Evolution of divergent daily temporal niches shaped by male-male competition can generate sympatric speciation

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Abstract

Specialisation into different ecological niches can participate to species divergence and co-existence in sympatry. Here, we focus on the partitioning into different timings of reproductive activities during the day, as observed in many insect species living in sympatry. We thus investigate the evolution of the reproductive activity timing of individuals within populations, using a comprehensive stochastic model. We model the evolution of (1) the timing of reproductive activity as a quantitative trait and (2) neutral loci that may generate genetic incompatibilities among divergent individuals. We specifically explore how male-male competition for female access can generate negative frequency-dependence on the timing of reproductive activities and fuel population divergence. Our simulations in finite populations highlight the strong effect of male-male competition and operational sex-ratio on the evolution of divergent temporal niches. They also show how genetic incompatibilities fuel the differentiation among populations with divergent temporal niches, but may impair their co-existence. We then compare our results on the evolution of daily temporal niches to simulations investigating the evolution of seasonal phenology and show the significant effect of overlapping *vs.* non-overlapping generations on the evolution of daily *vs.* seasonal niches. Our model therefore highlights male-male competition as an important factor shaping the evolution of diel niches, that may fuel sympatric speciation.

Introduction

The coexistence of multiple species in sympatry is usually thought to be linked to their partition into multiple ecological niches. Whether the ecological niches in sympatric species evolved in response to local interactions between species, or whether species diversification in sympatry results from specialization in different niches is a key question in community ecology. For instance, the competition for resources and the reproductive interference between species can fuel the evolution of species into divergent niches within the same environment (Soliva and Widmer 1999), with specialization into different resources (Kitajima and Poorter 2008). Within communities, species can also be partitioned into different temporal niches, with variations in breeding season (e.g. in birds, Karr 1976) or timing of daily activities (e.g. in tropical beetles, De Oliveira Ribeiro et al. 2022 or Lepidoptera, Beck and Linsenmair 2006). Plants flowering time is also a common example of differentiated reproductive timings, with strong genetic differentiation between closely-related, sympatric species, as for instance in *Howea* palms (Soliva and Widmer 1999), or *Gymnadenia* orchids (Savolainen et al. 2006). Notably in *Howea* palms, four loci were identified as containing genes under divergent selection, potentially associated with seasonal allochronic speciation. Temporal niches can thus be shaped by abiotic factors such as temperature, but also by interactions with closely-related species (see Taylor and Friesen 2017 for a review). In particular, reproductive interference between closely related species might favor the evolution of divergent phenology in sympatry (Devries et al. 2008). In turn, temporal segregation would also contribute to the speciation process itself, because of preferential reproduction among individuals sexually active at the same period of time (Devaux and Lande 2009). Nevertheless, the conditions facilitating allochronic speciation (Hendry and Day 2005) remain largely unexplored. Examples appear to be scarce, particularly in animals, suggesting either that allochronic speciation is inherently rare or challenging to detect, or that this speciation mechanism has been insufficiently studied. Interestingly, temporal partitioning of species activities throughout the day has been repeatedly reported in tropical insects (see for example Cavenay et al. 1995; De Oliveira Ribeiro et al. 2022;

Devries et al. 2008; Lamarre et al. 2015), but the evolutionary factors shaping this temporal structure are still largely unknown.

Selection promoting divergence in the timing of reproductive activities can stem from competition for accessing mating partners. In species with separated sexes, male-male competition can be strong, especially when the adult sex-ratio is unbalanced or when there is an asymmetry in the frequency of mating between males and females (Arak 1983; Sullivan-Beckers and Cocroft 2010). Competition for accessing available females may impact the evolution of males timing of activities: the evolution of protandry promoted by selection linked to limited female availability has indeed been documented in a number of plant (Forrest 2014; Zhao et al. 2020) and animal species (Morbey and Ydenberg 2001). Furthermore, when female availability is a limiting factor for male reproduction, intense competitive interactions may occur among males and the evolution of non-overlapping timing of courtship may then reduce the deleterious effects of male-male competition. Within species where female-attracting vocal cues are performed by males, such as in birds or frogs, non-overlapping timing of calls are observed among males (e.g. in *Seiurus aurocapillus*, (Ficken et al. 1985) or in *Hyperolius marmoratus* Grafe 1996). Such temporal partitioning is also observed among males from closely related sympatric species: in the hawaiian cricket (*Laupala* genus), males singing activity and insemination events temporally diverged between sympatric species (Danley et al. 2007). In many insect species, reproductive activities such as pheromone release (*e.g.* in Lepidoptera, Hall et al. 1987; Shorey 1973), patrolling for territory defense (*e.g.* in dragonflies, in Alcock 1989), or lekking/swarming (*e.g.* in fruit flies, Shelly and Whittier 1997) can be limited to a very short period of the day (Lamarre et al. 2015), potentially limiting interactions with heterospecific individuals.

Aggressive behaviors among males may contribute to temporal partition of sexual activities between sympatric species: for instance, aggressive behaviors between patrolling males, observed both within and between sympatric species of Morpho butterflies, may have contributed to the documented divergent timing of male patrolling behavior between sympatric species (Le Roy

et al. 2021). Antagonistic male-male interactions might thus contribute to the evolution of divergence in temporal niches: competitive interactions among males may generate negative density dependent selection on the timing of reproductive activities. In models investigating the evolution of seasonal patterns of reproduction in flowering plants, negative density-dependence acting on flowering time distribution, generated by pollinator limitation, was shown as a potential driver for allochronic speciation (Devaux and Lande 2009; Ye et al. 2014). In natural plant communities, competition stemming from shared pollinators was shown to structure seasonal divergence in blooming periods between species (Pleasants 1980). Competition for accessing suitable mating partners can therefore be a powerful driver for divergent evolution of timing of activities linked to reproduction, and might contribute to the speciation process.

The genetic basis underlying variation in the timing of reproductive activities among incipient species has scarcely been investigated. Nevertheless, in *Drosophila*, the circadian genes *period* and *timeless* were shown to control the daily mating hours and the sister-species *D. simulans* and *D. melanogaster*, observed in sympatry and exhibiting divergent timing of sexual activities (Sakai and Ishida 2001). The divergence in circadian clock between these *Drosophila* species was thus suggested to enhance reproductive isolation in sympatry. Similar mechanisms were also reported in the mouse *Acomys cahirinus*, where the regulation of genes affecting the circadian rhythm is found to impact the divergence in the timing of daily reproductive activities between populations (Wang et al. 2022). The genetic heritability of this reproductive timing has been documented in a few species, notably in birds (Evans et al. 2020; Hau et al. 2017). Studies on the daily free-running periods in birds (with *Parus major* in Helm and Visser 2010), or crickets (with *Dianemobius nigrofasciutus* in Shimizu and Masaki 1997) also showed high heritability of this key property of the circadian clock, with h^2 values for this trait as high as 0.86 ± 0.24. An important body of research on timing of moth pheromone release demonstrates how reproductive activity can be also restricted to specific time windows (Bento et al. 2001; Cardé et al. 1996; Heath et al. 1991), notably in *Spodoptera frugiperda* (Hänniger et al. 2017; Pashley et al. 1992; Schöfl et al.

2009). Importantly, the timing of pheromone release and response was shown to be genetically controlled (Rafaeli 2002). Polygenic control of diurnal timing of emergence was also reported in marine midges *Clunio marinus* (Kaiser et al. 2011). Notably, this emergence timing might also tune the timing of reproductive activities: since females are virgin at emergence, the timing of emergence generates a sudden burst of females available for mating and might therefore impact the timing of courtship in males. The variability and heritability of circadian activities therefore raise the possibility of an evolution of reproductive activities timing that may generate divergent evolution of temporal niches in sympatric species. Disentangling whether temporal segregation is the result of a reinforcement process caused by the poor hybrid fitness in cases of secondary contact between species, or whether such segregation is the main driver of speciation is then an important question. Convincing evidence for allochrony at seasonal scale causing speciation have been provided in birds such as *Oceanodroma castro*, where sympatric but genetically isolated populations show asynchronous breeding timings (Friesen et al. 2007). This has also been shown in insects (*Asphondylia* midges, Joy and Crespi 2007), with changes in temporal patterns of diapause potentially leading to exploitation of new ecological niches. Similarly in fungi (*Ampelomyces*, Kiss et al. 2011), genetic isolation between some closely related species is supposed to mainly result from temporal isolation. Allochronic shifts are also likely to contribute to reinforcement processes: for instance, pre-zygotic isolation caused by allochronic migrations is likely to reinforce genetic divergence between populations of the butterfly *Danaus chrysippus* (Smith et al. 2010). Allochrony is also shown to be an important factor fuelling population divergence, even when the initial trigger of divergence stems from another ecological factor (*e.g.* host shift, Tabuchi and Amano 2003), suggesting an effect of allochrony in the reinforcement process.

The level of post-zygotic isolation between sympatric species with divergent temporal niches is frequently unknown, but the accumulation of Bateson-Dobzhansky-Muller (*BDM* hereafter) incompatibilities (Orr and Turelli 2001) is likely to interact with the preferential reproduction between synchronously active individuals, therefore facilitating the emergence of reproductive

barriers between asynchronous populations. Such interactions between pre and post-zygotic barriers have been shown to fuel speciation in a model of neutral speciation triggered by isolation by distance (Baptestini et al. 2013). How much the interaction between genomic barriers and temporal isolation fuels speciation is still an open question.

Here, we built a general model to investigate the effect of male-male competition on the evolution of the temporal window of daily reproductive activities and its impact on the population divergence and speciation. We assumed a single haploid species, with two separate sexes, obligatory sexual reproduction and asymmetry in the frequency of mating between males and females. To investigate the interaction between the evolution of timing of activity and genetic incompatibilities, we also simulated the evolution of biallelic haploid loci within the genome. These loci either (1) had no impact on reproductive success or (2) generated incompatibilities preventing reproduction between genetically divergent individuals. Using an individual-based model, stochastic simulations were conducted to identify the evolutionary mechanisms promoting the emergence of divergent populations with segregated timings of reproductive activities in sympatry.

Methods

Model overview

We built a stochastic, individual-based birth-and-death process (*e.g.* Méléard 2016; Otto and Day 2011), to study the evolution of daily periods of reproductive activity within species, and test for the divergent evolution of allochronic populations, depending on the presence/absence of genetic incompatibilities acting as post-zygotic barriers. Within each individually-centered simulation, each individual of the population has a set of attributes (see Table A2), impacting its survival and reproductive success during the simulation.

The model, summarized in fig. 1, accurately fits to the life cycle of Lepidoptera, where immature caterpillar stages and sexually mature adult stage are strictly separated by the pupal stage. It can nevertheless be generalized to hemimetabolous and holometabolous insects, as they generally display life cycles with stereotypical timing of transitions between developmental stages. We considered a population where the adult emerges from the pupa only within a restricted period of the day, so that the emergence timing generates a burst of virgin females (and males) at a fixed given period within each day, centered around a time e. We then assume that the timing of reproductive activity, expressed in both males and females, is a single continuous heritable trait, represented by a single loci named h_a, with additive effect: offspring thus have a trait value drawn from a Normal distribution centered around the average values from both parents with standard deviation μ, accounting for the effects of random mutations. We then used individually-centred numerical simulations to track down the evolution of the distribution of the h_a trait within a population.

The model considered each day as a continuous time period from sunrise ($t = 0$) to sunset ($t = 1$), where an adult individual i is active only during its activity window, starting at time $t_1 = h_{a,i} - w_a$ and finishing at time $t_2 = h_{a,i} + w_a$. Since reproductive activities can only happen during the day, individuals with h_a values close to dawn and dusk thus have a shorter reproductive window. Each day, new adults can join the population after they emerge from their pupae, at a time drawn in a Normal law of mean e, and variance v_e. If an individual sexual activity period is earlier than its emergence timing, it can start mating only the day after its emergence day, within its reproductive activity window determined by h_a. Note that adults may survive several consecutive days, so that multiple generations of individuals can overlap temporally.

The simulation process used here followed the Doob-Gillespie algorithm (see Gillespie 1977; Tran 2006), that allows to simplify the way individual behaviors, whose probability depends on the individual attributes (Table A2) and on the parameters of the model (Table A1), actually

happen during the course of our stochastic simulations. Here, we only describes the probability of certain behaviors to happen to the different types of individuals for more clarity, but the details of the simulation process are provided in the Appendix A.

Individual behaviors

The behavior of each individual within the simulation depends on its attributes (see Table A2), that modulate its probability of survival and reproductive success at each time step.

Sex-dependent death rate

All individuals have a baseline death rate d during their adulthood, corresponding to death caused by factors like predation or senescence. During the reproductive period, individuals actively search for a partner, and thus are more likely to get attacked by predators, resulting in an increased death probability, modelled by an activity cost (named δ_e) that depends on the activity duration and applied to both males and females. Because males also engage in competitive interactions against each other, we assume they suffer from a supplementary cost that depends on the number of other males active within the same time window $N_a^{\♂}$, increasing their death rate during their activity period, with a rate $\delta_c N_a^{\♂}$. Egg-laying is also likely to generate a metabolic cost to females (named δ_l): we thus assumed that the more eggs a female lays, the more likely she is to die. These two sex-specific costs (δ_c and δ_l respectively) allowed to keep a balanced sex-ratio throughout the simulations.

Mating success

This model assumes differences in reproductive traits between males and females: males can mate indefinitely due to their ability to produce smaller and more quickly replenished gametes, while females have a limited number p of mating opportunities, due to a more costly production of gametes. They nevertheless stay fully receptive until this number is reached, and may produce offspring after the first mating event. The availability of females thus becomes the limiting factor

for male reproduction, generating intense male-male competition.

We assume that active males and available active females probability of mating depends on the current number of active individuals of the opposite sex, as well as an encountering rate β (see Table A1). Here we assume no spatial structure, so that there is equal encountering probability for all individuals being active at the same time. The mating rate is thus simply represented by $\beta \cdot N_a^{♂} \cdot N_a^{♀}$. It is important to note that while an increase in active males results in a higher overall mating rate per unit of time, the probability of any single male successfully mating decreases as the number of active males increases.

Each day, we assume that each mated female generates a number of offspring which depends on population density. This number depends on the parameter b (the mean number of offspring per female per day), on the carrying capacity of the environment (K) (see Table A1), and on the number of mated females alive at the start of the day ($N_m^{♀}$). As the number of mated females increases, each female produces fewer viable offspring, because of competition for resources. This reflects the limited availability of resources for the offspring, leading to higher mortality rates when too many offspring are born. Notably, since mated females incur a δ_l cost proportional to the number of eggs laid, in a high density population, females will have a longer life expectancy since they lay less eggs.

The number of offspring per female is drawn individually from a Poisson distribution of parameter λ_p. This parameter is computed using the following formula:

$$\lambda_p = b\left(1 - \frac{N_m^{♀}}{K}\right). \tag{1}$$

As we used parameters ensuring a mostly balanced sex-ratio, the number of mated females $N_m^{♀}$ is always inferior than the carrying capacity K in our simulations. We thus never encountered the case where λ_p is negative. Once a female has mated at least once, it can generate offspring every day after the mating day, until its death.

During the course of each simulation, the fertilization status f (see Table A2) of a female

may thus change: after completing p reproductive events, she transitions from being available to unavailable for mating. Her fertilization status changes from $f = 0$ to $f = 1$, fixed for the rest of her life, and is not receptive to any more males.

Offspring survival

To investigate the impact of post-zygotic incompatibilities on the divergent evolution of allochronic populations, we also assume B biallelic, unlinked, haploid loci that may influence the survival of the offspring produced by different parental pairs. These loci represent neutral, independent genetic elements scattered throughout the genome. In each of these haploid B loci, two alleles (0 or 1) can occur, and the viability of the offspring of a parental pair depends on the genetic distances across these B loci between the parents. This genetic distance was computed using the Hamming distance (Baptestini et al. 2013), between the genomes of two individuals x and y in the population following equation:

$$D_H = \frac{1}{B} \cdot \sum_{i=1}^{B} |x_i - y_i| \tag{2}$$

with x_i and y_i the allele values at the locus i for the individuals x and y respectively.

Note that $0 \leq D_H \leq 1$, and D_H = 1 is the maximum genetic divergence between two individuals.

For simplicity, we set a threshold value G above which mating between individuals with $D_H > G$ does not generate any viable offspring. While this threshold is probably more drastic than the actual effect of BDM incompatibilities actually arising in natural populations, this simplification does allow to relevantly implement reproductive barrier among genetically divergent individuals, and has been used in previous models (see Yamaguchi and Iwasa 2017 and de Aguiar et al. 2009 for instance). Simulations assuming a smooth decrease of offspring survival depending on the level of genetic incompatibility provided similar results as the ones obtained assuming a threshold (see fig. S1).

When the offspring does survive, it can eventually emerge as adult, at a time drawn in a truncated Normal law of parameters (e, v_e) bounded in $[0, 1]$ and its attributes are set up as follows:

- The sex of the individual is randomly chosen, assuming a balanced sex-ratio at birth. If the individual is a female, her fertilization status is initially set to 0.
- In cases where the mother has mated with multiple males ($p_n > 1$), one of them will be chosen uniformly at random to sire the offspring.
- We assume that the sexual activity time is a quantitative trait, and that the activity time of both parents will affect the activity time of the offspring evenly. We thus set the sexual activity timing parameters of the offspring i, $h_{a,i}$ (Table A2), using a truncated Normal distribution with parameters ($\frac{h_a^{father}+h_a^{mother}}{2}$, μ), bounded in $[0, 1]$. The parameter of μ represents segregation and mutational variance occurring in the genes controlling the circadian activity.
- For the B loci, we assumed a 50% chance to inherit either parental allele at each locus. Each of the B loci can thus freely recombine and independently mutate with a probability of μ_G.

Comparing daily vs. seasonal allochrony

In most simulations, we assumed overlapping generations, allowing individuals to survive several days. We also tested non-overlapping generations, analogous to a *seasonal* model with a non-perennial species. Individuals in this *seasonal* model all die at the end of each time period, meaning newly born individuals of the next generation do not overlap with the previous one. In the previous model (referred to as *daily* model hereafter), the time unit considered was a day, and in this seasonal version (referred to as *seasonal* model hereafter), each time unit is considered to be a year. Thus in the following time unit, offspring generated from reproduction within the previous day will again reach sexual maturity (at an emergence time drawn into a Normal law

of parameters (e, v_e)) and may mate afterwards within the same season.

Summary statistics drawn from simulation outcomes

To detect whether differentiated populations evolved during the course of a simulation, we track down the distribution of the trait h_a in the simulated populations and aim at detecting the number of peaks in this distribution. We used the *find_peaks* function from the "scipy.signal" package, to detect peaks and identify their position to define sub-populations. We set the *find_peaks* parameters to 0.5 for the *prominence* and 30 for the *distance*. *Prominence* is a measure of how much a peak stands out from the distribution. If the peak has a density value higher than 0.5, we take it into account, allowing us to ignore small size fluctuations within the h_a distributions. *Distance* on the other hand, measure the number of individual data points between two peaks. This allows us to ignore local maxima and focus on the main peaks within the h_a distribution. A *distance* of 30 means that there are 30 individuals with h_a values intermediate between two peaks. Since our carrying capacity is K=1000 for most simulations, and we never observed sub-population sizes get below one hundred, even for extreme values of δ_c (see fig. S3), 30 is a reasonable number to exclude local variation while still considering relevant information. A group of individuals with similar timing of activities that diverge from the ancestral population is then considered as an actual differentiated sub-population only when (1) it lasted more than forty days within the simulation and when (2) the position of the peak within the differentiated sub-population did not vary by more than 0.15 units of time over a day. Those requirements were determined from previous simulations, when searching for parameters that would guaranty large enough sub-population sizes and stable sub-populations over the length of a simulation. We must note that in our simulations, we only observed cases with either one or two peaks, (i.e. either one or two differentiated sub-populations), no matter the set of parameters used. We considered three categories of sub-populations in our model:

1. *Immediate* category, when the average reproductive activity within a sub-population was

centered around the timing of emergence e, with a leniency of ± 0.05.

2. *Dawn-shifted* category, when the average reproductive activity was earlier than the timing of emergence e, meaning mating starts happening on the day after the emergence day for those individuals.

3. *Dusk-shifted* category, when the average reproductive activity was later than the timing of emergence e, meaning freshly emerged individuals could start mating on the day of their emergence.

When differentiated sub-populations were observed at the end of a simulation, we quantified the level of genetic differentiation between the two sub-populations, using the F_{st} values computed from genetic variations observed at the B loci. We used the minima between the two peaks in the reproductive activity distribution curves to determine to which sub-population each individual belonged to. Individuals with h_a values greater or lesser than this minima are sorted to either sub-population. The F_{st} is then calculated according to the following equation, from Hudson et al. 1992:

$$F_{st} = \frac{\pi_{inter} - \pi_{intra}}{\pi_{inter}} \tag{3}$$

With π_{intra} and π_{inter} the average number of pairwise differences between two individuals of the same/different sub-population respectively

Note that under the assumption that intra-population variations are always smaller that inter-population variations, $0 \leq F_{st} \leq 1$, $F_{st} = 1$ is the maximum level of genetic differentiation between the two sub-populations. We also measured the level of linkage disequilibrium (LD) between each loci of the neutral genome and the reproductive activity timing h_a. We used a t-test to determine whether there was a significant difference in the reproductive activity timing between individuals displaying either the allele 0 or the allele 1 at each of their neutral loci. We then computed the number of neutral loci significantly linked to the locus controlling the timing of reproductive activity h_a. We then studied the percentage of simulations where linkage disequilibrium was

present (*i.e.* where at least one neutral locus exhibited significant *LD* with the timing of activity), and how many alleles were significantly linked to a certain reproductive activity timing throughout the whole population.

Finally, we characterized the shape of the distribution of reproductive activity timings within each sub-population. Using the *curve_fit* function from the "scipy.optimize" package, we fit a Gaussian curve on these distributions at the end of each simulation. When two sub-populations are detected, we separate our dataset and fit a curve to each of the two sub-population. We then evaluate the distribution width by using this standardized Gaussian curve, and measure the full width at half maximum (*FWHM*) to capture the shape of the curve. Additionally, when two sub-populations were present, we computed the distance between their respective h_a peak.

These metrics provide a basis for determining whether two sub-populations are distinctly differentiated or if their reproductive activity timings exhibit potential overlap.

Numerical simulations and equilibria

We ran each simulation for N = 500 time units for each repetition, ensuring that the equilibrium is reached for simulations (confirmed with simulations, see fig. S2), and used a range of reasonable parameters to ensure the emergence and coexistence of differentiated sub-populations (see fig. S4 for a study on the effects of the standard deviation μ of sexual activity timings, and fig. S5 for a study of the average generation time within simulation, depending on the proportion of loci necessary to generate incompatibilities G). We used the parameters and attribute range values provided in Tables A1 and A2. For simulation length purposes, we first used a low carrying capacity of the environment at $K = 1000$ individuals in most simulations. To test the impact of this parameter, we then ran a series of simulations assuming higher carrying capacities ($K = 2000$ and $K = 5000$), but did not detect significant difference between simulations (fig. S6A).
All simulations ended after 500 days, or when the population became extinct. We also tracked

down the evolution of the activity period trait h_a, and the genotypes at the B loci across all individuals.

The initial conditions for all simulations are a population of hundred individuals with a balanced sex-ratio, where all females are initially virgin. The initial values of h_a of all individuals are set with truncated in [0,1] Normal laws of parameters (0.5, μ). The neutral loci are initialized with values all equal to 0. A hundred replicates were run for each condition and the range of parameters used is given in Table A1. Python (3.11.7) was used for modeling purposes and data cleaning, using the packages "random", "numpy", "scipy" and "seaborn". R (4.4.0) was used to plot all results, using the "ggplot2" package.

Several series of simulations were run to investigate hypothesized mechanisms that may underlay the evolution of allochronic populations:

- *Effect of emergence time*: We simulated cases with varying values of the emergence time of adult individuals e, and differing values of the associated variance v_e. All other parameters remained fixed in those simulations, with values set-up to allow the persistence of stable populations within the simulations.

- *Male-male competition and male-female asymmetry*: We then estimated the respective effects of the cost of male-male competition and of the cost of male-female asymmetry in mating events on the evolution of differentiated populations. We thus ran simulations with different values of the strength of male-male competition (δ_c), and of the number of possible mating events throughout the life of females (p).

- *Effect of post-zygotic barriers*: we implemented genetic incompatibilities in our model, to evaluate the strength of the genetic differentiation between subpopulations using a F_{st} metric, and measured the importance of genetic barriers in population differentiation. To assess this differentiation, we ran simulations with varying values of the incompatibility threshold G and the male-male competition cost δ_c.

- *Daily vs. seasonal allochrony*: we finally compared simulations assuming either a *daily* or a *seasonal* model of temporal niche evolution, for different values of the adult emergence time (e) and strength of male-male competition (δ_c).

Results

Evolution of sub-populations with earlier reproductive activity

Assuming that females are able to mate at maximum once throughout their life ($p = 1$), and assuming no genetic incompatibilities, our simulations result in either a unimodal or a bimodal distribution of the timing of reproductive activities, depending on the timing of emergence of adults e (fig. 2).

- When a unimodal distribution of activity was observed, the average timing of reproductive activity tightly follows the timing of emergence for most e values (fig. S7A), and a single *immediate* population was thus observed. When the emergence occurs late during the day ($e \geq 0.8$), individuals are not active close to the emergence time happening at dusk, but rather at dawn (*i.e.* single *dawn-shifted* population). Since our model assumes no mating during the night, late reproductive periods are probably counter-selected. Late timing of adult emergence may thus favor the evolution of reproductive activities early in the morning.

- When a bimodal distribution in the timing of activity is observed, two sub-populations with different temporal niches (one with a *dawn-shifted* niche and one with an *immediate* niche) can co-exist. The sub-population with the *dawn-shifted* niche has an average timing of reproductive activity close to the start of the day, while the sub-population with an *immediate* niche displays an average timing of activity close to the moment of adult emergence, where more females are available (fig. S7B).

Characterisation of the distributions of the reproductive activity time h_a revealed that when

assuming no genetic incompatibilities, the average distance between peaks was superior to 0.4 (fig. S8A) and the average peak width ranged from 0.13 to 0.16 (fig. S8B). Our differentiated subpopulations thus likely have limited temporal niche overlap.

Interestingly, when the emergence of adults was assumed to occur either very early or very late during the day, the proportion of simulations where a bimodal distribution is observed decreases (fig. 2). Nevertheless, the outcomes of simulations assuming very early *vs*. very late emergence time differ. When emergence is very early, reproductive activity can start occurring within the same day, and selection thus favours the evolution of *immediate* temporal niches, allowing males to mate with virgin females immediately. The lack of available time earlier than the emergence time likely prevents the evolution of a second population with even earlier timing of activity. In contrast, when the emergence occurs very late in the day, we observed the evolution of a single *dawn-shifted* population. When emergence occur too close to the end of the day, males with *immediate* timing of reproductive activity have little mating opportunity before dusk. Individuals that are active the earliest on the following day become advantaged, because they are more likely to encounter the virgin females emerged the previous evening. Overall, these results suggest that the evolution of temporally differentiated reproductive sub-populations is heavily influenced by the timing of emergence (e). Specifically, emergence occurring in the middle of the day allows for temporal niche differentiation, as there is more available temporal space. On the contrary, extreme emergence times (either very early or very late) restrict reproductive timing variability, preventing the evolution of differentiated temporal niches.

Variation in the timing of adult emergence shapes population differentiation

Because the variability in the timing of adult emergence (v_e) throughout the day can impact the probability of encounter between males and available females, we run simulations for different levels of variability in the timing of emergence, assuming that females can only mate once ($p = 1$), and followed the distribution of the activity timing trait h_a through time.

Assuming that adults emerge around noon ($e = 0.5$), we run 100 simulations for each level

of variation in the timing of the emergence and observed three main evolutionary outcomes (fig. S9):

- When assuming low variability in the emergence timing ($v_e < 0.04$), a unimodal distribution of timing of reproductive activity is observed in a majority of simulations, with a single *immediate* population). The low variance in the timing of sexual activity in available females means that males are strongly selected to be active at this moment.

- When assuming moderate levels of variations in the emergence timing ($0.04 \leq v_e \leq 0.12$), most simulations result in a bimodal distribution of the sexual activity timing, generating sub-populations with different timings of reproduction, with a *dawn-shifted* sub-population co-existing with an *immediate* sub-population.

- When assuming high variability in the emergence timing ($v_e > 0.12$), a unimodal distribution of timing of reproductive activity is observed, with sexual activities occurring early in the morning (*dawn-shifted* population), away from the mean emergence time ($e = 0.5$). The high uncertainty in the timing of availability in available females likely promotes the evolution of the earliest possible timing of reproductive activities. The even temporal distribution of available females throughout the day no longer promotes sexual activities around the emergence peak, and only the advantage associated to be the first one to catch an available female remains in males. Male-male competition likely generates a race for earlier male reproductive activities, leading to the persistence of a single *dawn-shifted* population and limiting temporal differentiation.

Variation in the timing of adult emergence within population thus significantly affects the evolution of temporal niches.

Male-male competition and male-female asymmetry promoting the evolution of differentiated sub-populations

To test how much the density-dependent male-male competition generates negative frequency dependent selection on the timing of male sexual activity, we compared the proportion of simulations where a bimodal distribution of the timing of activities was observed at $N = 500$ days, when assuming different levels for the cost of male-male competition. Fig. 3A shows an increase of the probability of differentiation into two sub-populations when low competition exists ($\delta_c \leq 0.05$), compared to simulation without competition. However, when the competition becomes too intense ($\delta_c > 0.05$), the probability of observing differentiated populations decreases, reaching lower values than in simulations without competition (close to zero when $\delta_c = 1$). Such decrease may be explained by competitive exclusion between the two sub-populations (fig. 3A): when low competition was assumed ($\delta_c < 0.05$), the duration of coexistence between sub-populations is on average higher (fig. S6C) compared to simulations without any competition ($\delta_c = 0$), but decreases as the strength of male-male competition increases. When competition gets too intense ($\delta_c \geq 0.5$), the duration of coexistence became lower than in simulations assuming no competition, because of the intense competitive exclusion between the two sub-populations. The *dawn-shifted* sub-populations generally had a much smaller size as compared to *immediate* ones (see fig. S3A). This difference in population size increases with δ_c (fig. S3B), meaning that *dawn-shifted* sub-populations are much more likely to undergo extinction compared to *immediate* subpopulations. This decrease in coexistence explains the lower probability of observing differentiated sub-populations with high δ_c values. Males from the small *dawn-shifted* sub-populations suffer from an extreme cost in male-male competition, while they are not able to mate with as many females as compared to the individuals from the *immediate* sub-population.

Our model thus suggests that the competition between males can favour the evolution of differentiated timings of reproductive activities, because males with unusual timings of activity might benefit from reduced competition. Nevertheless, when male-male competition is too

high, the intense costs of antagonistic male interactions can prevent the persistence of the *dawn-shifted* sub-populations, therefore limiting the co-existence of sub-populations with differentiated temporal niches in sympatry.

Intriguingly, the evolution of differentiated sub-populations is still observed when male-male competition had no cost ($\delta_c = 0$, fig. 3A). In our initial simulations, we assumed that females could only mate once ($p = 1$), while males could mate multiple times over their lifespan. This asymmetry alone is sufficient to generate negative frequency-dependent selection on the timing of reproductive activities through male-male competition. We hypothesize that this competition is driven by a limited availability of females for mating, inherently creating male-male competition. This competition, in turn, fosters negative frequency-dependent selection, favoring reproductive activity at times when fewer males are competing simultaneously. To test for the effect of operational sex-ratio on negative density-dependent selection, we thus compare simulations allowing either a maximum of one mating event per female ($p = 1$) *vs.* multiple mating events per female (from $p = 2$ to $p = 5$), using $\delta_c = 0.1$ (fig. 3B). We indeed observe the significant effect of asymmetry in mating opportunity between males and females in the evolution of differentiated temporal niches: when the maximum number of partners possible for a female increases, the proportion of simulations with co-existing differentiated sub-populations decreases, from *circa* 75% when $p = 1$, to being almost never observed when $p = 5$. Female mating limitations thus strongly favors the emergence of bimodal distributions in the reproductive activity timing of individuals. Our model therefore suggests that intense male-male competition for access to available females is likely to promote the evolution of differentiated reproductive temporal niches in sympatry.

Genetic differentiation favored by competition and genetic incompatibilities

We then explore the effect of genetic incompatibilities in the evolution of differentiated sub-populations with divergent distributions in the timing of reproductive activities. We thus investigate the effect of the threshold of genetic divergence G, above which reproduction between

pairs of individuals becomes unsuccessful. Fig. S10 shows that G has a strong effect on the probability of evolution of differentiated sub-populations with divergent temporal niches:

- When the threshold G is low, *i.e.* when one to two allelic variations between parents at a single locus are sufficient to prevent the generation of viable offspring, the evolution of differentiated sub-populations is drastically limited. Such drastic incompatibilities may strongly limit reproduction and thus prevent the evolution of unusual timings of reproductive activity.

- When assuming intermediate values ($0.4 <= G <= 0.6$), the percentage of simulations where we observe the evolution of differentiated sub-populations becomes much more likely ($> 98\%$), but decreases when the threshold further increases. Note that when $G = 1$, genetic incompatibilities are totally lacking.

The evolution of differentiated populations is thus more likely to happen for moderate values of the threshold G, allowing sufficient successful mating, while preventing gene flown between sub-populations. The level of genetic differentiation between these sub-populations can be estimated using the fixation index (F_{st}).

When assuming genetic incompatibilities ($0 < G < 1$), the F_{st} values are higher when G is small (fig. 4A). Low values of G promote assortative mating between individuals with similar genotypes, driving the differentiation between *dawn-shifted* and *immediate* sub-populations. For $G = 0.2$, we observe a high variability in F_{st} values among simulations. This may be due to smaller population sizes (due to reproduction being drastically limited) enhancing genetic drift and thus inflating F_{st} values. When the threshold G becomes even higher ($G \geq 0.6$), F_{st} values become low, coinciding with the decrease in the probability of population differentiation shown in fig. S10.

When studying the effect of the genetic incompatibilities promoting the co-existence of the two sub-populations, we found that the duration of the co-existence of the two sub-populations

was maximal when $G = 0.5$ (fig. S6B). Notably, when $G = 1$, akin to simulations without any incompatibility, coexistence was much shorter. In extreme cases ($G = 0.1$), every simulation lead to the extinction of the whole population, because most individuals failed to generate any offspring (fig. S10). For $G = 0.2$, only 45% of simulations ended with a global extinction, while no extinction is observed for higher levels of G. Characterisation of our distributions revealed that with variations in the threshold of genetic divergence G underlying mate incompatibility (fig. S8A), the average temporal gap between the two peaks of temporal activity is superior to 0.35 and slightly decreases as G increases. The average peak width ranges from 0.11 to 0.13 (fig. S8B), and also slightly increases with G (notably for *dawn-shifted* sub-populations). While the effect is weak, stricter threshold (*i.e.* lower G values), promotes a larger temporal gap in reproductive activity timing between sub-populations, as well as narrower width of peaks. Genetic incompatibility thus seem to reinforce the temporal divergence between the two sub-populations, as well as the specialisation into narrower temporal niches.

Furthermore, the strength of male-male competition also had an effect on genetic differentiation between populations (captured by F_{st}), with genetic differentiation increasing with the intensity of competition (fig. 4B): F_{ST} values doubled in simulations with high competition ($\delta_c = 1$) as compared to simulations without ($\delta_c = 0$). Thus while high values of δ_c decreases the probability of population differentiation (see fig. 3A), in the few cases where sub-populations do evolve because of competitive exclusion (see section above), high levels of genetic differentiation are favored by the intense level of competition, counter-selecting intermediate values of h_a.

Finally, to investigate the coupling between pre and post-zygotic barriers to gene flow between the two sub-populations, we then examined the occurrence of linkage disequilibrium between the timing of reproductive activity (h_a) and the neutral genetic loci. Our analysis revealed that the number of simulations where at least one neutral locus was found significantly linked to the locus controlling the timing of reproductive activity was higher when assuming lower values of G (fig. 5A), *i.e.* when assuming that a low number of allelic differences immediately result in inviable offspring. Furthermore, for lower G values, a higher number of loci were also detected

in linkage disequilibrium with the locus controlling the temporal window of activity (fig. 5B). This is expected, as a stricter threshold for genetic incompatibilities is likely to fix different alleles at the different loci within the two populations. Stricter genetic incompatibilities are thus promoting more frequent linkage disequilibrium between loci acting as post-zygotic barrier and the locus controlling the timing of reproductive activity, acting as pre-zygotic barrier.

Genetic differentiation between sub-populations thus appears to be positively correlated to both the strength of male-male competition and the incompatibility threshold between divergent genomes. The linkage disequilibrium between h_a values at incompatibility loci generates a coupling of pre and post-zygotic barriers to gene flow between sub-populations that may further promote sympatric speciation.

Seasonal versus daily allochrony

To compare the evolution of divergence in the timing of reproductive activity at the *daily vs. seasonal* scale, we then compared simulations assuming over-lapping *vs.* non-overlapping generations respectively. In the simulations assuming non-overlapping generations (*i.e. seasonal* model), we observe that, similarly to the *daily* model, the evolution of the reproductive activity time strongly depends on the emergence timing e (fig. S11). However, in the *seasonal* model, whatever the e value, and assuming the level of competition between males previously used in simulations assuming the *daily* model ($\delta_c = 0.1$), bimodality in the distribution of the reproductive activity timing was almost never observed at the end of simulations (see fig. S12). In the *seasonal* model, individuals cannot be reproductively active before their timing of adult emergence, unlike in the *daily* model where they can search for mates the next morning. Earlier activity patterns are therefore probably strongly counter-selected in the *seasonal* model, and reproductive timing evolved toward values close to the emergence time e, leading to a single *immediate* population.

We then run simulations with larger strength of male-male competition and genetic incompatibilities in the *seasonal* model. Similarly to the *daily* model, the negative frequency depen-

dent selection, fueled by male-male competition, can promote the evolution of differentiated temporal niches, but only for extreme values of δ_c (fig. S13A). We observe up to *circa* 60% of simulations with coexisting sub-populations in our *seasonal* model, notably lower than in simulations assuming the *daily* model, where we reach almost 100% of simulations with differentiated sub-populations (fig. S10). Interestingly, when differentiated populations were observed in the *seasonal* model, the timing of reproductive activities of the two sub-populations differed from the *daily* model. We indeed observed the evolution of a *later* sub-populations, (fig. 6B and S13, akin to *dusk-shifted* sub-populations in the *daily* model), coexisting with a sub-population with the temporal niche located immediately after the time of adult emergence (akin to an *immediate* sub-population in the *daily* model). As the cost of competition increased, the activity timings of the *later* sub-population became closer to the end of the season. This strongly departs from the previous results obtained assuming *daily* model (as seen in fig. 6A), where new sub-populations have a temporal niche *earlier* than the sub-population active around the time of adult emergence. Since being active earlier than emergence is not a possibility in the *seasonal* model, individuals with later activity timings become favored, as they suffer from reduced survival costs incurred by male-male competition.

Discussion

Evolution of temporal niches of reproductive activities

Using our model of *daily* reproductive activity niche, we show that sub-populations with different timings of reproductive activities can evolve through time. Because we assumed that offspring have a timing of reproductive activity intermediate between their parents (*modulo* the mutational effect μ), our model limits the emergence of temporal differentiation within our simulated populations. Despite this reduced opportunity of divergence stemming from the genetic architecture assumed for the control of the timing activity in our model, we nevertheless frequently observed differentiation into two subpopulations. The differentiation into different temporal niches is

mainly due to the limited availability in females, but is also promoted by costs generated by antagonistic male-male interactions. Negative density-dependent selection acting on the timing of reproductive activities can therefore promote differentiation into different temporal niches. Another model recently investigated the ecological factors promoting daily allochronic speciation in the *Spodoptera frugiperda* moth (Van Doorn et al. 2024), by assuming divergent ecological selection favoring divergent adaptive timings of reproduction in the rice *vs*. corn eating populations. Nevertheless, in line with our own results, the operational sex-ratio (controlled in their model by monogamy *vs*. polygamy during the night) is tuning the intensity of male-male competition and the resulting negative frequency-dependent selection acting on the activity timing was a key parameter shaping the evolution of allochrony. In contrast with our general model assuming no ecological selection on the timing of reproductive activity, the divergent ecological selection assumed in the Van Doorn et al. (2024) model promoted the evolution of divergent expression of reproductive timing in males and females, stemming from a trade-off between natural and sexual selection.

Our model generates allochrony strictly based on male-male competition for virgin females, without assuming any other mechanisms generating disruptive selection. However, we did assume that the reproductive trait was controlled by the same locus in both males and females, an assumption that might be unrealistic in natural populations. Since the density-dependent selection act on the timing of activity of males but not on females, allowing for independent evolution of the activity timing between the two sexes might lead to different outcomes. To test this, we ran a set of one hundred simulations assuming independent control of the reproductive activity timing trait in males and females respectively. In this two-locus model, we found that when no genetic incompatibilities are assumed, we only observe a single population (fig. S14A). The lack of selection on females likely strongly contributes to this result, as even if males with early activity do mate with most of the females, female offspring will not be influenced by the trait of their father. The advantage of early timing of activity in males is thus greatly reduced. Nevertheless, when genetic incompatibilities are assumed, we observe the emergence

of differentiated sub-populations, although for a narrower range of incompatibility threshold values ($0.2 \leq G \leq 0.4$, see fig S14A), as compared to simulations assuming a common control of timing of activity in both sexes. Simulations with bimodal distributions mostly display *immediate* and *dawn-shifted* sub-populations (fig. S14B), with highly divergent temporal niches (fig. S14B and C). When assuming a common control of reproductive activities in males and females, the emergence of differentiated sub-populations is likely promoted by assortative mating between individuals with similar neutral genomes, stemming a from synchronicity of reproductive activities, so that the timing of reproductive activity acts as a grouping magic trait (Kopp et al. 2018). Such grouping mechanism might be reduced when the timing of activity evolves independently in males and females, therefore restricting the conditions enabling the evolution of differentiated timing of activity.

In previous models describing the evolution of flowering times, negative density dependent selection stemming from pollinator availability has already been described as involved in population subdivisions into different temporal niches (Devaux and Lande 2008). Nevertheless, this division was generally found symmetrical around the ancestral flowering time. In our model however, the evolution of differentiated temporal niche is not symmetrical. We indeed observed an asymmetrical distribution in the *daily* model, with new sub-populations having earlier activity timings, due to competition for available females. We never observed *dusk-shifted* sub-populations, where individuals would be selected to be active later than emergence in a day. This shows an asymmetric positive selection for earlier h_a values and not for later ones, because of male-male competition to access virgin females as soon as possible during the day. However, in the *seasonal* model, for similar sets of parameters, extreme values of male-male competition promoted the evolution of differentiated sub-populations with later activity timings. Our *seasonal* model therefore does not fit with the protandry actually observed at the seasonal scale for many species, from flowering plants (Zhao et al. 2020) to butterflies (Forsberg and Wiklund 1988). Here we indeed did not focus on the evolution of sexual maturity, but on the evolution of the timing of reproductive activity independently from the development until sexual maturity. In models

studying the evolution of protandry (*e.g.* applied to flowering time in plants (Forrest 2014) or to emergence time in butterflies (Iwasa et al. 1983)), the evolving trait is the timing of sexual maturity, akin to the parameter e in our model and the timing of reproductive activity is entirely controlled by the development time until sexual maturity. In our model however, the timing of reproductive activity (h_a) evolves independently from the timing of sexual maturity acquisition (e), which is assumed to be fixed. We therefore observed here strong discrepancy between the *daily* model, where sub-populations with reproductive activities occurring earlier can evolve with the *seasonal* model where only sub-population with delayed reproductive activities can be observed. Two mains factors are at play in the emergence of *late* temporal niches in our *seasonal* model: (1) individuals could not be active before the emergence timing, due to the non-overlapping generations assumed, and (2) male-male competition needed to incur a high cost so that individuals active later in the season had a better fitness, despite reduced access to available females. Daily and seasonal temporal niches for reproductive activity thus may be under different evolutionary constraints, especially in the case of non-perennial seasonal species.

In perennial species where individuals are potentially available for reproduction all year round, changes towards earlier breeding times during the year is shown to occur in wild populations of *Parus major* (Charmantier et al. 2008). Furthermore, at the daily scale, fitness advantages associated with earlier sexual activity (mate guarding and extra-pair mating) in males were reported in behavioral experiments in *Parus major* (Greives et al. 2015). These empirical results suggest that changes in the timing of reproductive activities can occur in the wild, because of both plasticity and/or genetic variations, and might be favored by selective pressures. In our model, we assumed that reproductive activity times were independent from the emergent time, which was fixed during our simulations. Nevertheless, the reproductive timing of activity (modeled here as h_a) and the emergence (e) are likely co-evolving in natural populations and are probably jointly influenced by the circadian clock, as shown in Drosophila (Calatayud et al. 2007; Kumara et al. 2015). Supplementary simulations allowing the emergence timing to evolve independently

of reproductive timing of activity demonstrated the emergence of differentiated sub-populations (fig. S15A), with both sub-populations evolving towards earlier reproductive timings (fig. S15B). Characterisation of the distribution of the activity timing trait confirmed that there exists minimal overlap between sub-populations (fig. S15C and D). Although emergence of differentiated sub-populations is more sparse than when the emergence timing was fixed (fig. 2 and S15A), these results demonstrate the strong effects of negative frequency dependence stemming from male-male competition on sub-population differentiation and coexistence. In this model, selection on being active as early as possible is strong in males given the absence of a fixed emergence timing during midday. The two sub-populations with earlier activity timings did not merge, even in the absence of genetic incompatibilities. This shows how negative frequency dependence can maintain two populations in sympatry, with separated temporal niches. The evolution of the temporal window of reproductive activity predicted by our model could thus happen in natural populations, if genetic variations involved in the circadian clock controls for the timing of reproductive behaviour, like courtship or mate searching activities.

Ecological factors promoting temporal divergence between sub-populations

In our model, the co-existence of sub-populations was generally transient, but varied depending on the strength of male-male competition δ_c and the threshold of genetic divergence G. We showed that moderate values of δ_c and G led to a longer duration of the co-existence for sub-populations. The limited duration of coexistence may be linked to the absence of joint evolution of other isolating mechanisms, such as host plant specialisation or coupling with abiotic factors. In our model, we indeed investigated the effect of neutral mutations triggering incompatibilities between divergent individuals. Nevertheless, if these mutations accumulating in the sub-populations with different temporal niches were under divergent selection, this may further reinforce co-existence of differentiated populations.

Temporal differentiation can be facilitated by variation in resource availability throughout the day, that may condition the timing of feeding *vs.* reproductive activities. In insects, host shifts may thus enhance the evolution of temporal niches. For instance, variation in the timing of flowering (afternoon *vs*. dusk) was reported among closely-related species of sphingophilous plants of the genus *Hemerocallis* (Hasegawa et al. 2006). Specialisation into these different plant species may induce temporal divergence in pollinators. Multiple other plants also display such daily variations flowering/pollen release patterns (Matsumoto et al. 2015; Stone et al. 1996), that may condition the evolution of daily temporal niche in pollinating insects. Temporal divergence may thus be promoted by both male-male competition and other ecological factors.

Abiotic factors such as temperature also may also enhance allochronic speciation, if the reproductive success is lower when individuals are not in their optimal temperature range (Dolgin et al. 2006; Keller and Seehausen 2012). Since thermal conditions usually vary both throughout a day and a year, the evolution of the temporal niches can be influence by variation in adaptation to thermal conditions. Differences in reproductive success was detected between sister species locally adapted to different thermal environments (Matute et al. 2009), probably as a by-product of divergent adaptation. As variations in selection of thermal resistance hinder local adaptation, species are likely to be adapted to a relatively small range of temperature conditions (Kawecki and Ebert 2004), and variations in thermal niches can be a strong barrier to reproduction. These temperature fluctuations are shown to be a source of diversification among species (Kleckova et al. 2015), with empirical data on animal and plant species (Keller and Seehausen 2012). The evolution of divergent thermal tolerance could co-evolve with the evolution of divergent temporal niches, at both the seasonal and daily scales.

Allochrony as a reinforcement mechanism in the divergence of species

Allochrony could also act as a reinforcement mechanism, when hybrids are already counter-selected because of post-zygotic barriers. In Butlin and Smadja (2018), such coupling between pre and post-mating barriers was shown to evolve, but disentangling whether allochrony is the driving force of speciation or just stem from reinforcement remains challenging (see Taylor and Friesen 2017).

To study the emergence of reproductive barriers in our population, we observed population dynamics with and without post-zygotic barriers to reproduction, represented by non-viable zygotes when the parents were genetically differentiated. When those genetic incompatibilities were introduced, the evolution of sub-populations with different temporal niches was more likely to happen for certain values of the genetic threshold G. More importantly, genetic incompatibilities seem mandatory to generate sub-populations differentiated on a genetic level, as the gene flow between sub-population keeps occurring in absence of these genetic incompatibilities. This is true only in the absence of other forces promoting ecological divergence. By testing the proportion of loci G required for incompatibilities, we found that intermediate values seemed to promote the longevity of small-sized *dawn-shifted* sub-populations. These values seem to allow a low level of gene flow that promoted co-existence, while allowing genetic differentiation between sub-populations. This is consistent with simulations for neutral speciation by distance (Baptestini et al. 2013, de Aguiar et al. 2009), showing similar results when incorporating a genetic mating distance G, with intermediate values of maximum genetic distance for reproduction producing higher counts of species. Temporal divergence could thus act as a coupled mechanism to other differentiation factors, by limiting gene flow between sub-populations.

Furthermore, during the differentiation into different temporal niches, offspring with intermediate temporal niches could suffer from elevated competition costs, as they would pay costs from negative interactions with individuals from both parental temporal niches. These interme-

diate offspring also have a low chance of occurring when genetic incompatibilities are added, since those two sub-populations are usually genetically differentiated, and hybrids were considered inviable. According to simulations performed by Liou and Price (1994), having inviable hybrids can lead to higher rates of speciation than with infertile ones, because the lack of individuals with intermediate phenotypes reduces competition (for resources/mating partners) for both sub-populations. This was also shown to make extinction less likely for sub-populations, thus promoting coexistence between divergent populations. This coexistence is thus likely conditioned by the availability of empty temporal niches. Indeed, our simulations showed that a certain width of temporal space is necessary for sub-populations to emerge earlier within the day, as they otherwise are too close to the alternative population and male-male competition may then lead to competitive exclusion. Smaller niches would result in more temporal space available for sub-populations to emerge, and thus provide more opportunities for speciation (Sexton et al. 2017). We indeed observed narrower temporal niches when implementing stricter threshold for genetic incompatibilities (fig. S8). Niche breadth is generally shown to be an important factor influencing speciation (Hardy and Otto 2014) and this effect is confirmed in our study, showing that gradual evolution of divergent temporal niches can be promoted by post-zygotic incompatibilities.

Our study therefore highlights the temporal variation in reproductive activity as an important component of the ecological niches, potentially reinforcing mating barriers between diverging sub-populations.

Data and Code Availability

All code and data is available anonymously at https://anonymous.4open.science/r/Daily-niche-model-0D05.

Literature Cited

Alcock, J. 1989. The mating system of Brechmorhoga pertinax (Hagen): The evolution of brief patrolling bouts in a territorial dragonfly (Odonata: Libellulidae). Journal of Insect Behavior 2:49–62.

Arak, A. 1983. Sexual selection by male–male competition in natterjack toad choruses. Nature 306:261–262.

Baptestini, E. M., M. A. de Aguiar, and Y. Bar-Yam. 2013. Conditions for neutral speciation via isolation by distance. Journal of Theoretical Biology 335:51–56.

Beck, J., and K. E. Linsenmair. 2006. Feasibility of light-trapping in community research on moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of southeast-asian hawkmoths (Lepidoptera: Sphingidae). The Journal of Research on the Lepidoptera 39:18–36.

Bento, J., Parra, J., Evaldo, F., Walder, J. & Leal, W. 2001. Sexual Behavior and Diel Activity of Citrus Fruit Borer Ecdytolopha aurantiana. Journal Of Chemical Ecology. 27:2053–2065

Brett, W. J. 1955. Persistent diurnal rhythmicity in Drosophila emergence. Annals of the Entomological Society of America 48:119–131.

Brumm H. 2006 Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. Journal of Comparative Physiology A 192:1279–1285.

Butlin, R. K., and C. M. Smadja. 2018. Coupling, reinforcement, and speciation. The American Naturalist 191:155–172.

Calatayud, P.-A., H. Guénégo, B. LeRü, J.-F. Silvain, and B. Frérot. 2007. Temporal patterns of emergence, calling behaviour and oviposition period of the maize stem borer, *Busseola fusca* (Fuller) (Lepidoptera: Noctuidae). Annales de la Société entomologique de France 43:63–68.

Cardé, R., Charlton, R., Wallner, W. Baranchikov, Y. 1996. Pheromone-Mediated Diel Activity Rhythms of Male Asian Gypsy Moths (Lepidoptera: Lymantriidae) in Relation to Female Eclosion and Temperature. Annals Of The Entomological Society Of America. 89:745-753

Caveney, S., C. H. Scholtz, and P. McIntyre. 1995. Patterns of daily flight activity in onitine dung beetles (Scarabaeinae: Onitini). Oecologia 103:444–452.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–803.

Danley, P. D., T. N. DeCarvalho, D. J. Fergus, and K. L. Shaw. 2007. Reproductive asynchrony and the divergence of hawaiian crickets. Ethology 113:1125–1132.

de Aguiar, M. A. M., M. Baranger, E. M. Baptestini, L. Kaufman, and Y. Bar-Yam. 2009. Global patterns of speciation and diversity. Nature 460:384–387.

De Oliveira Ribeiro, P. H., P. H. B. Togni, and M. R. Frizzas. 2022. Spatial and temporal segregation in dung beetles (Coleoptera: Scarabaeinae) in the cerrado of central brazil. Biodiversity and Conservation 31:2723–2740.

Devaux, C., and R. Lande. 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.

Devaux, C., and R. Lande. 2009. Selection on variance in flowering time within and among individuals. Evolution 64:1311–1320

Devries, P. J., G. T. Austin, and N. H. Martin. 2008. Diel activity and reproductive isolation in a diverse assemblage of neotropical skippers (Lepidoptera: Hesperiidae): Diel activity and reproductive isolation. Biological Journal of the Linnean Society 94:723–736.

Dolgin, E. S., M. C. Whitlock, and A. F. Agrawal. 2006. Male Drosophila melanogaster have higher mating success when adapted to their thermal environment. Journal of Evolutionary Biology 19:1894–1900.

Evans, S. R., E. Postma, and B. C. Sheldon. 2020. It takes two: Heritable male effects on reproductive timing but not clutch size in a wild bird population. Evolution 74:2320–2331.

Robert W. Ficken, James W. Popp and Paul E. Matthiae. 1985. Avoidance of Acoustic Interference by Ovenbirds. Wilson Ornithological Society 97:569–571

Forrest, J. R. 2014. Plant size, sexual selection, and the evolution of protandry in dioecious plants. The American Naturalist 184:338–351.

Forsberg, J., and C. Wiklund. 1988. Protandry in the Green-Veined White Butterfly, Pieris napi L. (Lepidoptera; Pieridae). Functional Ecology 2:81–88.

Friesen, V. L., A. L. Smith, E. Gomez-Dıaz, M. Bolton, R. W. Furness, J. Gonzalez-Solis, and L. R. Monteiro. 2007. Sympatric speciation by allochrony in a seabird. Proceedings of the National Academy of Sciences 104:18589–18594.

Gillespie, D. T. 1977. Exact stochastic simulation of coupled chemical reactions. The Journal of Physical Chemistry 81:2340–2361.

Grafe, T. U. 1996. The function of call alternation in the african reed frog (Hyperolius marmoratus): Precise call timing prevents auditory masking. Behavioral Ecology and Sociobiology 38:149–158.

Greives, T. J., S. A. Kingma, B. Kranstauber, K. Mortega, M. Wikelski, K. Van Oers, A. C. Mateman, G. A. Ferguson, G. Beltrami, and M. Hau. 2015. Costs of sleeping in: circadian rhythms influence cuckoldry risk in a songbird. Functional Ecology 29:1300–1307.

Hall, D. R., A. Cork, R. Lester, and P. Zagatti. 1987. Sex pheromones of rice moth, Corcyra Cephalonica Stainton. Journal of Chemical Ecology 13:1575-1589.

Hänniger, S., P. Dumas, G. Schöfl, S. Gebauer-Jung, H. Vogel, M. Unbehend, D. G. Heckel and A. T. Groot. 2017. Genetic basis of allochronic differentiation in the fall armyworm. BMC Evolutionary Biology 17:68.

Hardy, N. B., and S. P. Otto. 2014. Specialization and generalization in the diversification of phytophagous insects: Tests of the musical chairs and oscillation hypotheses. Proceedings of the Royal Society B: Biological Sciences 281:20132960.

Hasegawa, M., T. Yahara, A. Yasumoto, and M. Hotta. 2006. Bimodal distribution of flowering time in a natural hybrid population of daylily (Hemerocallis fulva) and nightlily (Hemerocallis citrina). Journal of Plant Research 119:63–68.

Hau, M., D. Dominoni, S. Casagrande, C. L. Buck, G. Wagner, D. Hazlerigg, T. Greives, and R. A. Hut. 2017. Timing as a sexually selected trait: The right mate at the right moment. Philosophical Transactions of the Royal Society B: Biological Sciences 372:20160249.

Heath, R., Mclaughlin, J., Proshold, F., and Teal, P. 1991. Periodicity of Female Sex Pheromone Titer and Release in Heliothis subflexa and H. virescens (Lepidoptera: Noctuidae). Annals Of The Entomological Society Of America. 84:182–189

Helm, B., and M. E. Visser. 2010. Heritable circadian period length in a wild bird population. Proceedings of the Royal Society B: Biological Sciences 277:3335–3342.

Hendry, A. P., and T. Day. 2005. Population structure attributable to reproductive time: Isolation by time and adaptation by time. Molecular Ecology 14:901–916.

Hudson, R. R., M. Slatkin, and W. P. Maddison. 1992. Estimation of levels of gene flow from DNA sequence data. Genetics 132:583–589.

Iwasa, Y., F. J. Odendaal, D. D. Murphy, P. R. Ehrlich, and A. E. Launer. 1983. Emergence patterns in male butterflies: A hypothesis and a test. Theoretical Population Biology 23:363–379.

Joy, J. B., and B. J. Crespi. 2007. Adaptive radiation of gall-inducing insects within a single host-plant species. Evolution, 61:784–795.

Kaiser, T. S., D. Neumann, and Heckel D. G. 2001. Timing the tides: Genetic control of diurnal and lunar emergence times is correlated in the marine midge Clunio marinus. BMC Genetics 12:49.

Karr, J. R. 1976. Seasonality, resource availability, and community diversity in tropical bird communities. The American Naturalist 110:973–994.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Keller, I., and O. Seehausen. 2012. Thermal adaptation and ecological speciation. Molecular Ecology 21:782–799.

Kiss, L., A. Pintye, M. G. Kovacs, and T. Jankovics. 2011. Temporal isolation explains host-related genetic differentiation in a group of widespread mycoparasitic fungi. Molecular Ecology 20: 1492–1507

Kitajima, K., and L. Poorter. 2008. Functional basis for resource niche partitioning by tropical trees. Tropical forest community ecology. 1936:160–181

Kleckova, I., M. Cesanek, Z. Fric, and L. Pellissier. 2015. Diversification of the cold-adapted butterfly genus Oeneis related to holarctic biogeography and climatic niche shifts. Molecular Phylogenetics and Evolution, 92:255–265.

Kopp, M., M. R. Servedio, T. C. Mendelson, R. J. Safran, R. L. Rodríguez, M. E. Hauber, E. C. Scordato, et al. 2018. Mechanisms of Assortative Mating in Speciation with Gene Flow: Connecting Theory and Empirical Research. The American Naturalist 191:1–20.

Kumara, A. D. N. T., M. Chandrashekharaiah, K. Subaharan, and A. K. Chakravarthy. 2015. Peri-

odicity of adult emergence and sexual behaviour of coconut black headed caterpillar, Opisina arenosella Walker (Lepidoptera: Oecophoridae). Phytoparasitica 43:701–712.

Lamarre, G. P. A., I. Mendoza, R. Rougerie, T. Decaens, B. Hérault, and F. Bénéluz. 2015. Stay out (almost) all night: Contrasting responses in flight activity among tropical moth assemblages. Neotropical Entomology 44:109–115.

Le Roy, C., C. Roux, E. Authier, H. Parrinello, H. Bastide, V. Debat, and V. Llaurens. 2021. Convergent morphology and divergent phenology promote the coexistence of Morpho butterfly species. Nature Communications. 12:1–9

Limborg, M. T., R. K. Waples, J. E. Seeb, and L. W. Seeb. 2014. Temporally isolated lineages of pink salmon reveal unique signatures of selection on distinct pools of standing genetic variation. Journal of Heredity 105:835–845.

Liou, L. W., and T. D. Price. 1994. Speciation by reinforcement of premating isolation. Evolution, 48:1451–1459.

Matsumoto, T., A. A. Yasumoto, K. Nitta, S. K. Hirota, T. Yahara, and H. Tachida. 2015. Difference in flowering time can initiate speciation of nocturnally flowering species. Journal of Theoretical Biology 2015:61–71.

Matute, D. R., C. J. Novak, and J. A. Coyne. 2009. Temperature-based extrinsic reproductive isolation in two species of Drosophila. Evolution 63:595–612.

Orr, H. A., and M. Turelli. 2001. The evolution of postzygotic isolation: Accumulating Dobzhansky-Muller incompatibilities. Evolution 55:1085–1094.

Otto, S. P., and T. Day. 2011. A biologist's guide to mathematical modeling in ecology and evolution. Princeton University Press.

Pashley, D. P., A. M. Hammond, and T. N. Hardy. 1992. Reproductive Isolating Mechanisms in

Fall Armyworm Host Strains (Lepidoptera: Noctuidae). Annals of the Entomological Society of America 85:400–405.

Pleasants, J. M. 1980. Competition for bumblebee pollinators in rocky mountain plant communities. Ecology 61:1446–1459.

Rafaeli, A. 2002 Neuroendocrine Control of Pheromone Biosynthesis in Moths. International Review of Cytology 213:49–91.

Sakai, T., and N. Ishida. 2001. Circadian rhythms of female mating activity governed by clock genes in Drosophila. Proceedings of the National Academy of Sciences 98:9221–9225.

Savolainen, V., Anstett, M., Lexer, C., Hutton, I., Clarkson, J., Norup, M., Powell, M., Springate, D., Salamin, N. and Baker, W. 2006. Sympatric speciation in palms on an oceanic island. Nature 441:210-213

Schöfl, G., D. G. Heckel, and A. T. Groot. 2009. Time-shifted reproductive behaviours among fall armyworm (Noctuidae: *Spodoptera frugiperda*) host strains: evidence for differing modes of inheritance. Journal of Evolutionary Biology 22:1447–1459.

Sexton, J. P., J. Montiel, J. E. Shay, M. R. Stephens, and R. A. Slatyer. 2017. Evolution of ecological niche breadth. Annual Review of Ecology, Evolution, and Systematics 48:183–206.

Shelly, T. E., and T. S. Whittier. 1997. Lek behavior of insects. Pages 273–293 in J. C. Choe and B. J. Crespi, eds. The evolution of mating systems in insects and arachnids (1st ed.) Cambridge University Press.

Shimizu, T., and S. Masaki. 1997. Geographical and species variation in circadian rhythm parameters in nemobiine crickets. Physiological Entomology 22:83–93.

Smith, D. A. S., I. J. Gordon, and J. A. Allen. 2010. Reinforcement in hybrids among once isolated semispecies of *Danaus chrysippus* (L.) and evidence for sex chromosome evolution. Ecological Entomology 35:77–89.

Shorey, H. H. 1973. Behavioral responses to insect pheromones. Annual Review of Entomology 18:349–380.

Soliva, M., and A. Widmer. 1999. Genetic and floral divergence among sympatric populations of Gymnadenia conopsea s.l. (Orchideaceae) with different flowering phenology. International Journal of Plant Sciences 160:897–905.

Stone, G., P. Willmer, and S. Nee. 1996. Daily partitioning of pollinators in an African acacia community. Proceedings of the Royal Society of London. Series B: Biological Sciences 263:1389–1393.

Sullivan-Beckers, L., and R. B. Cocroft. 2010. The importance of female choice, male-male competition, and signal transmission as causes of selection on male mating signals: identifying sources of selection on mating signals. Evolution 64:3158–3171.

Méléard, S. 2016. Modèles aléatoires en Ecologie et Evolution, vol. 77. Springer Berlin, Heidelberg ed. Springer Berlin Heidelberg.

Tabuchi, K., and H. Amano. 2003. Host-associated differences in emergence pattern, reproductive behavior and life history of Asteralobia sasakii (Monzen) (Diptera: Cecidomyiidae) between populations on Ilex crenata and I. integra (Aquifoliaceae). Applied Entomology and Zoology 38:501–508.

Taylor, R. S., and V. L. Friesen. 2017. The role of allochrony in speciation. Molecular Ecology 26:3330–3342.

Tran, V. C. 2006. Modèles particulaires stochastiques pour des problèmes d'évolution adaptative et pour l'approximation de solutions statistiques. Ph.D. thesis. Université de Nanterre - Paris X.

Van Doorn, G., Schepers, J., Hut, R. and Groot, A. 2024 Sex-specific expression of circa-

dian rhythms enables allochronic speciation. Evolution Letters, Advance online publication. 10.1093/evlett/qrae049

Wang, Y., Z. Qiao, L. Mao, F. Li, X. Liang, X. An, S. Zhang, X. Liu, Z. Kuang, N. Wan, E. Nevo, and K. Li. 2022. Sympatric speciation of the spiny mouse from evolution canyon in Israel substantiated genomically and methylomically. Proceedings of the National Academy of Sciences 119:e2121822119.

Yamaguchi, R. & Iwasa, Y. 2017 A tipping point in parapatric speciation. Journal Of Theoretical Biology. 421:81–92

Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673.

Ye, Z.-M., W.-K. Dai, X.-F. Jin, R. W. Gituru, Q.-F. Wang, and C.-F. Yang. 2014. Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant–plant interactions? Plant Ecology 215:3–13.

Zhao, Z., M. Hou, Y. Wang, and G. Du. 2020. Phenological variation of flower longevity and duration of sex phases in a protandrous alpine plant: Potential causes and fitness significance. BMC plant biology 20:1–10.

Figure legends

Figure 1: **Schematic view of the model describing variations in activity patterns in a butterfly population with two main sub-populations, with individuals with early and late adult reproductive activity times represented by blue and orange butterflies respectively.** The scheme describes a typical day in our simulation, where two sub-populations have successfully differentiated. Individuals active at the same time can participate in male-male competition, or mating with individuals of the opposite sex. Once mated, females become unavailable for reproduction and lay eggs that will give rise to new individuals. These non-sexually mature individuals (represented as pupae on the scheme) will become mature adults over the next few days. At the same time $t = e$ each day, some sexually mature adults can emerge from the previously produced pupae. If an individual activity timing is later than the emergence timing, it will be become active within the same day, potentially mating right after emergence. In contrast, individuals emerging after their activity timings will start mating only the following day.

Figure 2: **Emergence of sub-populations with different temporal niches depending on the timing of emergence of adults.** (A) Percentage of simulations where either one or two sub-populations were observed after 500 days, for 100 replicates per value of the timing of adult emergence e. (B), (C) and (D) are distributions outcomes of simulations for each type of distribution. Two types of unimodal distribution of the timing of reproductive activity can be observed after 500 days: (B) a single *dawn-shifted* population, where the average time of reproductive activity is below the emergence time e or (C) a single *immediate* population. Bimodal distribution of timing of activities leading to the co-existence of two sub-populations can also be observed (D), with both *dawn-shifted* and *immediate* sub-populations. The vertical dotted line in (B), (C) and (D) show the emergence timing in our examples ($e = 0.9, 0.3$ and 0.5 respectively). All simulations were run assuming the same values in the other parameters : $\beta = 3, \delta_c = 0.1, G = 1, v_e = 0.05, p = 1, K = 1000$.

Figure 3: **Effects of the male-male competition and male-female asymmetry on the evolution of sub-populations with different temporal niches.** (A) Effect of the intensity of male-male competition (δ_e) on the percentage of simulations where a bimodal distribution was observed after 500 days, for 100 replicates per condition. Intermediate values (around $\delta_c = 0.05$) lead to the higher percentage of simulations with coexistence of *dawn-shifted* and *immediate* sub-populations. Note that x-values are provided using a log_{10} scale. (B) Effect of maximum mates per female on the percentage of simulations where a bimodal distribution was observed after 500 days for 100 replicates per condition.

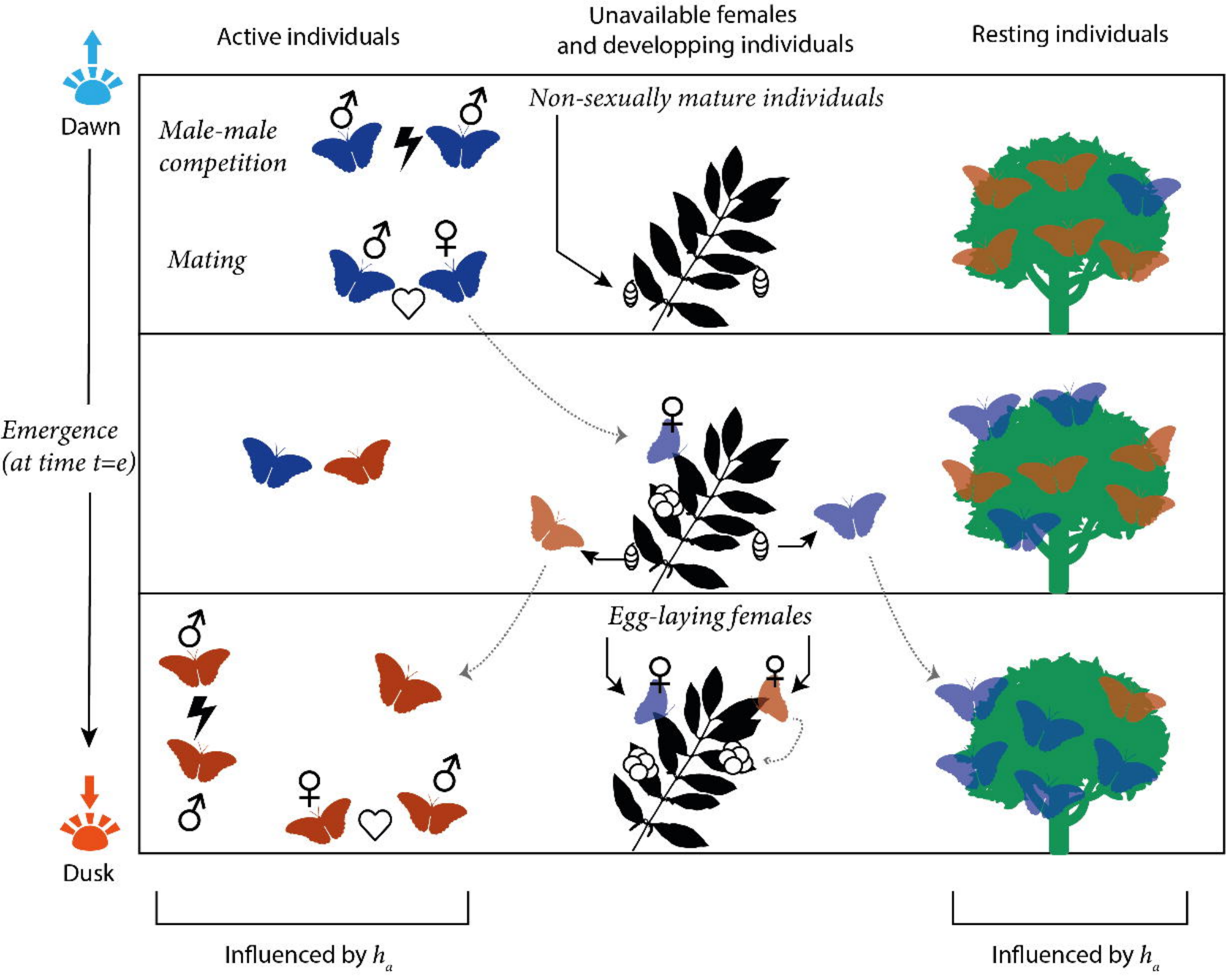
Error bars show the standard deviation (SD) computed over the 100 replicates per value of each parameter. All simulations were run assuming the same values in the other parameters $\delta_c = 0.1$, except in 3A, $\beta = 3$, G = 1, $e = 0.5, v_e = 0.05, p = 1$, except in 3B, $K = 1000$

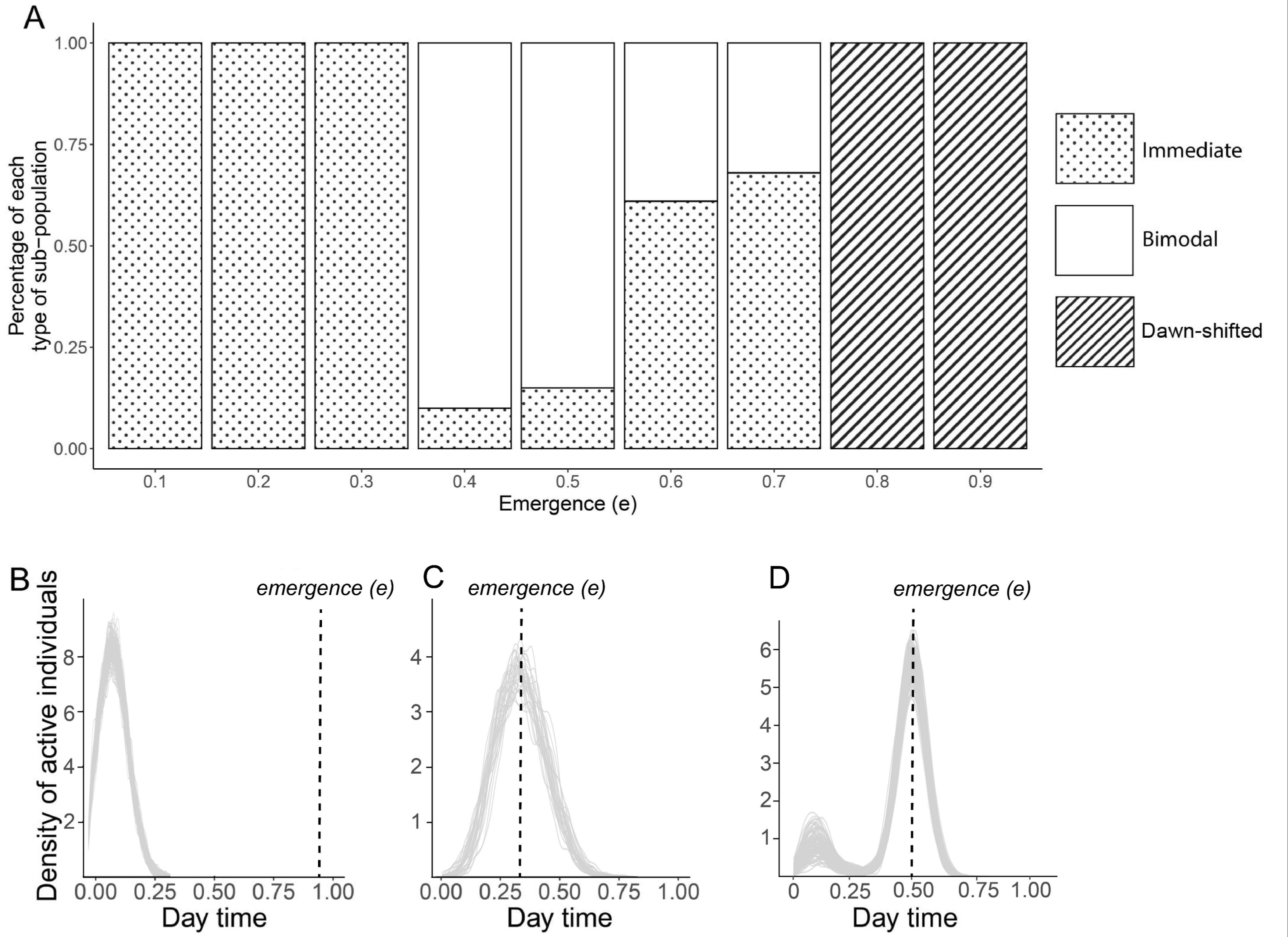
.

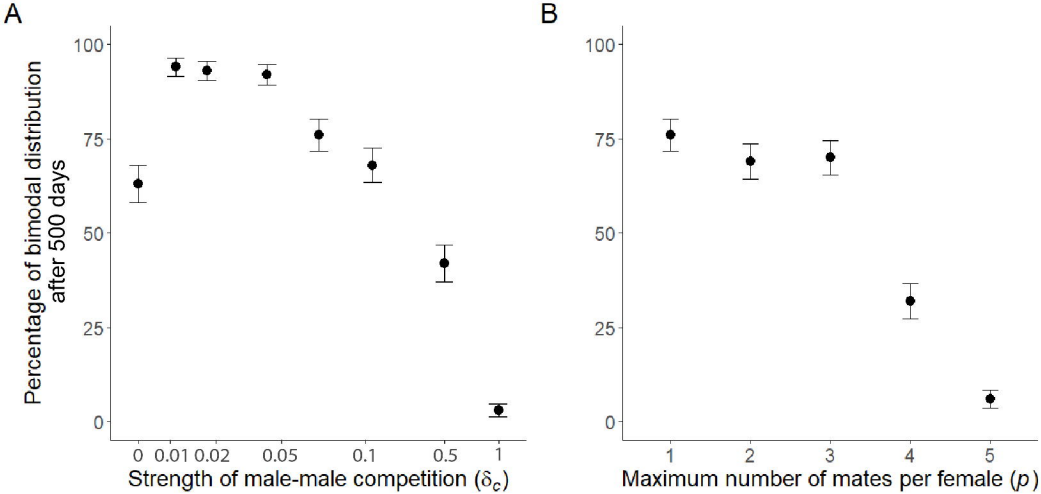
Figure 4: **Effect of genetic incompatibility and male-male competition on the genetic differentiation between sub-populations with different temporal niches.** The average F_{st} between sub-populations where a bimodal distribution was observed after 500 days, assuming genetic incompatibilities is shown, for 1000 replicates per values. (A) Effect of the proportion of loci G required for mating incompatibilities on the level differentiation between sub-populations, estimated by F_{ST}. While very small values of G do not sustain population differentiation, moderate values of G promote high F_{st} values between sub-populations. (B) Effect of male-male competition intensity δ_c on the F_{st} values between differentiated populations. When the male-male competition intensifies, average F_{st} between sub-populations increases.
Error bars show the SD computed over the 100 replicates per value of each parameter. All simulations were run assuming the same values in the other parameters: $\beta = 3, \delta_c = 0.1, G = 0.4$ for fig. $4B, e = 0.5, v_e = 0.05, p = 1, K = 1000$.

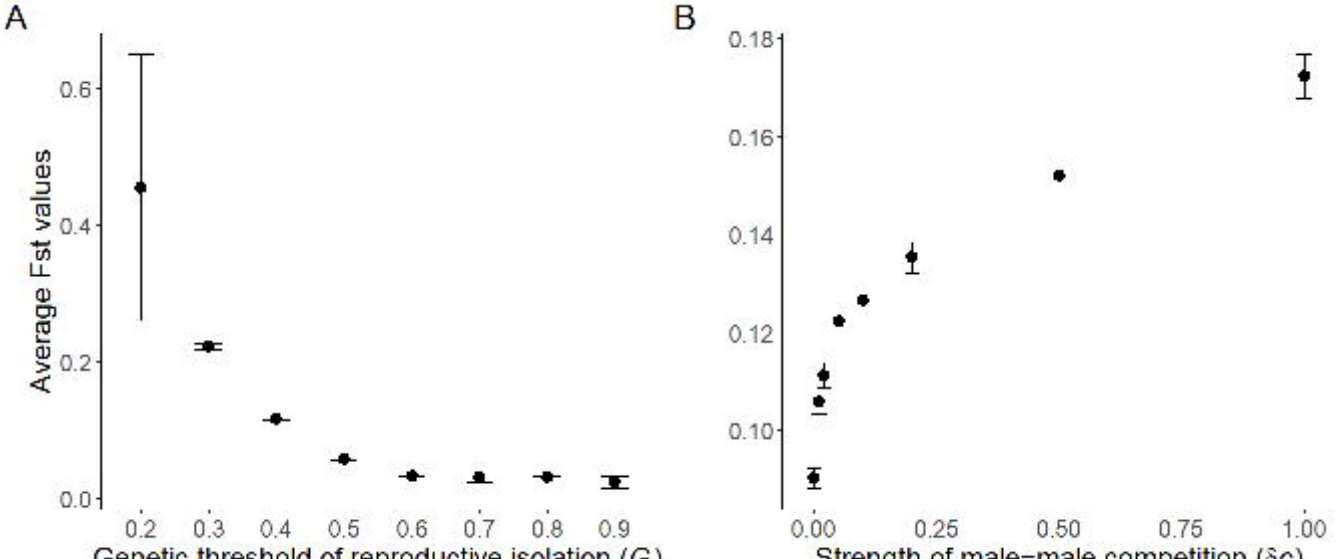
Figure 5: **Characterisation of the linkage disequilibrium between activity time and the neutral loci, depending on the proportion of loci necessary to generate incompatibilities G**. Using point-biserial correlation, we assessed the presence of linkage disequilibrium at each locus by testing whether the mean average reproductive activity differed significantly between individuals with a value of 1 and those with a value of 0 at this locus. We quantified (A) the percentage of simulations ending with differentiated sub-populations and displaying at least one locus with linkage disequilibrium, (B) the average number of loci exhibiting linkage disequilibrium when it arose. We can observe that for lower values of G, sub-populations exhibit linkage disequilibrium more frequently, but also that more loci display linkage disequilibrium on average. Stricter genetic incompatibilities are thus promoting linkage disequilibrium more frequently, as well as more strongly. Error bars show the SD computed over the 100 replicates per value of G. All simulations were run assuming the same values in the other parameters: $\delta_c = 0.1, \beta = 3, e = 0.5, v_e = 0.05, p = 1, K = 1000$.

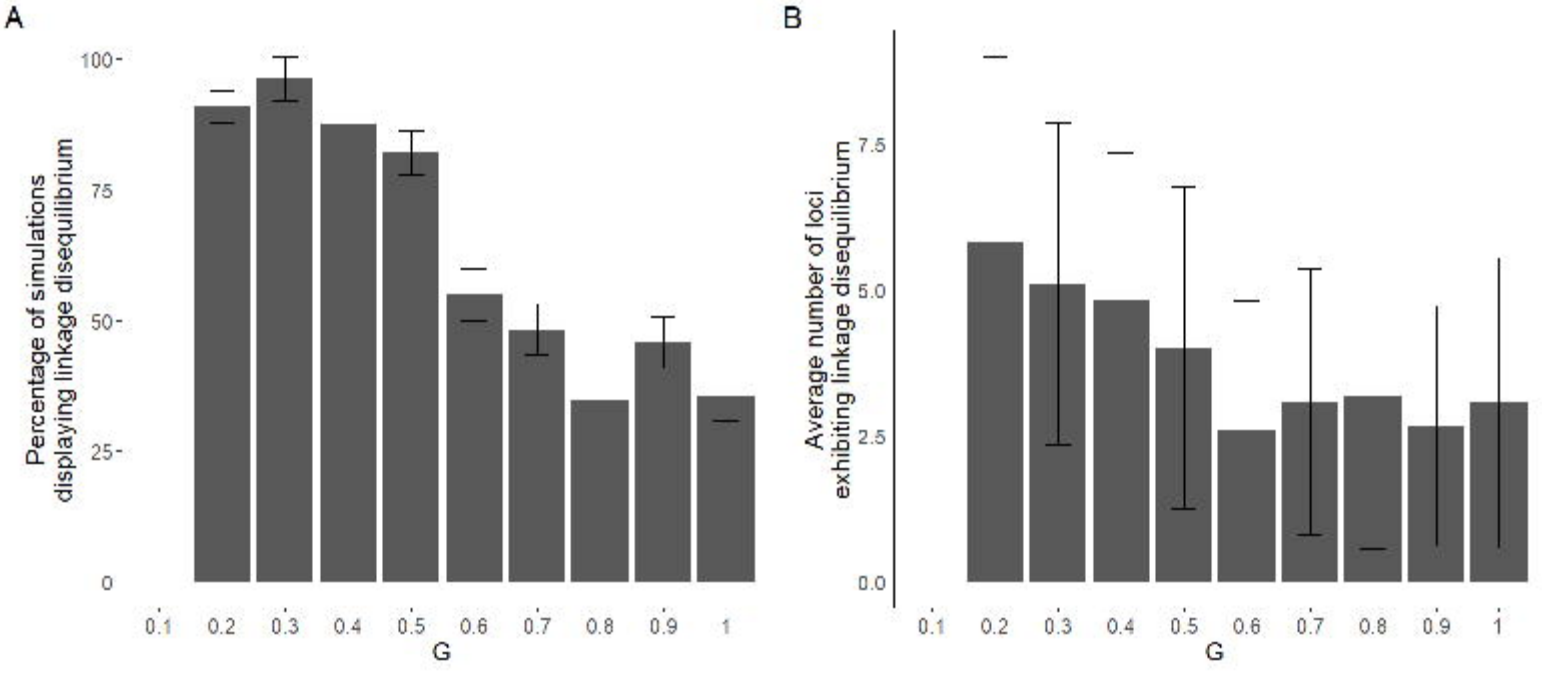
Figure 6: **Comparison of bimodal simulation outcomes, assuming either the *daily* or the *seasonal* model.** Distributions of the timing of reproductive activities from 100 simulations when differentiated sub-population evolve in (A) the *daily* model assuming over-lapping days and $\delta_c = 0.1$ and (B) the *seasonal* model, assuming non-over-lapping days and $\delta_c = 5$. The emergence time $e = 0.5$ is shown by a dotted line. In simulations assuming the *daily* model, we observe the evolution of a sub-population displaying earlier reproductive activity as compared to the alternative sub-population where reproductive activities occurred around the emergence time. In simulations assuming the *seasonal* model, both sub-populations were active after the emergence time e. All simulations were run assuming the same parameter values: $\beta = 3, \delta_c = 0.1$ in fig. 6A, and 5 in fig.6B, $G = 0.4, e = 0.5, v_e = 0.05, p = 1, K = 1000$.

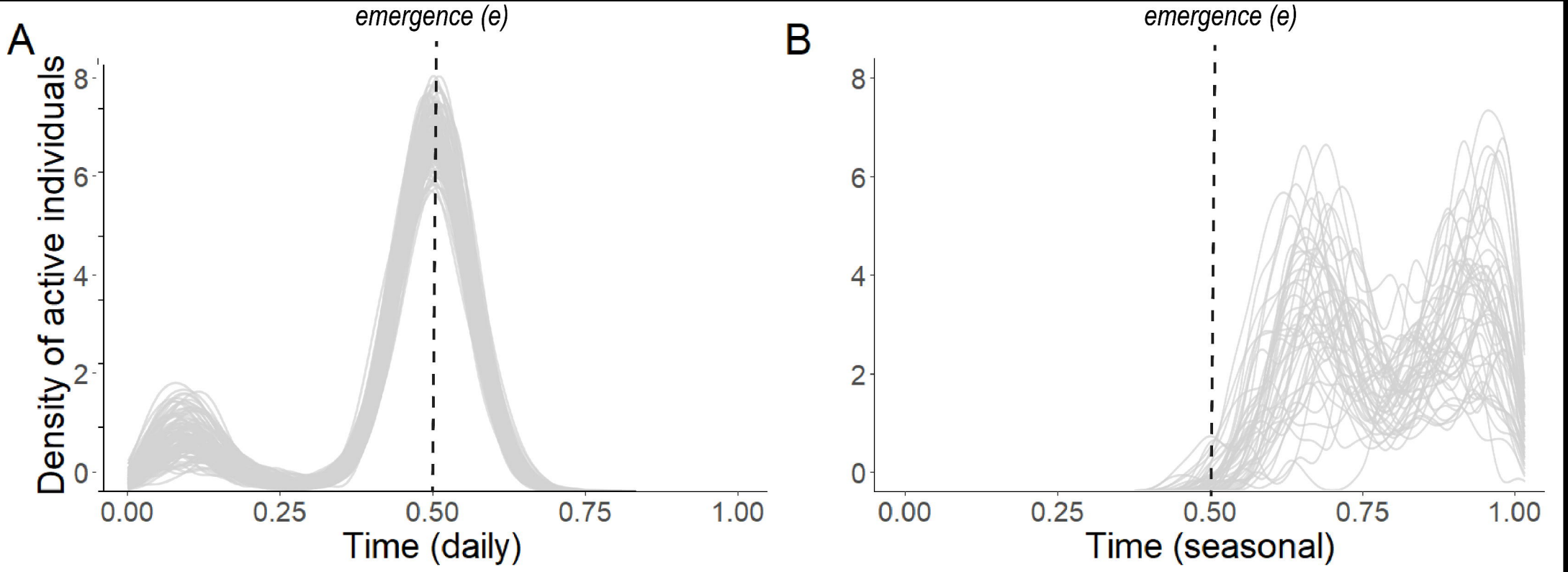

Active individuals
Unavailable females
and developping individuals
Resting individuals
Dawn
Male-male
competition
Non-sexually mature individuals
Mating
Emergence
(at time t=e)
Egg-laying females
Dusk
Influenced by h_a
Influenced by h_a


A
Percentage of each type of sub−population
1.00
0.75
0.50
0.25
0.00
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Emergence (e)
Immediate
Bimodal
Dawn-shifted
B
Density of active individuals
emergence (e)
Day time
C
emergence (e)
Day time
D
emergence (e)
Day time


A
B
Percentage of bimodal distribution after 500 days
100
75
50
25
0
0
0.01
0.02
0.05
0.1
0.5
1
Strength of male-male competition (δ_c)
1
2
3
4
5
Maximum number of mates per female (p)


A
Average Fst values
0.0
0.2
0.4
0.6
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Genetic threshold of reproductive isolation (G)
B
0.10
0.12
0.14
0.16
0.18
0.00
0.25
0.50
0.75
1.00
Strength of male−male competition (δc)


A
Percentage of simulations displaying linkage disequilibrium
100
75
50
25
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
G
B
Average number of loci exhibiting linkage disequilibrium
7.5
5.0
2.5
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
G


A
emergence (e)
Density of active individuals
8
6
4
2
0
0.00
0.25
0.50
0.75
1.00
Time (daily)
B
emergence (e)
8
6
4
2
0
0.00
0.25
0.50
0.75
1.00
Time (seasonal)