isolation.

Table S3. Measures of PMPZ isolation in other taxa were combined into 3 categories. Numbers in parentheses are counts of studies using each measure.

Measure	Includes
Fertilisation success	Fertilisation success (4)
Molecular divergence	Molecular divergence (3)
Gametic interactions	Observing gamete interactions (4)

Table S4. Search terms used to access Web Of Science on 26/05/2022.

Search term
“gametic isolation” AND “reproductive isolation” AND speciation
“gametic isolation”
“gametic isolation” AND speciation
gamet* AND speciation
pollen AND speciation
pollen AND “reproductive isolation”
“pollen-pistil” AND “reproductive isolation” AND speciation
sperm AND speciation
sperm AND “reproductive isolation”
“reproductive isolation” AND speciation AND post-mat*
“reproductive isolation” AND speciation AND postmat*
“reproductive isolation” AND speciation AND post-cop*
“reproductive isolation” AND speciation AND postcop*
“reproductive isolation” AND speciation AND post-pollination
“reproductive isolation” AND speciation AND postpollination
“reproductive isolation” AND speciation AND pre-zygot*
“reproductive isolation” AND speciation AND prezygot*
“gametic incompatibility”
“reproductive isolation” AND “postmating prezygotic”
“reproductive isolation” AND “post-mating prezygotic”

Figure S1. Measures of PMPZ isolation in other eukaryotes.

Stacked bars show the number of studies in which each grouped measure (see Table S3) has been measured.

Figure S2. PMPZ isolation and flowering plants. Two common experimental setups for measuring PMPZ isolation in angiosperms. (A) A crossability experiment, whereby reciprocal hand-pollinations are performed using heterospecific pollen only (reciprocal cross not shown). Measures of PMPZ isolation (including pollen performance, fruit set, and seed set) are taken and compared to an intraspecific baseline (intraspecific cross not shown). There are three possible outcomes when measuring seed set in a crossability experiment: (i) full seed set (implies no PMPZ isolation, but PMPZ isolation can be present under competitive conditions, see B); (ii) reduced seed set resulting from PMPZ isolation; and (iii) reduced seed set resulting from post-zygotic embryo abortion (i.e., not PMPZ isolation). Note that (i) and (ii) are confounded unless embryo abortion is rigorously accounted for. (B) A pollen competition experiment, whereby a mix (typically 50:50) of heterospecific and conspecific pollen are applied to stigmas of one or both species. Paternity is then assigned to seeds using paternity analysis. Reduced hybrid seed formation can result from (i) reduced ability of heterospecific pollen to obtain fertilisation (PMPZ isolation) or (ii) reduced seed set from postzygotic embryo abortion. As in A, without additional data on where failure is occurring, these outcomes are confounded.