

The role of allochrony in speciation

Rebecca S. Taylor  | Vicki L. Friesen

Department of Biology, Queen's University,
Kingston, ON, Canada

Correspondence

Rebecca S. Taylor, Department of Biology,
Queen's University, Kingston, ON, Canada.
Email: 13rst@queensu.ca

Funding information

Ontario Trillium Scholarship

Abstract

The importance of sympatric speciation – the evolution of reproductive isolation between codistributed conspecific individuals – in generating biodiversity is highly controversial. Allochrony, or differences in breeding time (phenology) between conspecific individuals, has the potential to lead to reproductive isolation and therefore speciation. We critically review the literature to test the importance of allochronic speciation over the three timescales over which allochrony can occur – over the day, between seasons or between years – and explore what is known about genomic mechanisms underlying allochrony in the diverse taxa in which it is found. We found that allochrony can be a key contributor to reproductive isolation, especially if populations have little overlap in breeding time and therefore little potential for gene flow, and may sometimes be the initial or key driver of speciation. Shifts in phenology can be caused by several factors, including a new ecological opportunity, environmental change, or reinforcement. The underlying genomic basis of allochrony has been studied mostly in insects, highlighting the need for genomic studies in other taxa; nonetheless, results to date indicate that several cases of allochrony involve changes in circadian genes. This review provides the first comprehensive discussion of the role of allochrony in speciation and demonstrates that allochrony as a contributor to divergence may be more widespread than previously thought. Understanding genomic changes and adaptations allowing organisms to breed at new times may be key in the light of phenological changes required under climate change.

KEYWORDS

allochronic speciation, breeding time, magic traits, phenology, speciation with gene flow, sympatric speciation

1 | INTRODUCTION

Speciation in sympatry, that is the evolution of reproductive isolation without geographic impediments to gene flow, presents theoretical challenges to evolutionary theory, largely because it requires the evolution of assortative mating within an initially panmictic population (Coyne & Orr, 2004). Specialization of individuals to different niches or resources could lead to sympatric speciation if assortative mating also develops (Dieckmann & Doebeli, 1999; Servedio, Van Doorn, Kopp, Frame, & Nosil, 2011; Box 1, panel a). However, recombination will tend to separate genes controlling

adaptation to a particular niche from those causing assortative mating (Dieckmann & Doebeli, 1999; Servedio et al., 2011). But if the trait under disruptive selection also causes assortative mating, a so-called “magic trait”, then recombination is no longer a problem (Gavrilets, 2004). While there is much contention about the frequency of sympatric speciation in nature, researchers generally agree that speciation in the face of gene flow is more likely if it entails a magic trait (Bolnick & Fitzpatrick, 2007; Dieckmann & Doebeli, 1999; Gavrilets, 2004; Servedio et al., 2011). Magic traits leading to divergence could be more common than initially thought, leading to the suggestion that “magic” traits are

misnamed (Servedio & Kopp, 2012; Servedio et al., 2011) and should be renamed “multiple effect traits” (Smadja & Butlin, 2011).

Perhaps the most intuitive multiple effect (or magic) trait is divergence in breeding time, or allochrony (Servedio et al., 2011). Allochrony can act over different timescales – over the day, between seasons or between years – and clearly can automatically result in assortative mating. In some cases, differences in phenology may be the initial driver of speciation (Box 1, panel b). True allochronic speciation was originally described as “all speciation resulting *initially* from temporal separation” of populations (Alexander & Bigelow, 1960; emphasis added), even though other barriers to reproduction will develop as populations diverge. Allochrony can also be an important driver contributing to divergence as a by-product of, or act concurrently with, another multiple effect trait (e.g. host preference in *Rhagoletis* host races; Feder et al., 1994), or act to reinforce divergence at any stage along the speciation continuum; that is, there are more ways that allochrony can contribute to speciation than the initiation of reproductive isolation. However, these cases are not “true” allochronic speciation, and it is important to elucidate at what point allochrony acted.

In this review, we explore whether temporal variation in breeding time has made significant contributions to the generation of reproductive isolation (i.e. the disruption of gene flow or migration). For each of the three timescales over which allochrony can occur, we discuss evidence for a role for allochrony in speciation and provide examples. We then explore proposed mechanisms of divergence, and investigate whether similarities exist in genetic mechanisms across timescales and taxa, or whether genes controlling allochrony and mate choice may be linked.

1.1 | Theory of allochrony

Hendry and Day (2005) demonstrated that heritable variation in reproductive times can potentially lead to genetic divergence between individuals breeding at different times, even in the absence of selection (“isolation by time”). They also showed that “adaptation by time” could occur if individuals adapt to the environmental conditions that occur at the time of their breeding. Both processes could lead to reproductive isolation and are more likely to evolve with high heritability of reproductive time (Hendry & Day, 2005).

Whereas allochrony itself is common, whether (and how much) allochrony contributes to speciation is less clear (Box 1). To demonstrate true allochronic speciation, studies need to demonstrate three key things:

1. The species, or incipient species, were/are sister taxa, at least at the time of speciation. This can be tested through phylogenetics.
2. Allochrony was the initial cause of divergence. Allochrony must not have followed from other factors (e.g. a host shift), and must not be a result of reinforcement after speciation was complete. This can be difficult to test in taxa that have many pre- and postzygotic isolating mechanisms.

3. Breeding time must have a heritable component (Hendry & Day, 2005). Ideally, the genomic basis of the change in breeding time would be known.

Allochronic speciation traditionally received little study as it was thought to be uncommon in nature (Santos et al., 2007; Yamamoto & Sota, 2009), and reviews of multiple effect traits only give brief mention of allochrony as a mechanism of divergence (Bolnick & Fitzpatrick, 2007; Dieckmann, Doebeli, Metz, & Tautz, 2004; Gavrillets, 2004; Servedio & Kopp, 2012; Servedio et al., 2011; Smadja & Butlin, 2011). However, compelling examples of divergence driven by allochrony are accumulating for a diversity of taxa.

For this review, we searched the words “allochrony”, “allochronic”, “breeding phenology” and “breeding time” using the Web of Science (<https://webofknowledge.com/>). Examples of species or populations diverging in association with differences in breeding time were reviewed critically, including study details and support for allochronic speciation based on the three key points listed above. Approximately 200 articles were evaluated (see Table S1 for full results), and 64 case studies were found, of which nine appear to be true or incipient allochronic speciation (in bold in Table S1) and a further eight may be true allochronic divergence but further study is needed (in italics in Table S1).

2 | ROLE OF ALLOCHRONY IN SPECIATION

2.1 | Speciation by daily allochrony

We found 10 case studies involving separation of species by breeding time over a daily cycle (Table S1). Daily allochrony seems less likely to lead to divergence than seasonal or yearly allochrony, but could be more common than previously thought, especially within insects and coral species. For example, Devries, Austin, and Martin (2008) sampled over 400 species of Neotropical skippers (Lepidoptera: Hesperiidae) and found that species pairs in at least seven genera had significant differences in timing of flight activity of males (Devries et al., 2008). Further study is needed in these skippers to determine how important allochrony was as an initial driver of divergence versus secondary reinforcement or niche partitioning to reduce competition. However, temporal structure clearly occurs within insect communities and perhaps is quite common within sympatric species assemblages.

Similarly, allochronic separation in spawning times likely played a role in speciation in *Acropora* corals (Fukami, Omori, Shimoike, Haya-shibara, & Hatta, 2003) and may be common in coral species given the short persistence time of coral gametes at viable concentrations for fertilization in the water column, potentially less than 2 hr (Fukami et al., 2003; Levitan et al., 2004). Although ruling out allochrony acting through reinforcement after speciation is difficult (Fukami et al., 2003), further investigation into the role of even small separations in spawning times in divergence between corals is needed.

2.2 | Speciation by seasonal allochrony

Seasonal separation of breeding times was the most common mode of allochronic divergence we uncovered, with 47 case studies (12 involving a host shift) encompassing fish, insects, birds, plants, fungi and corals (Table S1). Many interesting examples of seasonal populations are emerging among insect species. One that best satisfies the criteria for true allochronic speciation is the pine processionary moth (*Thaumetopoea pityocampa*). This species has one population with the usual winter larval development and one with summer larval development on the same plant host species in Portugal. The reproductive periods of the two populations do not overlap, and genetic data suggest they are sister taxa (Santos et al., 2007). Summer and winter populations are differentiated at microsatellite loci and so represent “phenological races”, and emergence time has been shown to be highly heritable (Branco, Paiva, Santos, Burban, & Kerdelhué, 2017; Santos, Burban, et al., 2011). Hybrids produced in laboratory experiments had intermediate emergence times, suggesting codominance in the genes controlling emergence (Branco et al., 2017). The lower genetic diversity of the summer population suggests it formed from a founder event (Santos, Burban, et al., 2011). Laboratory studies show that summer population larvae, which face 6.6°C higher average temperatures during development, have increased thermal tolerance (Santos, Paiva, Tavares, Kerdelhué, & Branco, 2011). Furthermore, the summer population has fewer, larger eggs with egg scales that differ in shape and colour, possible adaptations to increase egg temperature suggesting potential adaptation by time (Santos, Paiva, Rocha, Kerdelhué, & Branco, 2013).

Emergence time is likely a plastic trait affected by environmental conditions, and a few individuals emerge in late summer, possibly due to a longer larval development or delayed pupal diapause (Burban et al., 2016). Some hybridization occurs between summer and winter populations, although this is not thought to be driven by the late emerging summer individuals, which were caught in a different area (Burban et al., 2016). The hybrids were found at the northern and southern range limits of the expanding summer population and so may be due to the colonization process before reproductive isolation develops (Burban et al., 2016). The winter population size is low within the central range of the summer population, warranting further investigation to understand whether competition with the newer summer individuals is affecting the winter population (Burban et al., 2016). This is one example of true incipient allochronic speciation that has been thoroughly investigated and almost fully addresses our three key points. If ongoing work on pine processionary moths uncovers the genomic mechanisms involved in the life cycle change, the three criteria will be fully satisfied.

Another convincing case of incipient allochronic isolation is the winter geometrid moth, *Inurois punctigera*, found throughout Japan (Yamamoto & Sota, 2009). In southern Japan, winter geometrid moths emerge to reproduce throughout the winter. However, in areas with the most extreme temperatures reproduction does not occur during mid-winter. As a result, two breeding populations exist: one each in early and late winter. These seasonal populations are

genetically differentiated (Yamamoto & Sota, 2009) and may have arisen multiple times in parallel throughout Japan (Yamamoto & Sota, 2012). A slight isolation-by-time structure occurs in populations breeding continuously over the winter, and so emergence time appears to be genetically controlled (Yamamoto & Sota, 2009). Segregation of breeding time may have contributed to speciation in other *Inurois* species also showing early and late winter breeding (Yamamoto, Beljaev, & Sota, 2016), and so allochronic isolation may have occurred multiple times within the genus.

Although not considered true allochronic speciation, many phytophagous insects undergo shifts in breeding time after a host shift, which contributes to reproductive isolation (Table S1 section 2b for seasonal examples involving a host shift). Examples vary in the amount and importance to reproductive isolation of phenology differences between host races. The most well-studied example is *Rhagoletis pomonella*, where a host shift from hawthorn (*Crataegus* spp.) to apple (*Malus pumila*) occurred. The change to an apple host secondarily caused an earlier emergence time, which together led to the formation of two host races (Feder et al., 1994; Box 2).

In many salmonid species, particularly in the genus *Oncorhynchus*, distinct “early” and “late” run breeding populations exist within the same river and often differ genetically (Table S1). Salmon have highly heritable breeding times (reviewed in Hendry & Day, 2005), which facilitates genetic divergence of populations. The lack of gene flow between seasonal populations in salmon seems to have led to adaptation by time in some cases. For example, early breeding sockeye salmon (*O. nerka*) live longer, associated with their increased need to defend nests against later returning fish (Hendry, Morbey, Berg, & Wenburg, 2004).

Different migratory strategies also can lead to assortative mating by inducing differences in breeding time (Table S1). For example, a proportion of European blackcaps (*Sylvia atricapilla*) breeding in Germany started overwintering in Britain and Ireland around 50 years ago, whereas the rest of the breeding population overwinters in Iberia, and individuals appear to mate assortatively by overwintering area due to differences in return dates (Bearhop et al., 2005). Many seasonal migrant populations, or species, have periods of both allopatry and sympatry throughout the annual cycle. Divergence between such lineages is known as heteropatric speciation, and allochrony could be a contributor in many cases (Winker, 2010).

Evidence suggests that true allochronic speciation is occurring in multiple populations within the band-rumped storm-petrel (*Hydrobates* spp.) species complex. On at least four archipelagos, this seabird has developed two seasonal breeding populations (Friesen et al., 2007). Genetic evidence suggests that seasonal populations within archipelagos are sister taxa and so arose by parallel evolution in sympatry (Friesen et al., 2007). In the Azores, hot and cool populations differ in neutral genetic markers as well as vocalizations, morphology and diet, suggesting adaptation by time (Bolton et al., 2008). Genetically differentiated seasonal populations also exist in the Leach's storm-petrel (*H. leucorhoa*; Friesen et al., 2007) and possibly other storm-petrel species (Spear & Ainley, 2007).

A similar example of seasonal allochronic speciation involves the coral species *Acropora samoensis* in Western Australia. A genetic analysis of sympatric spring and autumn spawning cohorts revealed the two to be highly differentiated, potentially to species level (Rosser, 2015).

Reviews of multiple effect (magic) traits usually use plant flowering time differences as their example involving phenology (e.g. Kisdi & Priklopil, 2011; Servedio et al., 2011), something that could be relatively common (see Table S1 for examples). Devaux and Lande (2008) used a theoretical model to test factors that might promote allochronic speciation in plants, treating flowering time as a quantitative trait. They found that individual plants could cluster in flowering time, particularly when plants have (i) a finite population size; (ii) a long flowering season but with each individual plant having a short flowering time; and (iii) high mutational variance in flowering time. Clusters formed even in the absence of selection; adding weak disruptive selection to the model “promoted long-lived transient clusters” (Devaux & Lande, 2008). Interestingly, temporal isolation has been suggested as a way of reducing gene flow between crops and their wild relatives (Ohigashi, Mizuguti, Yoshimura, Matsuo, & Miwa, 2014).

2.3 | Speciation by yearly allochrony

While we found fewer potential examples, allochronic speciation can involve cohorts that breed in different years (seven case studies, Table S1). Yearly allochrony includes perhaps the most famous example of true allochronic speciation: several species of periodical cicadas (*Magicicada* spp.) with two life cycles, emerging after 13 or 17 years, occur in North America (Marshall & Cooley, 2000). These species have a complex phylogeographic structure (being largely parapatric) and co-emerge every 221 years allowing potential for hybridization; however, the evolution of this group seems to have involved multiple allochronic life cycle shifts, with each species most closely related to another of an alternative life cycle. These life cycle changes have been important drivers of diversification in this group (Sota et al., 2013; see Box S1 for a detailed description).

Within plants, the evolution of “flowering waves” in bamboo (subfamily Bambusoideae) is often compared to evolution in periodical cicadas. Bamboo species are semelparous and live for decades before having a mass flowering event (Franklin, 2004). This synchrony is thought to be under genetic control; however, flowering occurs in different patches of bamboo in successive years (hence “flowering waves” Franklin, 2004; de Carvalho et al., 2013). Allochronic patches could be examples of incipient allochronic speciation and occur in many bamboo species across the world (Table S1). However, further study is needed to determine whether offset populations are genetically differentiated, so demonstrating isolation by time, to confirm whether allochrony is leading to divergence.

Some organisms have a two-year life cycle, with individuals that breed in alternate years being reproductively separated from each other. The White Mountain arctic butterfly (*Oeneis melissa semidea*), a threatened butterfly endemic to four sedge meadows in New

Hampshire, USA, provides an example (Gradish, Keyghobadi, & Otis, 2015). While no genetic differentiation was found between meadows, sympatric allochronic cohorts exhibit moderate differentiation (Gradish et al., 2015). Pink salmon (*O. gorbuscha*) provide another example of populations breeding in alternate years, in addition to seasonal allochrony (above); yearly cohorts are genetically differentiated, and genetic differentiation is stronger between cohorts than among populations breeding within the same year in different rivers (Aspinwall, 1974). Other potential examples of yearly allochrony within organisms with a strict multiyear development time remain to be fully explored with respect to the three criteria, for example Childers canegrub (*Antitrogus parvulus*; Logan, Allsopp, & Zalucki, 2003; Table S1).

3 | GENOMIC CONTROL OF BREEDING TIME

3.1 | Daily allochrony

The genomic mechanisms controlling daily reproductive cycles have been studied primarily in *Drosophila* species (Sakai & Ishida, 2001; Tauber et al., 2003) and the melon fly, *Bactrocera cucurbitae* (Fuchikawa et al., 2010; Miyatake et al., 2002). Mutations affecting the expression of the circadian genes *period* and *timeless* were shown to affect the frequency of flies mating at different times of day in *D. melanogaster* as null mutant flies lacked circadian rhythms (Sakai & Ishida, 2001; see Figure 1 for a description of the circadian clock mechanism). Interestingly, the gene *period* seems also to affect reproductive isolation: not only was it involved in the timing of locomotor and mating activities, but also transgenic *D. melanogaster* and *D. pseudoobscura* flies with the same *period* genotype mated preferentially even with males with their wings removed to remove the effect of courtship songs (Tauber et al., 2003).

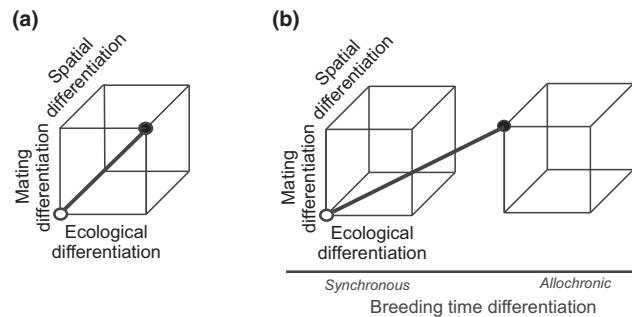
The role of the *period* gene and timing of mating was also investigated in *Bactrocera cucurbitae*. Two laboratory lines were established, one each with a short (S-strain) or long (L-strain) developmental time, which created reproductive isolation (Miyatake et al., 2002). The *period* gene was found to have different daily fluctuations in expression levels between these two lines (Miyatake et al., 2002), although the amino acid sequences were identical (Fuchikawa et al., 2010), suggesting that regulation of the *period* gene may be important. Another circadian gene, *cryptochrome*, had two amino acid substitutions, and L-strain flies had lower *cryptochrome* mRNA levels than S-strain flies. Consistent results were found for two related allochronic sister species, *B. neohumeralis* and *B. tryoni*: expression of *cryptochrome* was higher in *B. neohumeralis*, which mates earlier in the day, as do S-strain *B. cucurbitae* individuals (Fuchikawa et al., 2010).

3.2 | Seasonal allochrony

Most insights into genomic mechanisms underlying seasonal allochrony come from insects, for example the European corn borer

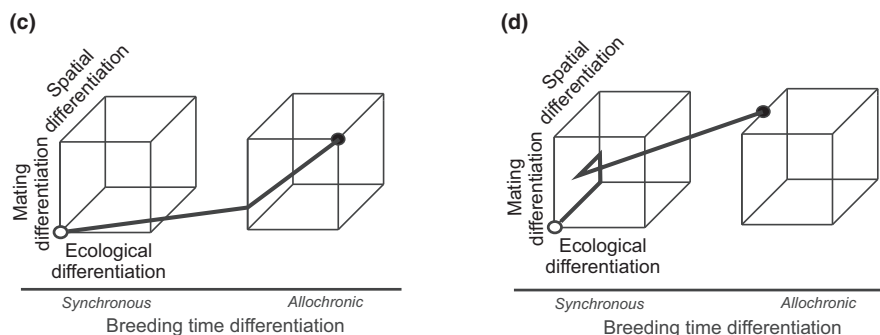
BOX 1 Allochrony and a process-based classification of speciation

To help visualize and classify the complexity of speciation processes, Dieckmann et al. (2004) proposed representing speciation as a three-dimensional cube, where axes represent the extent of population differentiation with respect to ecology, mate choice and geographic distribution (space, e.g. sympatry vs. allopatry), and the origin represents undifferentiated populations (open circle, panel a; simplified from Dieckmann et al. (2004), who show various speciation scenarios). Differentiation in either space or ecology can be driven by genetic drift, selection or external forces (e.g. geographic isolation; not shown), ultimately resulting in reproductive isolation (solid circle). Panel a shows sympatric speciation through ecological differentiation.



Superficially, breeding time could be interpreted either as an alternative to spatial differentiation, or as a type of ecological differentiation. However, breeding time can act either in concert with or independent of each of the three axes, potentially contributing to differentiation in ecology ("adaptation by time", Hendry & Day, 2005), mating ("isolation by time", Hendry & Day, 2005), or space, and resulting from either genetic drift or selection (Hendry & Day, 2005). Thus, breeding time contributes a fourth dimension to the cube (panel b), where allochrony may occur over the day, between seasons, or between years. (For simplicity, only the two extremes of breeding time differentiation are shown – complete breeding synchrony and complete allochrony.)

Under true allochronic speciation, allochrony is the initial cause of mating differentiation (see Introduction; panel b). However, spatial, mating and/or ecological differentiation can potentially accompany allochrony and contribute to mating isolation (panel c). Furthermore, as discussed in Dieckmann et al. (2004), speciation can involve two (or more) phases, where allochrony may initiate speciation but reproductive isolation is only completed under the action of spatial or ecological differentiation. Alternatively, speciation may be initiated by spatial or ecological differentiation, but be completed through the evolution of allochrony, for example following secondary contact where allochrony is a result of reinforcement (panel d).



(*Ostrinia nubilalis*) and *Rhagoletis pomonella*. Phenological shifts in insects are often associated with genes controlling diapause duration, timing of diapause termination and circadian rhythms, and may be associated with genomic inversions (e.g. the European corn borer,

Box 3). In *Rhagoletis* flies, six allozyme loci and multiple areas of the genome correlate with eclosion time and key diapause traits (Dambroski & Feder, 2007; Feder, Powell, Filchak, & Leung, 2010; Feder et al., 1997). Genomic inversions on chromosomes 1, 2 and 3,

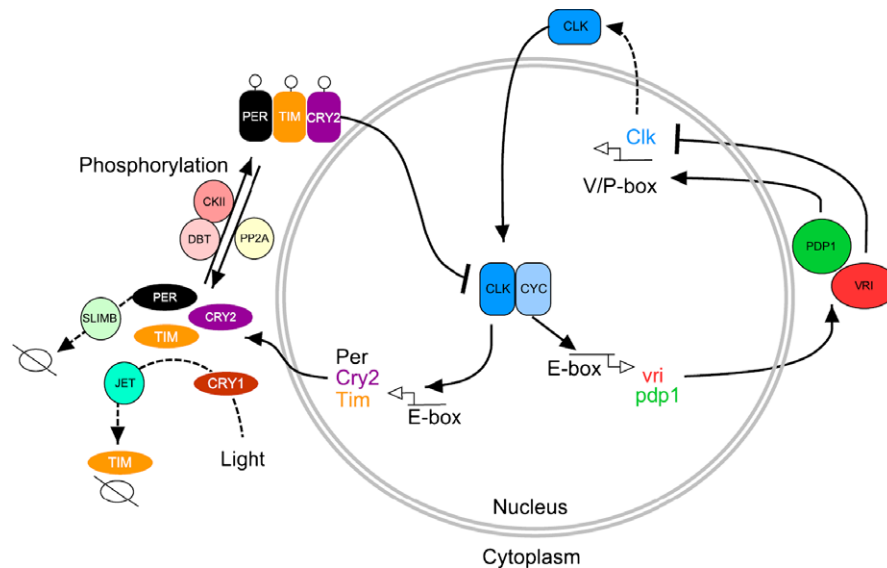


FIGURE 1 Circadian clock mechanism, here shown for Lepidoptera, modified from Derks et al. (2015). *Clock* (CLK) and *cycle* (CYC) heterodimerize and drive the transcription of *period* (PER), *timeless* (TIM) and *cryptochrome 2* (CRY2). Within insects, *period* and *timeless* are mostly transcribed at night. *Cryptochrome 2* inhibits transcription of *clock* and *cycle* in a feedback loop. *Period* and *timeless* bind together, and *Casein kinase II* (CKII), *discs overgrown* (DBT) and the *protein phosphatase 2A* (PP2A) are involved in their post-translational modifications and activation. *Cryptochrome 1* (CRY1) is activated by light and modulates the degradation of *timeless* by *jetlag* (JET). *Slimb* (SLIMB) stimulates the degradation of *period*. In a second feedback loop, *vri* and *par domain protein 1* (PDP1) regulate the expression of *clock*

covering a large part of the genome, correlate with diapause traits (Feder, Roethele, Filchak, Niedbalski, & Romero-Severson, 2003; see also Box 3). Further investigation would be interesting to determine whether genes for host response to fruit volatiles also map to these areas (Feder et al., 2003), in the same way that diapause and behavioural genes map to the same inversion in the European corn borer (Wadsworth, Li, & Dopman, 2015). Using gene expression, Ragland, Egan, Feder, Berlocher, and Hahn (2011) found many genes and pathways potentially important in controlling timing of diapause termination in *Rhagoletis*, a first step in determining specific pathways allowing adaptation to host phenology.

Large areas of the *R. pomonella* genome are diverging between host races (Michel et al., 2010). In an experiment in which prewintering period was altered, Egan et al. (2015) found significant allele shifts at 312 single nucleotide polymorphisms (SNPs) widely distributed throughout the genome. The direction and magnitude of allele frequency changes in all 32,455 SNPs was the same in the selection experiment as between wild apple and hawthorn flies (Egan et al., 2015); however, *Rhagoletis* flies have very high levels of linkage disequilibrium across the genome (partly due to inversions mentioned above), which may be strengthening the patterns seen (Egan et al., 2015).

The above experiment also suggests that standing genetic variation is likely the source of allele frequency differences between host races (Egan et al., 2015; Powell et al., 2013). In addition, the areas of the genome that are diverging between apple and hawthorn host races are similar to those divergent in the reproductively isolated *Rhagoletis* flies attacking *Cornus florida* (Powell et al., 2013). *Rhagoletis* flies have a complex biogeographic history, which has

increased levels of standing genetic variation (Egan et al., 2015). For example, the inversions between apple and hawthorn host races appear to have originated 1.5 million years ago in Mexico, then spread into North American flies. This historic variation may have enabled *Rhagoletis* flies to form host races rapidly (Barrett & Schluter, 2008), so the ability of species to adapt rapidly to a new breeding time may depend on high levels of standing genetic variation.

Circadian genes, already implicated in diapause regulation and therefore seasonal allochrony in insects, were not expressed during diapause termination in *Rhagoletis*. However, genes that are secondary modulators of circadian genes did change expression levels during this phase (Ragland et al., 2011). Circadian genes are therefore potentially important in determining seasonal timing in *R. pomonella*; however, much more investigation is needed to understand their role in regulating diapause (Ragland et al., 2011).

Genomic mechanisms generating seasonal allochrony in noninsect taxa remain largely unexplored, with two exceptions. In cryptic seasonal populations of *Acropora samoensis* (above), the gene *PaxC* appeared to be under selection as the *PaxC* intron had no shared alleles between the seasonal cohorts. *PaxC* in cnidarians is a homolog of *Pax6*, a gene involved with eye development in vertebrates, leading Rosser (2015) to suggest *PaxC* may be involved in sensing light, and changes in light intensity are likely a cue for spawning time. A further study on *A. tenuis* supported the idea of *PaxC* functioning in spawning time (Rosser, 2016), which could be investigated in other corals.

Brieuc, Ono, Drinan, and Naish (2015) used genomic techniques to locate loci putatively in, or linked to, regions controlling

variation in run timing in Chinook salmon (*O. tshawytscha*). They found a number of potential loci on numerous chromosomes throughout the genome. A cluster of particularly interesting predictor loci mapped to one 2-centimorgan region, although the bias in distribution of predictor loci could be due to an ancestral genome duplication in salmon. Altogether, multiple loci of both large and small effect appear to control run timing in Chinook salmon (Brieuc et al., 2015). The results demonstrate how even low-density markers from across the genome in nonmodel organisms can further our knowledge of mechanisms involved with timing of breeding. More genomic study is needed, and is now easier, to further elucidate genomic architecture controlling breeding time in a wider variety of taxa.

3.3 | Yearly allochrony

We could not find any studies investigating the genetic control of breeding time under yearly allochrony, a clear gap in our knowledge of allochronic speciation.

4 | DISCUSSION AND SYNTHESIS

4.1 | Role of allochrony in speciation

This review uncovered many examples for which allochrony contributed to the development of reproductive isolation, including several examples of true allochronic speciation (Table S1). Phytophagous insects are well studied and demonstrate that temporal differences are often important for creating reproductive isolation. However, many factors other than allochrony can promote reproductive isolation during sympatric speciation, and the role of allochrony in initiating speciation is often unclear, particularly when it is acting concurrently with other isolating factors as is often the case. For example, how many sister species of skippers with different breeding times only developed reproductive isolation because of temporal shifts in breeding (Devries et al., 2008)? This is challenging to study when speciation is complete.

Clearly allochronic speciation requires more focused study, with authors testing hypotheses about allochrony and specifically weighing the importance of allochrony versus other potential forces driving divergence. Authors rarely do this (but with some exceptions, e.g. studies on the pine processionary moth, see Table S1). We hope that future investigations will try to address the three points listed in the introduction. Nonetheless, existing studies allow some synthetic insights. *First, the less that breeding time overlaps, the more likely full speciation appears to be.* For example, among seven examples of yearly allochrony (where, if taxa have a fixed annual life cycle, breeding time cannot overlap), three have allochrony as the initial driver (representing true or incipient allochronic speciation), two are likely true allochronic speciation but require further investigation, and two seem to have plasticity in life cycle length which would tend to inhibit genetic divergence (but see Levis & Pfennig, 2016). Across all timescales,

none of the five case studies that appear to be true complete allochronic speciation have any overlap in breeding time. In fact, all nine examples of true or incipient allochronic speciation have no or very little overlap in time, suggesting that allochrony is more likely to initiate divergence when there is a strong shift in breeding time. This supports theory developed by Hendry and Day (2005).

Given speciation appears more likely with no overlap in breeding time, it seems yearly allochrony is the least “leaky” to gene flow, assuming strictly heritable life cycle length, whereas daily allochrony is likely the most “leaky”. Only in coral species did we find possible true allochronic speciation over a daily cycle (Table S1), and daily allochronic speciation may require quite specific conditions (e.g. the very short persistence time of coral gametes in the water column, see above). Migration rate, or levels of gene flow, has been measured between allochronic populations (for example Burban et al., 2016; Feder et al., 1994; Friesen et al., 2007). However, to our knowledge, no studies have directly estimated the initial reduction in migration caused by allochrony in comparison with other factors, but future study would be beneficial here to explicitly test whether the less the overlap in time, the lower the actual migration and gene flow between the allochronic populations.

That speciation is more likely to occur with no overlap in breeding time relates to allochrony acting as a multiple effect trait. If breeding time overlaps then selection for increased assortative mating beyond that generated by allochrony is not inevitable. There is often a cost to being choosy during mating (Gavrilets, 2004, 2005), and so when both populations co-occur for at least some of their breeding period, assortative mating may not evolve. For example, apple and hawthorn host races of *R. pomonella* have 4% current gene flow per population and may never fully speciate, as breeding times still overlap (Egan et al., 2015; Feder et al., 1994; Ragland, Sim, Goudarzi, Feder, & Hahn, 2012). Perhaps the cost of choosiness to *Rhagoletis pomonella* apple and hawthorn host races is too high, even though hybrids could be less fit with respect to developmental profile, timing or host plant (Dambroski & Feder, 2007; Feder et al., 2010).

Allochrony has the potential to at least contribute to population divergence under any geographic mode of speciation, including in sympatry, parapatry and allopatry, and can also facilitate reinforcement following secondary contact (Box 1). For example, according to the Asynchrony of Seasons Hypothesis, populations of a species adapting to different local precipitation regimes, and therefore breeding at different times, could diverge genetically (Martin, Bonier, Moore, & Tewksbury, 2009). The Asynchrony of Seasons Hypothesis was tested using data from 57 New World bird species (Quintero, González-Caro, Zalamea, & Cadena, 2014). Increased spatial asynchrony in precipitation was related to increased genetic distance between populations (after accounting for geographic and ecological distances), which could clearly lead to adaptation by time as described by Hendry and Day (2005). Populations can still exchange genes; the key is that asynchrony due to locally adapted phenologies reduces interbreeding between populations (Martin et al., 2009;

BOX 2 How important is allochrony in reproductive isolation of host races of *Rhagoletis pomonella*?

The best-known example of speciation with gene flow in a phytophagous insect is the *R. pomonella* host shift from hawthorn (*Crataegus* spp.) to apple (*Malus pumila*), approximately 150 years ago. Apple trees fruit about 3 weeks earlier than hawthorns, and so apple-infesting flies emerge earlier to match their host phenology (Ragland et al., 2012). Adult flies only live for about 1 month (Ragland et al., 2012), creating significant temporal isolation between the host races. The two are genetically differentiated (Powell et al., 2014) even with gene flow of around 4% per generation (Egan et al., 2015; Feder et al., 1994).

Adaptive changes in key diapause traits, allowing them to match host phenology, appear to be important for the fitness of these flies on their respective hosts. Genetic factors involved in diapause depth seem to be “uncoupled” from those controlling diapause termination time and post diapause development (Dambroski & Feder, 2007). This implies that, to successfully adapt life cycle timing to host phenology, multiple regions of the genome may be involved. Timing therefore creates both a strong barrier to gene flow, and postzygotic isolation (in addition to prezygotic isolation caused by lack of overlap in adult flight time), as hybrids would have a mismatched developmental profile on the wrong host plant (Dambroski & Feder, 2007; Feder et al., 2010).

However, allochronic separation, and adaptation to different phenologies, is not the only cause of differentiation in *R. pomonella*. Each host race has a behavioural preference for the odour of their host plants, probably for the fruit volatiles, contributing to premating isolation (Linn et al., 2004). F1 hybrids were demonstrated to lose the behavioural response to fruit volatiles, suggesting the preference has a genetic basis and can also cause postzygotic isolation (Linn et al., 2004).

When considering the importance of both adaptation to host phenology and preference for fruit volatiles in the development of reproductive isolation, other examples of *R. pomonella* host switching are helpful. In the southern USA, *Rhagoletis* has formed host races on western mayhaw (*Crataegus opaca*), blueberry hawthorn (*C. brachyacantha*), southern red hawthorn (*C. mollis* var. *texana*) and green hawthorn (*C. viridis*; Powell et al., 2014). A relationship between eclosion time and genetic differentiation is found in the host races. However, the host plants separated the most in time (*C. opaca* and *C. viridis*) had flies that were most similar genetically and in eclosion characteristics. These two plants are separated in fruiting time by 6 months, and such a large time difference may limit differentiation by allochrony as, for example, host races may develop a bivoltine life cycle (i.e. having two generations per year; Powell et al., 2014).

Differences in the host plant volatiles and preferences are found between the southern host races. However, no relationship between genetic differentiation and response to host volatiles was found (Powell et al., 2014). Thus, both shifts in life cycle timing and odour preferences may generate reproductive isolation between *R. pomonella* host races throughout its range. The pre- and postzygotic isolation formed through allochronic separation and genetic adaptations to a shifted life cycle (adaptation by time) appear to play a key role. Given the relationship between emergence time and genetic differentiation, and the fact that multiple unrelated genes seem to be involved (Dambroski & Feder, 2007; Feder et al., 2010; Powell et al., 2014), allochrony is possibly essential for enough reduction in gene flow to allow incipient speciation to occur. *Rhagoletis* flies infesting dogwood (*Cornus florida*) have higher levels of genetic and ecological divergence and appear to have completely speciated in sympatry (Powell et al., 2014), and so over time, the reduction in gene flow between host races caused by allochrony can facilitate the formation of new species.

Interestingly, a specialist parasitoid wasp, *Diachasma alloeum*, has formed incipient species on different host races in the *Rhagoletis* complex. Divergence of the parasitoid is also driven by preference for fruit volatiles and differences in eclosion time, and a relationship between microsatellite loci and eclosion time was found (Forbes, Powell, Stelinski, Smith, & Feder, 2009). Further study also found sequential divergence of two other parasitoids, *Utetes canaliculatus* and *Diachasmimorpha mellea*, on members of the *Rhagoletis* species complex in a similar way (although *D. mellea* did not have a relationship between microsatellite loci and eclosion time, Hood et al., 2015). Temporal isolation and habitat isolation together were found to contribute 70–94% of the reproductive isolation between hosts in *D. alloeum*, 85–99% in *U. canaliculatus* and 79–90% in *D. mellea* (Hood et al., 2015), demonstrating the power of allochronic differences in life cycles to contribute to genetic differentiation not only between populations, but also across trophic levels.

Quintero et al., 2014). Therefore, allochrony, rather than geographic distance, would appear to be an important factor facilitating speciation (Quintero et al., 2014).

While not explored in detail here, within insects a narrower window of resource availability may promote allochrony, whereas increased temporal divergence between resources may favour the development of a bivoltine or multivoltine life cycle instead (J. Feder, personal communication). For example, if host plants are available too close in time to allow the evolution of bivoltinism, the formation of two univoltine host races may occur instead, such as the apple and hawthorn *Rhagoletis* flies. However, increased temporal divergence between resources, or increased season length, may allow the development of bivoltinism (Levy, Kozak, Wadsworth, Coates, & Dopman, 2015), potentially explaining patterns seen in other hawthorn *Rhagoletis* host races (Powell, Forbes, Hood, & Feder, 2014; Box 2). Also, generalist insects may be less likely to diverge allochronically than those specifically adapted to one host plant.

4.2 | Causes of allochrony

This review supports theory that allochrony can be caused by a variety of environmental and evolutionary factors. It could just happen by chance, with individuals becoming offset in breeding time. For example, the pine processionary moth summer population is thought to have evolved from a sudden mutational change shifting breeding time in a founder event (Burban et al., 2016). Allochrony could develop simply if breeding time is heritable and assortative mating occurs because of temporal isolation over the breeding season (Hendry & Day, 2005), as is possible in some plants (Devaux & Lande, 2008). Alternatively, a new ecological opportunity may cause individuals to breed at a different time, as in many phytophagous insects colonizing a new host plant (e.g. Ragland et al., 2012). Similarly, multiple temporal peaks in the availability of resources such as food can cause, or at least help maintain, distinct breeding populations (e.g. band-rumped storm-petrels; Monteiro & Furness, 1998). Finally, environmental changes can cause shifts in life cycles as seen in the Japanese winter geometrid moth (Yamamoto & Sota, 2012), periodical cicadas (Marshall, Cooley, & Hill, 2011) and bamboo (Franklin, 2004).

Given that many ecological causes of allochrony exist and that it has been found in a wide diversity of taxa, it probably is an important contributor to speciation. In the words of Dopman, Robbins, and Seaman (2010), “although accounts of temporal isolation may be numerically rare, the phylogenetic breadth of taxa that experience temporal isolation suggests that this paucity reflects limited study rather than low evolutionary frequency”. Many more examples probably remain to be discovered.

4.3 | Mechanisms underlying allochrony

This review attempted to explore whether genomic mechanisms underlying allochronic shifts would differ over different timescales, and whether taxonomic variation in mechanisms occurs. However, only within insects has allochrony been studied in detail and so

whether the genetic control of allochrony is similar among taxa is largely unknown. *Within insects, mechanisms underlying allochrony at different timescales appear to overlap, and the genes involved may be physically if not functionally linked.* Circadian genes are clearly important in controlling both daily and seasonal reproductive cycles (Fuchikawa et al., 2010; Levy et al., 2015; Ragland et al., 2011; Tauber et al., 2003). Genes underlying the control of diapause are important in insect life cycles, with circadian genes possibly being involved with circannual rhythms (Dambroski & Feder, 2007; Dopman, Pérez, Bogdanowicz, & Harrison, 2005; Levy et al., 2015; Ragland et al., 2011; Wadsworth, Woods, Hahn, & Dopman, 2013). More work is needed to discover whether circadian genes play a role in divergence in noninsect taxa; for example, no difference was found in the circadian genes *clock* or *per2* between seasonal populations of band-rumped or Leach's storm-petrels (V. L. Friesen, unpublished data).

Much more is known about genomic mechanisms of seasonal allochrony than daily or yearly allochrony. For example, chromosomal rearrangements and patterns of genome wide divergence may be involved in many cases of allochronic separation, but the importance is not known (Feder et al., 2003, 2014; Powell et al., 2013; Wadsworth et al., 2015). Studies on *R. pomonella* indicate that large areas of divergence can evolve rapidly throughout the genome (Feder et al., 2014; Powell et al., 2013). Whether this can be generalized outside insect taxa, and whether it depends on high levels of standing genetic variation, is unknown; differentiation is more likely to be genome wide when differences between populations are due to polygenic traits, as is likely the case in allochronic speciation and adaptation by time (Egan et al., 2015). Processes such as physical linkage of genes within inversions, and involvement of sex chromosomes may be general to any type of speciation with gene flow (Feder et al., 2014; Seehausen et al., 2014), and appear to exist among examples of allochronic speciation. Similarly, standing genetic variation may be needed for rapid changes in breeding time (Feder et al., 2014; Powell et al., 2013), but this needs to be investigated further.

Allochronic populations with no overlap in breeding time could be compared to allopatric populations, separated in time instead of in space (temporal allopatry; Box 1). For example, in organisms with a 2-year life cycle, the genomic architecture controlling breeding time will probably be the same between the two cohorts, but as they exist in different temporal demes, they cannot interbreed. Allochronic divergence is therefore unusual as, in some cases, neutral genetic divergence, for example genetic drift and the build-up of genomic incompatibilities such as Bateson–Dobzhansky–Muller incompatibilities (Orr, 1996), could occur if there is no gene flow between the temporal populations. Further study would be interesting to test whether intrinsic genetic incompatibilities are present in examples with strict, nonoverlapping breeding times.

4.4 | Climate change

Global changes in climate have, and will continue to have, an impact on the phenology of many species (Visser & Both, 2005), and so will

likely affect the process of allochronic isolation. Seasonal allochrony seems most likely to be affected, as exemplified by incipient allochronic isolation in the winter geometrid moth (Yamamoto & Sota, 2009). If winter temperatures increase in northern Japan, the moths will likely breed continuously as in southern areas, reducing the potential for allochronic isolation. Similarly, the summer population of the pine processionary moth may be impacted by warming temperatures. Godefroid et al. (2016) modelled the potential distribution of the summer populations, and found its current distribution to be restricted to coastal areas due to unsuitable climate inland, despite their adaptations to higher temperatures (Santos, Paiva, et al., 2011; see above). Predicted increases in temperature within their current range could be detrimental to the survival of the summer population (Godefroid et al., 2016).

The life history of phytophagous insects in general may be shaped by changes in climate. As warmer year-round temperatures

and an extended availability of host plants seems to favour the evolution of multivoltinism (Levy et al., 2015), perhaps additional generations will be selected for instead of divergence driven by a host shift (J. Feder, personal communication), although other factors, such as adaptations to a specific host plant will also play a role.

In most cases, seasonal allochronic populations are driven by, or at least persist because of, suitable environmental conditions or resources and so future changes in climate will likely have a wide impact. Predicting exactly what will happen will be more difficult for many of the other examples, however. For example, the impact climate change will have on seasonal breeding populations of band-rumped storm-petrels, or salmon species, is less clear. Note that although daily and yearly allochrony seem less likely to be affected, exceptions do exist. Extreme climate conditions are thought to have played a role in periodical cicada life cycle shifts (see Box S1). Why a 17-year life cycle is

BOX 3 Genomic mechanisms controlling allochrony in the European corn borer

The European corn borer was introduced into North America approximately 100 years ago. Two strains exist: E and Z. Females of different strains produce, and males respond to, different sex pheromones (Dopman et al., 2010), which is clearly important in assortative mating. But allochrony also creates some isolation between strains. In North America, allochronic separation is related to voltinism, or the number of generations per year (Dopman et al., 2010). Populations in New York state comprise three races that are temporally separated: bivoltine Z, bivoltine E and univoltine Z, which emerges between the two bivoltine generations (Dopman et al., 2005). Work so far has demonstrated the importance of the Z (sex) chromosome in creating differences in breeding cycle (Dopman et al., 2010). The sex-linked locus *Tpi* differs between the three races and is linked to a major genetic factor controlling postdiapause development time, *Pdd* (Dopman et al. 200; Wadsworth & Dopman, 2015). There are two codominant alleles at the *Pdd* region: one causing earlier adult flight time (*Pdd*^S) and one later adult flight time (*Pdd*^L). The delay in emergence between uni- and bivoltine strains was found to be due to the timing of the diapause termination phase (Wadsworth et al., 2013), which supports the importance of shifts in diapause in creating temporal isolation between insect lineages. An inversion including approximately 20% of the Z chromosome was found to contain genes for temporal isolation (including *Pdd*) and behavioural isolation (e.g. male response to E or Z pheromones). This rearrangement suppresses recombination, facilitating divergence between strains (Wadsworth et al., 2015).

Transcriptome sequencing at different times of diapause identified 48 candidate genes within the *Pdd* region with either fixed amino acid differences between the earlier emerging E-strain individuals and the later emerging Z-strain individuals, or differences in expression levels between the two (Wadsworth & Dopman, 2015). The *Pdd* region appears to act as a genetic switch to activate postdiapause development, delayed in the Z-strain relative to the E-strain moths and so driving timing differences (Wadsworth & Dopman, 2015).

Evidence for a role for circadian genes in controlling voltinism, and therefore seasonal isolation, has been found. *Period* and *cryptochrome1* were both associated with changes in voltinism with latitude in the European corn borer, with *period* mapping to the Z chromosome (Levy et al., 2015). In the transcriptome study by Wadsworth and Dopman (2015), the major pathways identified as likely candidates operating in *Pdd* were involved in insulin signalling and circadian rhythms. They found a glycine to arginine amino acid change within the *Period* gene between the Z-strain and E-strain individuals, and *Period* was upregulated in E-strain moths on both day 1 and day 7 after long-day exposure (Wadsworth & Dopman, 2015).

More study would help determine the importance of other circadian genes in breeding phenology in the European corn borer, and to explore the other pathways highlighted in the transcriptome sequencing, for example those involved in insulin signalling, to further resolve the genetic differences underlying the shift in emergence time between the E- and Z-strain moths.

advantageous in more northern areas is unknown (Koyama et al., 2015), but perhaps an increase in temperature across North America will affect the distribution of the 13- and 17-year cicada species.

Further study to understand the genomic mechanisms underlying shifts in breeding time may enable us to predict which species may be better able to adapt to rapid environmental changes. For example, is overall standing genetic variation, as well as genetic diversity at particular areas of the genome (perhaps in circadian pathways), important in facilitating breeding time changes?

5 | CONCLUSIONS AND FUTURE DIRECTIONS

Allochrony clearly is an important contributor to speciation. When writing about allochrony as a “magic trait”, authors primarily cite differences in plant flowering time or discuss insects as their examples (e.g. Kisdi & Priklopil, 2011; Servedio & Kopp, 2012; Servedio et al., 2011). However, this review shows that allochrony can be caused by numerous factors and has occurred in a large array of taxa, suggesting that it is evolutionarily significant and not “magic” in the sense that it is not special or necessarily uncommon. We believe that more study in this area will demonstrate it to be more important than previously thought and, although true allochronic speciation may not be widespread, many more examples will likely be found. In the future, authors need to explicitly weigh the importance of allochrony in driving divergence, addressing the three key points listed in the introduction. The potential impact of allochronic shifts across trophic levels, as shown in *Rhagoletis* parasitoids (Box 2), is an interesting avenue for research. Further investigation into the link between the amounts of temporal overlap, gene flow and reproductive isolation would also be beneficial. *In particular, there may be many more unstudied organisms with strict multiyear life cycles that could be examples.* In addition, explicit comparison of the importance of allochrony relative to other potential isolating forces in populations demonstrating allochronic differences would improve our understanding of the evolutionary significance of allochrony.

Elucidating whether breeding time is heritable or plastic in taxa with allochronically diverged populations will help resolve how allochronic populations evolve and persist. Does plasticity help with the initial shift as in periodical cicadas? But if plasticity persists could this prevent genetic divergence, as is likely in Atlantic salmon (*Salmo salar*; Johnston et al., 2014)? Further investigations, particularly with genomic techniques, are needed to help understand both whether genes involved in allochronic speciation tend to be physically linked, and the potential importance of standing genetic variation in allowing shifts in breeding time. Understanding genomic changes and adaptations allowing organisms to breed at new times will clarify allochronic speciation itself but also aid our understanding of phenological shifts in general, and may be key in the light of phenological changes required under climate change.

ACKNOWLEDGEMENTS

We would like to thank Louis Bernatchez, Tim Birt, Francis Bonier, Jeffrey Feder, Bronwyn Harkness, Andrew Hendry, Haley Kenyon, Per Lundberg, Trevor Price, Drew Sauve and three anonymous reviewers for their helpful comments on earlier versions of this review. We would also like to thank Stewart Berlocher and Sandra Smit for sharing figures. We acknowledge financial support from the Ontario Trillium Scholarship.

AUTHOR CONTRIBUTION

The article was conceived by V.L.F. and R.S.T. The article was researched and written by R.S.T., and V.L.F. edited the manuscript.

DATA ACCESSIBILITY

All data come from published articles.

REFERENCES

- Alexander, R. D., & Bigelow, R. S. (1960). Allochronic speciation in field crickets, and a new species, *Acheta veletis*. *Evolution*, 14, 334–346.
- Aspinwall, N. (1974). Genetic analysis of North American populations of the pink salmon, *Oncorhynchus gorbuscha*, possible evidence for the neutral mutation-random drift hypothesis. *Evolution*, 28, 295–305.
- Barrett, R. D., & Schluter, D. (2008). Adaptation from standing genetic variation. *Trends in Ecology and Evolution*, 23, 38–44.
- Bearhop, S., Fiedler, W., Furness, R. W., Votier, S. C., Waldron, S., Newton, J., ... Farnsworth, K. (2005). Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, 310, 502–504.
- Bolnick, D. I., & Fitzpatrick, B. M. (2007). Sympatric speciation: Models and empirical evidence. *Annual Review of Ecology, Evolution and Systematics*, 38, 459–487.
- Bolton, M., Smith, A. L., Gómez-Díaz, E., Friesen, V. L., Medeiros, R., Briéd, J., ... Furness, R. W. (2008). Monteiro's storm-petrel *Oceanodroma monteiroi*: A new species from the Azores. *Ibis*, 150, 717–727.
- Branco, M., Paiva, M. R., Santos, H. M., Burban, C., & Kerdelhué, C. (2017). Experimental evidence for heritable reproductive time in 2 allochronic populations of pine processionary moth. *Insect Science*, 24, 325–335.
- Brieuc, M. S. O., Ono, K., Drinan, D. P., & Naish, K. A. (2015). Integration of Random Forest with population-based outlier analyses provides insight on the genomic basis and evolution of run timing in Chinook salmon (*Oncorhynchus tshawytscha*). *Molecular Ecology*, 24, 2729–2746.
- Burban, C., Gautier, M., Leblois, R., Landes, J., Santos, H., Paiva, M.-R., ... Kerdelhue, C. (2016). Evidence for low-level hybridization between two allochronic populations of the pine processionary moth, *Thaumetopoea pityocampa* (Lepidoptera: Notodontidae). *Biological Journal of the Linnean Society*, 119, 311–328.
- de Carvalho, A. L., Nelson, B. W., Bianchini, M. C., Plagnol, D., Kuplich, T. M., & Daly, D. C. (2013). Bamboo-dominated forests of the southwest Amazon: Detection, spatial extent, life cycle length and flowering waves. *PLoS ONE*, 8, e54852.
- Coyne, J. A., & Orr, H. A. (2004). *Speciation*. Sunderland, MA: Sinauer Associates.
- Dambroski, H. R., & Feder, J. L. (2007). Host plant and latitude-related diapause variation in *Rhagoletis pomonella*: A test for multifaceted life history adaptation on different stages of diapause development. *Journal of Evolutionary Biology*, 20, 2101–2112.

- Derks, M. F., Smit, S., Salis, L., Schijlen, E., Bossers, A., Mateman, C., ... Megens, H. J. (2015). The genome of Winter Moth (*Operophtera brumata*) provides a genomic perspective on sexual dimorphism and phenology. *Genome Biology and Evolution*, 7, 2321–2332.
- Devaux, C., & Lande, R. (2008). Incipient allochronic speciation due to non-selective assortative mating by flowering time, mutation and genetic drift. *Proceedings of the Royal Society B: Biological Sciences*, 275, 2723–2732.
- Devries, P. J., Austin, G. T., & Martin, N. H. (2008). Diel activity and reproductive isolation in a diverse assemblage of Neotropical skippers (Lepidoptera: Hesperidae). *Biological Journal of the Linnean Society*, 94, 723–736.
- Dieckmann, U., & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400, 354–357.
- Dieckmann, U., Doebeli, M., Metz, J. A. J., & Tautz, D. (2004). *Adaptive speciation*. Cambridge: Cambridge University Press.
- Dopman, E. B., Pérez, L., Bogdanowicz, S. M., & Harrison, R. G. (2005). Consequences of reproductive barriers for genealogical discordance in the European corn borer. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 14706–14711.
- Dopman, E. B., Robbins, P. S., & Seaman, A. (2010). Components of reproductive isolation between North American pheromone strains of the European corn borer. *Evolution*, 64, 881–902.
- Egan, S. P., Ragland, G. J., Assour, L., Powell, T. H., Hood, G. R., Emrich, S., ... Feder, J. L. (2015). Experimental evidence of genome-wide impact of ecological selection during early stages of speciation-with-gene-flow. *Ecology Letters*, 18, 817–825.
- Feder, J. L., Nosil, P., Wacholder, A. C., Egan, S. P., Berlocher, S. H., & Flaxman, S. M. (2014). Genome-wide congealing and rapid transitions across the speciation continuum during speciation with gene flow. *Journal of Heredity*, 105, 810–820.
- Feder, J. L., Opp, S. B., Wlazlo, B., Reynolds, K., Go, W., & Spisak, S. (1994). Host fidelity is an effective premating barrier between sympatric races of the apple maggot fly. *Proceedings of the National Academy of Sciences of the United States of America*, 91, 7990–7994.
- Feder, J. L., Powell, T. H. Q., Filchak, K., & Leung, B. (2010). The diapause response of *Rhagoletis pomonella* to varying environmental conditions and its significance for geographic and host plant-related adaptation. *Entomologia Experimentalis et Applicata*, 136, 31–44.
- Feder, J. L., Roethele, J. B., Filchak, K., Niedbalski, J., & Romero-Severson, J. (2003). Evidence for inversion polymorphism related to sympatric host race formation in the apple maggot fly, *Rhagoletis pomonella*. *Genetics*, 163, 939–953.
- Feder, J. L., Stolz, U., Lewis, K. M., Perry, W., Roethele, J. B., & Rogers, A. (1997). The effects of winter length on the genetics of apple and hawthorn races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Evolution*, 51, 1862–1876.
- Forbes, A. A., Powell, T. H. Q., Stelinski, L. L., Smith, J. J., & Feder, J. L. (2009). Sequential sympatric speciation across trophic levels. *Science*, 323, 776–779.
- Franklin, D. C. (2004). Synchrony and asynchrony: Observations and hypotheses for the flowering wave in a long-lived semelparous bamboo. *Journal of Biogeography*, 31, 773–786.
- Friesen, V. L., Smith, A. L., Gómez-Díaz, E., Bolton, M., Furness, R. W., González-Solis, J., & Monteiro, L. R. (2007). Sympatric speciation by allochrony in a seabird. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 18589–18594.
- Fuchikawa, T., Sanada, S., Nishio, R., Matsumoto, A., Matsuyama, T., Yamagishi, M., ... Miyatake, T. (2010). The clock gene cryptochrome of *Bactrocera cucurbitae* (Diptera: Tephritidae) in strains with different mating times. *Heredity*, 104, 387–392.
- Fukami, H., Omori, M., Shimoike, K., Hayashibara, T., & Hatta, M. (2003). Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Marine Biology*, 142, 679–684.
- Gavrilets, S. (2004). *Fitness landscapes and the origin of species*. Princeton, NJ: Princeton University Press.
- Gavrilets, S. (2005). 'Adaptive speciation' – It is not that easy: A reply to Doebeli et al. *Evolution*, 59, 696–699.
- Godefroid, M., Rocha, S., Santos, H., Paiva, M.-R., Burban, C., Kerdelhué, C., ... Rossi, J.-P. (2016). Climate constrains range expansion of an allochronic population of the pine processionary moth. *Diversity and Distributions*, 22, 1288–1300.
- Gradish, A. E., Keyghobadi, N., & Otis, G. W. (2015). Population genetic structure and genetic diversity of the threatened White Mountain arctic butterfly (*Oeneis melissa semidea*). *Conservation Genetics*, 16, 1253–1264.
- Hendry, A. P., & Day, T. (2005). Population structure attributable to reproductive time: Isolation by time and adaptation by time. *Molecular Ecology*, 14, 901–916.
- Hendry, A. P., Morbey, Y. E., Berg, O. K., & Wenburg, J. K. (2004). Adaptive variation in senescence: Reproductive lifespan in a wild salmon population. *Proceedings of the Royal Society B: Biological Sciences*, 271, 259–266.
- Hood, G. R., Forbes, A. A., Powell, T. H., Egan, S. P., Hamerlinck, G., Smith, J. J., & Feder, J. L. (2015). Sequential divergence and the multiplicative origin of community diversity. *Proceedings of the National Academy of Sciences of the United States of America*, 112, E5980–E5989.
- Johnston, S. E., Orell, P., Pritchard, V. L., Kent, M. P., Lien, S., Niemelä, E., ... Primmer, C. R. (2014). Genome-wide SNP analysis reveals a genetic basis for sea-age variation in a wild population of Atlantic salmon (*Salmo salar*). *Molecular Ecology*, 23, 3452–3468.
- Kisdi, E., & Priklopil, T. (2011). Evolutionary branching of a magic trait. *Journal of Mathematical Biology*, 63, 361–397.
- Koyama, T., Ito, H., Kakishima, S., Yoshimura, J., Cooley, J., Simon, C., & Sota, T. (2015). Geographic body size variation in the periodical cicadas *Magicicada*: Implications for life cycle divergence and local adaptation. *Journal of Evolutionary Biology*, 28, 1270–1277.
- Levis, N. A., & Pfennig, D. W. (2016). Evaluating 'plasticity-first' evolution in nature: Key criteria and empirical approaches. *Trends in Ecology & Evolution*, 31, 563–574.
- Levitan, D. R., Fukami, H., Jara, J., Kline, D., McGovern, T. M., McGhee, K. E., ... Knowlton, N. (2004). Mechanisms of reproductive isolation among sympatric broadcast-spawning corals of the *Montastraea annularis* species complex. *Evolution*, 58, 308–323.
- Levy, R. C., Kozak, G. M., Wadsworth, C. B., Coates, B. S., & Dopman, E. B. (2015). Explaining the sawtooth: Latitudinal periodicity in a circadian gene correlates with shifts in generation number. *Journal of Evolutionary Biology*, 28, 40–53.
- Linn, C. E., Dambroski, H. R., Feder, J. L., Berlocher, S. H., Nojima, S., & Roelofs, W. L. (2004). Postzygotic isolating factor in sympatric speciation in *Rhagoletis* flies: Reduced response of hybrids to parental host-fruit odors. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 17753–17758.
- Logan, D. P., Allsopp, P. G., & Zalucki, M. P. (2003). Overwintering, soil distribution and phenology of Childers cane grub, *Antitrogus parvulus* (Coleoptera: Scarabaeidae) in Queensland sugarcane. *Bulletin of Entomological Research*, 93, 307–314.
- Marshall, D., & Cooley, J. R. (2000). Reproductive character displacement and speciation in periodical cicadas, with description of a new species, 13-year *Magicicada neotredecim*. *Evolution*, 54, 1313–1325.
- Marshall, D. C., Cooley, J. R., & Hill, K. B. R. (2011). Developmental plasticity of life-cycle length in thirteen-year periodical cicadas (Hemiptera: Cicadidae). *Annals of the Entomological Society of America*, 104, 443–450.
- Martin, P. R., Bonier, F., Moore, I. T., & Tewksbury, J. J. (2009). Latitudinal variation in the asynchrony of seasons: Implications for higher rates of population differentiation and speciation in the tropics. *Ideas in Ecology and Evolution*, 2, 9–17.

- Michel, A. P., Sim, S., Powell, T. H. Q., Taylor, M. S., Nosil, P., & Feder, J. L. (2010). Widespread genomic divergence during sympatric speciation. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 9724–9729.
- Miyatake, T., Matsumoto, A., Matsuyama, T., Ueda, H. R., Toyosato, T., & Tanimura, T. (2002). The period gene and allochronic reproductive isolation in *Bactrocera cucurbitae*. *Proceedings of the Royal Society B: Biological Sciences*, 269, 2467–2472.
- Monteiro, L. R., & Furness, R. W. (1998). Speciation through temporal segregation of Madeiran storm petrel (*Oceanodroma castro*) populations in the Azores? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 353, 945–953.
- Ohigashi, K., Mizuguti, A., Yoshimura, Y., Matsuo, K., & Miwa, T. (2014). A new method for evaluating flowering synchrony to support the temporal isolation of genetically modified crops from their wild relatives. *Journal of Plant Research*, 127, 109–117.
- Orr, H. A. (1996). Dobzhansky, Bateson, and the genetics of speciation. *Genetics*, 144, 1331–1335.
- Powell, T. H. Q., Forbes, A. A., Hood, G. R., & Feder, J. L. (2014). Ecological adaptation and reproductive isolation in sympatry: Genetic and phenotypic evidence for native host races of *Rhagoletis pomonella*. *Molecular Ecology*, 23, 688–704.
- Powell, T. H. Q., Hood, G. R., Murphy, M. O., Heilveil, J. S., Berlocher, S. H., Nosil, P., & Feder, J. L. (2013). Genetic divergence along the speciation continuum: The transition from host race to species in *Rhagoletis* (Diptera: Tephritidae). *Evolution*, 67, 2561–2576.
- Quintero, I., González-Caro, S., Zalamea, P. C., & Cadena, C. D. (2014). Asynchrony of seasons: Genetic differentiation associated with geographic variation in climatic seasonality and reproductive phenology. *American Naturalist*, 184, 352–363.
- Ragland, G. J., Egan, S. P., Feder, J. L., Berlocher, S. H., & Hahn, D. A. (2011). Developmental trajectories of gene expression reveal candidates for diapause termination: A key life-history transition in the apple maggot fly *Rhagoletis pomonella*. *Journal of Experimental Biology*, 214, 3948–3960.
- Ragland, G. J., Sim, S. B., Goudarzi, S., Feder, J. L., & Hahn, D. A. (2012). Environmental interactions during host race formation: Host fruit environment moderates a seasonal shift in phenology in host races of *Rhagoletis pomonella*. *Functional Ecology*, 26, 921–931.
- Rosser, N. L. (2015). Asynchronous spawning in sympatric populations of a hard coral reveals cryptic species and ancient genetic lineages. *Molecular Ecology*, 24, 5006–5019.
- Rosser, N. L. (2016). Demographic history and asynchronous spawning shape genetic differentiation among populations of the hard coral *Acropora tenuis* in Western Australia. *Molecular Phylogenetics and Evolution*, 98, 89–96.
- Sakai, T., & Ishida, N. (2001). Circadian rhythms of female mating activity governed by clock genes in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 9221–9225.
- Santos, H., Burban, C., Rousselet, J., Rossi, J.-P., Branco, M., & Kerdelhué, C. (2011). Incipient allochronic speciation in the pine processionary moth (*Thaumetopoea pityocampa*, Lepidoptera, Notodontidae). *Journal of Evolutionary Biology*, 24, 146–158.
- Santos, H. M., Paiva, M. R., Rocha, S., Kerdelhué, C., & Branco, M. (2013). Phenotypic divergence in reproductive traits of a moth population experiencing a phenological shift. *Ecology and Evolution*, 3, 5098–5108.
- Santos, H., Paiva, M. R., Tavares, C., Kerdelhué, C., & Branco, M. (2011). Temperature niche shift observed in a Lepidoptera population under allochronic divergence. *Journal of Evolutionary Biology*, 24, 1897–1905.
- Santos, H., Rousselet, J., Magnoux, E., Paiva, M.-R., Branco, M., & Kerdelhué, C. (2007). Genetic isolation through time: Allochronic differentiation of a phenologically atypical population of the pine processionary moth. *Proceedings of the Royal Society B: Biological Sciences*, 274, 935–941.
- Seehausen, O., Butlin, R. K., Keller, I., Wagner, C. E., Boughman, J. W., Hohenlohe, P. A., ... Widmer, A. (2014). Genomics and the origin of species. *Nature Reviews Genetics*, 15, 176–192.
- Servedio, M. R., & Kopp, M. (2012). Sexual selection and magic traits in speciation with gene flow. *Current Zoology*, 58, 510–516.
- Servedio, M. R., Van Doorn, G. S., Kopp, M., Frame, A. M., & Nosil, P. (2011). Magic traits in speciation: 'magic' but not rare? *Trends in Ecology and Evolution*, 26, 389–397.
- Smadja, C. M., & Butlin, R. K. (2011). A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology*, 20, 5123–5140.
- Sota, T., Yamamoto, S., Cooley, J. R., Hill, K. B. R., Simon, C., & Yoshimura, J. (2013). Independent divergence of 13- and 17-y life cycles among three periodical cicada lineages. *Proceedings of the National Academy of Sciences of the United States of America*, 110, 6919–6924.
- Spear, L. B., & Ainley, D. G. (2007). Storm-petrels of the Eastern Pacific Ocean: Species assembly and diversity along marine habitat gradients. *Ornithological Monographs*, 62, 1–77.
- Tauber, E., Roe, H., Costa, R., Hennessy, J. M., & Kyriacou, C. P. (2003). Temporal mating isolation driven by a behavioral gene in *Drosophila*. *Current Biology*, 13, 140–145.
- Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: The need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, 272, 2561–2569.
- Wadsworth, C. B., & Dopman, E. B. (2015). Transcriptome profiling reveals mechanisms for the evolution of insect seasonality. *Journal of Experimental Biology*, 218, 3611–3622.
- Wadsworth, C. B., Li, X., & Dopman, E. B. (2015). A recombination suppressor contributes to ecological speciation in *OSTRINIA* moths. *Heredity*, 114, 593–600.
- Wadsworth, C. B., Woods, W. A., Hahn, D. A., & Dopman, E. B. (2013). One phase of the dormancy developmental pathway is critical for the evolution of insect seasonality. *Journal of Evolutionary Biology*, 26, 2359–2368.
- Winker, K. (2010). On the origin of species through heteropatric differentiation: A review and a model of speciation in migratory animals. *Ornithological Monographs*, 69, 1–30.
- Yamamoto, S., Beljaev, E. A., & Sota, T. (2016). Phylogenetic analysis of the winter geometrid genus *Inurois* reveals repeated reproductive season shifts. *Molecular Phylogenetics and Evolution*, 94, 47–54.
- Yamamoto, S., & Sota, T. (2009). Incipient allochronic speciation by climatic disruption of the reproductive period. *Proceedings of the Royal Society B: Biological Sciences*, 276, 2711–2719.
- Yamamoto, S., & Sota, T. (2012). Parallel allochronic divergence in a winter moth due to disruption of reproductive period by winter harshness. *Molecular Ecology*, 21, 174–183.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Taylor RS, Friesen VL. The role of allochrony in speciation. *Mol Ecol*. 2017;26:3330–3342. <https://doi.org/10.1111/mec.14126>