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COALESCENT PROCESSES IN SUBDIVIDED POPULATIONS SUBJECT TO RECURRENT MASS EXTINCTIONS

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Abstract

We investigate the infinitely many demes limit of the genealogy of a sample of individuals from a subdivided population that experiences sporadic mass extinction events. By exploiting a separation of time scales that occurs within a class of structured population models generalizing Wright's island model, we show that as the number of demes tends to infinity, the limiting form of the genealogy can be described in terms of the alternation of instantaneous *scattering* phases that depend mainly on local demographic processes, and extended *collecting* phases that are dominated by global processes. When extinction and recolonization events are local, the genealogy is described by Kingman's coalescent, and the scattering phase influences only the overall rate of the process. In contrast, if the demes left vacant by a mass extinction event are recolonized by individuals emerging from a small number of demes, then the limiting genealogy is a coalescent process with simultaneous multiple mergers (a Ξ -coalescent). In this case, the details of the within-deme population dynamics influence not only the overall rate of the coalescent process, but also the statistics of the complex mergers that can occur within sample genealogies. These results suggest that the combined effects of geography and disturbance could play an important role in producing the unusual patterns of genetic variation documented in some marine organisms with high fecundity.

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1 Introduction

In this article, we investigate a class of population genetics models that describe a population of individuals subdivided into D demes which are subject to sporadic mass extinction events. In general, we will think of these demes as corresponding to geographically distinct subpopulations such as occur in Wright's island model [Wright, 1931], but this structure could also arise in other ways, such as through the association of homologous chromosomes within different individuals of a diploid species. Whatever the source of the structure, many species are subject to recurrent disturbances which, if severe enough, can result in the extinction of a large proportion of the population [Sousa, 1984]. Important sources of widespread disturbance include fire, severe storms, drought, volcanic eruptions, earthquakes, insect outbreaks, and disease epidemics. Our goal in this paper is to characterize the effects that such events have on the genealogy of a sample of individuals or genes collected from the entire population. Specifically, we will identify a set of conditions which will guarantee that in the limit of infinitely many demes, the genealogy of the sample converges to a process which alternates between two phases: an extended phase during which ancestral lineages occupy distinct demes, and an effectively instantaneous phase that begins each time two or more lineages are gathered into the same deme and ends when these are again scattered into different subpopulations through a combination of mergers and migrations. The existence of this limit is a consequence of the separation of time scales between demographic events occurring within individual demes and those affecting the global dynamics of the population.

This study was partly motivated by recent investigations of the population genetics of several marine organisms whose genealogies appear to depart significantly from Kingman's coalescent (see Section 1.2). Based on their analysis of sequence polymorphism in a population of the Pacific oyster, Eldon and Wakeley [2006] and more recently Sargsyan and Wakeley [2008] suggest that the genealogies of some marine organisms with high fecundity and sweepstakes recruitment may be better described by a class of coalescent processes that generalize Kingman's coalescent by allowing for simultaneous multiple mergers. Indeed, in such organisms, the capacity of individuals to spawn millions of offspring makes it possible, in theory at least, for a substantial fraction of the population to be descended from a single parent. However, depending on the life history and ecology of the species in question, this could happen in several different ways. One possibility is that on rare occasions, individuals give birth to such a large number of offspring that even with random, independent survival of young, these cohorts constitute a sizable proportion of the next generation. Such a scenario has been studied by Schweinsberg [2003], who showed that coalescents with multiple and simultaneous mergers arise naturally when the offspring distribution has a polynomial tail. Another possibility is that on rare occasions a small number of individuals could contribute disproportionately many of the surviving offspring not because they are exceptionally fecund, but because of mass reproductive failure or death in other parts of the population. What distinguishes these two scenarios is whether individuals win the recruitment sweepstakes by producing an exceptionally large number of offspring relative to the long-term average, or by simply giving birth to an average (or even below-average) number of offspring at a time when most other individuals experience an exceptional failure of reproduction.

The multiple mergers that occur in the models investigated in this paper arise through a combination of both of these factors: mass extinctions create large swathes of unoccupied territory which is then instantaneously repopulated by individuals emerging from finitely many demes. Of course, one weakness of this study is that we do not identify the biological mechanism responsible for re-

stricting recolonization in this way, and in fact it seems difficult to formulate such a mechanism that is both realistic and consistent with the metapopulation models considered in this paper. However, there are several scenarios under which similar dynamics could arise in a spatially extended population in which disturbance events tend to affect contiguous demes. For example, if dispersal distances are short, then recolonization of vacant habitat in a one-dimensional population such as along a shoreline or a riparian corridor could be dominated by individuals recently descended from the small number of demes bordering the affected area. Similar reasoning might also apply to organisms with fractal-like distributions, such as aquatic or littoral species in estuarine environments or possibly even HIV-1 populations in the lymphatic system of an infected host. Alternatively, if regrowth from the margins is slow or even impossible (e.g., because surviving demes are separated from vacant demes by inhospitable habitat), then a few long-distance migrants could be responsible for repopulating empty demes even in species with two-dimensional distributions. Furthermore, in this case, we might also predict that the number of demes contributing recolonizers would be negatively correlated with the fecundity of the organism, since less time would be available for additional migrants to enter the affected region before the first migrant propagule had completely repopulated the region. Although the mathematical analysis is much more challenging than that given here, spatially-explicit models incorporating these features are currently under development (Alison Etheridge, pers. comm.).

1.1 Wright's island model with mass extinctions

To motivate both the class of models studied in this paper as well as the separation of time scales phenomenon that leads to the infinitely-many demes limit, let us begin by considering a version of Wright's island model with mass extinctions. Suppose that a population of haploid organisms is subdivided into D demes, each of which contains N individuals. We will assume that individuals reproduce continuously, i.e., generations are overlapping, and that at rate 1 each individual gives birth to a single offspring which settles in that same deme with probability $1 - m$ and otherwise migrates to one of the other $D - 1$ demes, chosen uniformly at random. In either case, we will assume that the deme size is constant and that a newborn individual immediately replaces one of the existing N members of the deme in which it settles. Notice that if $m = 0$, then this model reduces to a collection of D independent Moran models in populations of constant size N , whereas if $N = m = 1$, it describes the usual Moran model in a single population of size D . However, in the following discussion we will assume that $m > 0$ and that D is very much larger than N .

Before we account for mass extinctions, let us consider the genealogy of a sample of n individuals chosen uniformly at random from the entire population. We first observe that, looking backwards in time, each lineage migrates out of its current deme at rate $(D - 1)Nm/ND \approx m$. Furthermore, if two lineages occupy different demes, then for these to coalesce, one of the two must migrate into the deme where the other lineage currently resides, an event that occurs approximately at rate m/D ; here we have neglected terms of order D^{-2} and will continue to do so without further comment. When two lineages are collected in the same deme, then they can either coalesce immediately, which happens with probability $1/N$, or they can cohabit within that deme for some random period of time until either they coalesce or they migrate into different demes. Since two lineages occupying the same deme coalesce at rate $2(1 - m)/N$, and each lineage, independently of the other, migrates out of the deme at rate m , the probability that the two coalesce rather than migrate is $\chi = (1 - m)/(1 - m + Nm)$. Putting these observations together, it follows that every time two lineages are collected

within the same deme by migration, the total probability that they coalesce rather than migrate into different demes is $1/N + (1 - 1/N)\chi = 1/(1 - m + Nm)$, and the time that elapses between entry into the same deme and either coalescence or escape is a mixture of a point mass at 0 (in case they coalesce at the entry time) and an exponential random variable with mean $N/(2mN + 2(1 - m))$. In particular, notice that typically much less time is required for two lineages occupying the same deme to either coalesce or escape (of order N) than is needed for two lineages occupying different demes to be collected into the same deme (of order D). It is this disparity between the rate of events happening within individual demes and the rate at which lineages are gathered together that gives rise to a separation of time scales in the island model. If we rescale time by a factor of D and let the number of demes tend to infinity, then the time required for two lineages sampled from different demes to coalesce is exponentially distributed with mean $(1 - m + Nm)/2m$.

To complete our description of the coalescent process in this model, we need to consider the possibility of more complex coalescent events. We first observe that if n individuals are sampled from D demes, then the probability that all of these individuals reside in different demes will be close to one if D is much greater than n . Furthermore, because lineages occupying different demes coalesce and migrate independently of one another, it is straightforward to show that the probability that three or more lineages ancestral to our sample are collected into the same deme is of order D^{-2} or smaller. Likewise, it can be shown that the probability of having multiple pairs of lineages collected into several demes at the same time is similarly negligible. From these observations, it follows that only pairwise coalescence events matter in the infinitely-many demes limit, and that if there are n ancestral lineages, then at rate $\binom{n}{2}2m/(1 - m + Nm)$, two of these, chosen uniformly at random, coalesce, leaving $n - 1$ ancestral lineages. In other words, the genealogy for this model can be approximated by a scalar time change of Kingman's coalescent, with a rate that depends on both the migration rate and the deme size. This result is essentially due to Wakeley and Aliacar [2001], who considered a similar model with non-overlapping generations and Wright-Fisher sampling.

Now let us introduce mass extinction events into this model. Fix $e > 0$ and $y \in [0, 1)$, and suppose that at rate e/D , the metapopulation suffers a disturbance which causes each deme to go extinct, independently of all others, with probability y . For example, we could consider a model in which the demes represent small islands or keys in the Caribbean and the disturbances are hurricanes that completely inundate those islands lying in their path. Here we are reverting to the original time units, i.e., time has not yet been rescaled by a factor of D , and we have chosen the disturbance rate so that mass extinctions occur at rates commensurate with coalescence in the pure island model. In keeping with the assumption that deme size is constant, we will assume that all of the islands that are left vacant by a mass extinction are immediately recolonized by offspring dispersing out of a single source deme that is chosen uniformly at random from among the demes unaffected by the disturbance. In addition, we will assume that the parent of each colonizing individual is chosen uniformly at random from the N members of the source deme. Of course, the entire metapopulation could be extirpated by a mass extinction if $y > 0$, but the probability of this outcome is exponentially small in D and can be disregarded as D tends to infinity.

Suppose that a mass extinction occurs at a time when there are n ancestral lineages occupying distinct demes. Bearing in mind that we are now looking backwards in time, all of the lineages belonging to demes that are affected by the disturbance will move into the source deme, where those sharing the same parent will immediately coalesce. Thus, one reason that multiple mergers can occur in this model is because of the very highly skewed distribution of recolonizing offspring contributed both by individuals and demes following a mass extinction. Suppose that there are n_1

distinct lineages remaining in the source deme once we account for this initial set of coalescences. These lineages will undergo a random sequence of migration and coalescence events until there is only one lineage remaining within the source deme. For example, if $n_1 = 4$, then one possible outcome would see one lineage migrate out of the deme followed by a pair of binary mergers, leaving only one lineage within the source deme. Whatever the sequence, the amount of time required to scatter the lineages into different demes will be of order $O(1)$, whereas the time until either the next mass extinction event or the next binary merger involving lineages outside of the source deme will be of order $O(D)$. Thus, if we again rescale time by a factor of D , then any sequence of coalescence and migration events involving a source deme will effectively be instantaneous when we let D tend to infinity. This is the second way in which multiple merger events can arise in this model. Furthermore, varying the migration rate and deme size changes not only the overall rate of coalescence, but also the relative rates of the different kinds of multiple merger events that can occur. For example, if Nm is very small, then the coalescent process will be close to a Λ -coalescent (which has multiple mergers, but not simultaneous multiple mergers) because most lineages that are collected into a source deme by a mass extinction event will coalesce before any escape by migration. However, as N increases, so will the probability that multiple lineages enter into and then escape from the source deme without coalescing. This suggests that at moderate values of Nm , mass extinctions may be likely to result in simultaneous mergers (i.e., the coalescent is a Ξ -coalescent), while for very large values of Nm , multiple mergers of all types will be unlikely and the coalescent process will tend towards Kingman's coalescent.

1.2 Neutral genealogies and coalescents

In the last twenty years, coalescent processes have taken on increasingly important role in both theoretical and applied population genetics, where their relationship to genealogical trees has made them powerful tools to study the evolution of genetic diversity within a population. Under the assumption of neutrality, allelic types do not influence the reproduction of individuals and it is therefore possible to separate 'type' and 'descent'. This allows us to study the genealogy of a sample of individuals on its own and then superimpose a mechanism describing how types are transmitted from parent to offspring, justifying the interest in investigating genealogical processes corresponding to particular reproduction mechanisms without explicit mention of types. We refer to Nordborg [2001] for a review of coalescent theory in population genetics.

Beginning with the coalescent process introduced by Kingman [1982] to model the genealogy of a sample of individuals from a large population, three increasingly general classes of coalescent processes have been described. A key feature shared by all three classes is the following consistency property: the process induced on the set of all partitions of $\{1, \dots, n\}$ by the coalescent acting on the partitions of $\{1, \dots, n+k\}$ (obtained by considering only the blocks containing elements of $\{1, \dots, n\}$) has the same law as the coalescent acting on the partitions of $\{1, \dots, n\}$. In terms of genealogies, this property means that the genealogy of n individuals does not depend on the size of the sample that contains them. To describe these continuous-time Markov processes, it will be convenient to introduce some notation. For all $n \in \mathbb{N}$, we denote the set of all partitions of $[n] \equiv \{1, \dots, n\}$ by \mathcal{P}_n . In the following, the index n of the set of partitions in which we are working will be referred to as the **sample size**, an element of $\{1, \dots, n\}$ will be called an **individual**, and 'block' or '**lineage**' will be equivalent terminology to refer to an equivalence class. If $\zeta \in \bigcup_n \mathcal{P}_n$, then $|\zeta| = k$ means that the partition ζ has k blocks. Also, for $\zeta, \eta \in \mathcal{P}_n$ and $k_1, \dots, k_r \geq 2$, we will write $\eta \subset_{k_1, \dots, k_r} \zeta$ if

η is obtained from ζ by merging exactly k_1 blocks of ζ into one block, k_2 into another block, and so on. Kingman's coalescent is defined on P_n for all $n \geq 1$, as a Markov process with the following Q -matrix: if $\zeta, \eta \in P_n$,

$$q_K(\zeta \rightarrow \eta) = \begin{cases} 1 & \text{if } \eta \subset_2 \zeta, \\ -\binom{|\zeta|}{2} & \text{if } \eta = \zeta, \\ 0 & \text{otherwise.} \end{cases}$$

A more general class of exchangeable coalescents, allowing mergers of more than two blocks at a time, was studied by Pitman [1999] and Sagitov [1999]. These coalescents with multiple mergers (or Λ -coalescents) are in one-to-one correspondence with the finite measures on $[0, 1]$ in the following manner: for a given coalescent, there exists a unique finite measure Λ on $[0, 1]$ such that the entries $q_\Lambda(\zeta \rightarrow \eta)$ of the Q -matrix of the coalescent, for $\zeta, \eta \in P_n$, are given by

$$q_\Lambda(\zeta \rightarrow \eta) = \begin{cases} \int_0^1 \Lambda(dx) x^{k-2} (1-x)^{b-k} & \text{if } \eta \subset_k \zeta \text{ and } |\zeta| = b, \\ -\int_0^1 \Lambda(dx) x^{-2} (1 - (1-x)^{b-1} (1-x+bx)) & \text{if } \eta = \zeta \text{ and } |\zeta| = b, \\ 0 & \text{otherwise.} \end{cases}$$

Kingman's coalescent is recovered by taking $\Lambda = \delta_0$, the point mass at 0. Lastly, a third and wider class of coalescents was introduced by Möhle and Sagitov [2001] and Schweinsberg [2000], for which mergers involving more than one ancestor are allowed. These coalescents with simultaneous multiple mergers (or Ξ -coalescents) are characterized in Schweinsberg [2000] by a finite Borel measure on the infinite ordered simplex

$$\Delta = \left\{ (x_1, x_2, \dots) : x_1 \geq x_2 \geq \dots \geq 0, \sum_{i=1}^{\infty} x_i \leq 1 \right\}.$$

Indeed, to each coalescent corresponds a unique finite measure Ξ on Δ of the form $\Xi = \Xi_0 + a\delta_0$, where Ξ_0 has no atom at zero and $a \in [0, \infty)$, such that the transition rates of the coalescent acting on P_n are given by

$$q_\Xi(\zeta \rightarrow \eta) = \int_{\Delta} \frac{\Xi_0(d\mathbf{x})}{\sum_{j=1}^{\infty} x_j^2} \left(\sum_{l=0}^s \sum_{i_1 \neq \dots \neq i_{r+l}} \binom{s}{l} x_{i_1}^{k_1} \dots x_{i_r}^{k_r} x_{i_{r+1}} \dots x_{i_{r+l}} (1 - \sum_{j=1}^{\infty} x_j)^{s-l} \right) + a \mathbb{I}_{\{r=1, k_1=2\}}$$

if $\eta \subset_{k_1, \dots, k_r} \zeta$ and $s \equiv |\zeta| - \sum_{i=1}^r k_i$. The other rates (for $\eta \neq \zeta$) are equal to zero. The Λ -coalescents are particular cases of Ξ -coalescents, for which $\Xi(x_2 > 0) = 0$.

As mentioned above, coalescent processes can be used to describe the genealogy of large populations. Indeed, a large body of literature has been devoted to describing conditions on the demography of a population of finite size N that guarantee that the genealogical process of a sample of individuals converges to a coalescent as N tends to infinity. Such limiting results for populations with discrete non-overlapping generations are reviewed in Möhle [2000], and some examples can be found for instance in Schweinsberg [2003], Eldon and Wakeley [2006] and Sargsyan and Wakeley [2008]. In these examples, the shape of the limiting coalescent is related to the propensity of individuals to produce a non-negligible fraction of the population in the next generation.

However, the representation of the genealogy as a coalescent requires in particular that any pair of lineages has the same chance to coalesce. This condition breaks down when the population is

structured into subpopulations, since then coalescence will occur disproportionately often between lineages belonging to the same deme. To model these kinds of scenarios, structured analogues of coalescent processes were introduced [see e.g. Notohara, 1990; Wilkinson-Herbots, 1998], which allow lineages both to move between demes as well as coalesce within demes. Various state spaces have been used to describe a structured coalescent, such as vectors in which the i 'th component gives the lineages (or their number) present in deme i , or vectors of pairs 'block \times deme label'. All these representations of a structured genealogy take into account the fact that the reproductive or dispersal dynamics may differ between demes, hence the need to keep track of the location of the lineages. In contrast, several papers investigate models where the structure of the genealogy collapses on an appropriate time scale, i.e., the limiting genealogy no longer sees the geographical division of the population. In Cox [1989], demes are located at the sites of the torus $\mathbb{T}(D) \subset \mathbb{Z}^d$ of size D and each site can contain at most one lineage. Lineages move between sites according to a simple random walk, and when one of them lands on a site already occupied, it merges instantaneously with the inhabitant of this 'deme'. These coalescing random walks, dual to the voter model on the torus, are proved to converge to Kingman's coalescent as $D \rightarrow \infty$. More precisely, Cox shows that if $n < \infty$ lineages start from n sites independently and uniformly distributed over $\mathbb{T}(D)$, then the process counting the number of distinct lineages converges to the pure death process that describes the number of lineages in Kingman's coalescent. This analysis is generalized in Cox and Durrett [2002] and Zähle et al. [2005], where each site of the torus now contains $N \in \mathbb{N}$ individuals and a Moran-type reproduction dynamics occurs within each deme. Again, the limiting genealogy of a finite number of particles sampled at distant sites is given by Kingman's coalescent, and convergence is in the same sense as for Cox' result. Other studies of systems of particles moving between discrete subpopulations and coalescing do not require that the initial locations of the lineages be thinned out. In Greven et al. [2007], demes are distributed over the grid \mathbb{Z}^2 and the process starts with a Poisson-distributed number of lineages on each site of a large box of size $D^{\alpha/2}$, for some $\alpha \in (0, 1]$. The authors show that the total number of lineages alive at times of the form D^t converges in distribution as a process (indexed by $t \geq \alpha$) to a time-change of the block counting process of Kingman's coalescent, as $D \rightarrow \infty$. See Greven et al. [2007] for many other references related to these ideas.

Our emphasis in this paper will be on the separation of time scales phenomenon and the way in which local and global demographic processes jointly determine the statistics of the limiting coalescent process. Consequently, we shall always assume that the demes comprising our population are exchangeable, i.e., the same demographic processes operate within each deme, and migrants are equally likely to come from any one of the D demes. In this simplified setting, we only need to know how lineages are grouped into demes, but not the labels of these demes.

1.3 Separation of time scales

A separation of time scales can be said to occur whenever different components of a stochastic process evolve at rates which greatly differ in their magnitudes. This concept is usually invoked when there is a sequence of stochastic processes $(X_t^D, t \geq 0)$ on a space E as well as a function $\eta : E \rightarrow E'$ and an increasing sequence $r_D \rightarrow \infty$ such that the processes $(X_{r_D^{-1}t}^D, t \geq 0)$ have a non-trivial limit $(X_t^{\text{fast}}, t \geq 0)$ determined by the **fast** time scale, while the processes $(\eta(X_t^D), t \geq 0)$ (which are only weakly influenced by the fast evolution) have another non-trivial limit $(X_t^{\text{slow}}, t \geq 0)$ determined by the **slow** time scale. It is often the case that the processes $(X_t^D, t \geq 0)$ have the Markov

property but do not converge to a limit, while the slow processes $(\eta(X_t^D), t \geq 0)$ do converge, but are not Markovian.

Separation of time scales techniques were first introduced into population genetics by Ethier and Nagylaki [1980], and since then have been used to study the genealogical processes of structured populations in several different settings. Nordborg and Krone [2002] consider a population of total size N , evolving according to a Wright-Fisher model [see Fisher, 1930; Wright, 1931] and distributed over $D < \infty$ demes. These demes are in turn structured into groups of demes, within which individuals migrate faster (at a rate of order $N^{-\alpha}$ for an $\alpha \in [0, 1]$) than from one group to another (which occurs at a rate $O(N^{-1})$). When all demes are connected by fast migration, they show that structured genealogy collapses to an unstructured Kingman's coalescent as N tends to infinity, due to the fact that migration is so fast compared to the coalescence rate (of order N^{-1}) that the population becomes well-mixed before the first coalescence event occurs. When several groups of demes are connected by slow migration, the genealogical process converges to a structured coalescent, in which groups of demes act as panmictic populations and coalescence of lineages within a group is faster than between two groups. These results are made possible by the fact that the blocks of the partition induced by the genealogy are not affected by a migration event. Since only migration occurs on the fast time scale and coalescence is on the slow time scale, forgetting about the location of the lineages gives a sequence of (non-Markov) processes which converge on the slow time scale to a Markov process.

Another kind of separation of time scales was studied by Wakeley and co-authors in a series of papers [see in particular Wakeley, 1998, 1999, 2004; Wakeley and Aliacar, 2001]. In these models, a population evolving in discrete non-overlapping generations occupies D demes, labeled $1, \dots, D$. Deme i contains a population of N_i adults and receives M_i migrants each generation. Then, a Wright-Fisher resampling within each deme brings the population sizes back to their initial values. Other mechanisms can also be taken into account, such as extinction of a group of demes followed by instantaneous recolonization. Allowing D to tend to infinity greatly simplifies the analysis of the genealogical processes, and in particular gives rise to a decomposition of the genealogy of a sample of individuals into two different phases, occurring on two time scales. Following the terminology introduced in Wakeley [1999], the first phase to occur is the **scattering phase**, in which lineages occupying the same deme coalesce or move to **empty** demes ('empty' meaning that none of the sampled lineages are in this deme). In the limit, this phase occurs on the fast time scale and is therefore viewed as instantaneous. At the end of the scattering phase, all remaining lineages lie in different demes. The **collecting phase** is the following period of time during which lineages are gathered together into the same demes by migration or extinction/recolonization, where they may merge. The limiting genealogical process is a coalescent on the slow time scale, which ends when the number of lineages reaches one.

As we have already mentioned, apart from an initial instantaneous burst of mergers (which only occurs if multiple individuals are sampled from the same deme) all of the genealogical processes obtained in this setting are scalar time changes of Kingman's coalescent. Indeed, in the forwards in time evolution, migrants and colonizers are assumed to come from the whole population or from a non-vanishing fraction of the demes and so, with probability one, only two of the finitely many lineages of the sample are brought into the same deme at a time in the limit. Subsequently, the two lineages either coalesce or are scattered again, but in any case the outcome is at most a binary merger. In this paper, we shall study coalescent processes that arise in population models which include mass extinctions and general recolonization mechanisms, and describe the conditions in

which it corresponds to an unstructured Ξ -coalescent on the slow time scale. To this end, we will speak of ‘scattering’ and ‘collecting’ phases in a more general sense. We prefer to call the ‘collecting phase’ the period of time during which lineages wander among empty demes until a migration or extinction event brings several lineages into the same deme. We shall show that, once such a ‘geographical collision’ has occurred, an instantaneous scattering phase follows at the end of which all lineages have merged or moved to empty demes. Another collecting phase then starts and so on until the most recent common ancestor of the sample has been reached and there is only one lineage remaining.

1.4 Framework and main results

Fix $n \in \mathbb{N}$ and consider the genealogy of a sample of n individuals from a population of $D > n$ demes (the following framework also allows $D = \infty$). In the following, we shall suppose that demes are exchangeable in the sense given in Section 1.2. We shall work in the space \mathbb{P}_n^s defined as follows:

Definition 1. Let $\tilde{\mathbb{P}}_n^s$ be the set

$$\tilde{\mathbb{P}}_n^s \equiv \{(\{B_1, \dots, B_{i_1}\}, \dots, \{B_{i_{n-1}+1}, \dots, B_{i_n}\}) : 0 \leq i_1 \leq \dots \leq i_n \leq n, \\ \emptyset \neq B_j \subset [n] \forall j \in \{1, \dots, i_n\}, \{B_1, \dots, B_{i_n}\} \in \mathbb{P}_n\}$$

of n -tuples of sets (we allow some of the components of the n -tuple to be empty), and let us define the equivalence relation \sim on $\tilde{\mathbb{P}}_n^s$ by $\xi \sim \xi'$ if and only if there exists a permutation σ of $[n]$ such that, if $\mathcal{B}_1 \equiv \{B_1, \dots, B_{i_1}\}, \dots, \mathcal{B}_n \equiv \{B_{i_{n-1}+1}, \dots, B_{i_n}\}$ are the components of the vector ξ , then $\xi' = (\mathcal{B}_{\sigma(1)}, \dots, \mathcal{B}_{\sigma(n)})$. The quotient of $\tilde{\mathbb{P}}_n^s$ by \sim is denoted by \mathbb{P}_n^s .

We call any $(\{B_1, \dots, B_{i_1}\}, \dots, \{B_{i_{n-1}+1}, \dots, B_{i_n}\}) \in \tilde{\mathbb{P}}_n^s$ an **unordered structured partition of $[n]$** .

In view of the application we have in mind, each component \mathcal{B}_j represents a particular deme containing some of the lineages ancestral to the sample, and the blocks B_k (for $k \in \{1, \dots, i_n\}$) specify the partition of the sample determined by the ancestors alive at a particular time. Empty components are used to guarantee a constant vector size, n , independent of the index D used later. In the following, we omit the term ‘unordered’ when referring to the structured partitions of Definition 1.

The finite set \mathbb{P}_n^s is endowed with the discrete topology, which is equivalent to the quotient by \sim of the discrete topology on $\tilde{\mathbb{P}}_n^s$.

Definition 2. A Markov process \mathcal{P} on \mathbb{P}_n^s for which blocks can only merge and change component is called a **structured genealogical process**.

To illustrate the possible transitions, let us take $n = 5$ and consider the following sequence of events:

$$\begin{aligned} (\{\{1\}\}, \{\{2\}\}, \{\{3\}\}, \{\{4\}\}, \{\{5\}\}) &\stackrel{(i)}{\rightarrow} (\{\{1\}, \{2\}\}, \{\{3, 4\}\}, \{\{5\}\}, \emptyset, \emptyset) \\ &\stackrel{(ii)}{\rightarrow} (\{\{1\}\}, \{\{2\}\}, \{\{3, 4, 5\}\}, \emptyset, \emptyset) \\ &\stackrel{(iii)}{\rightarrow} (\{\{1, 2, 3, 4, 5\}\}, \emptyset, \emptyset, \emptyset, \emptyset). \end{aligned}$$

In this example, we start from the configuration in \mathbb{P}_5^s where each lineage is alone in its deme. During transition (i), either $\{1\}$ or $\{2\}$ changes component and both blocks end up in the same

deme (which creates an empty component in our representation), but remain distinct. In contrast, either $\{3\}$ or $\{4\}$ also moves (emptying another component), but then the two blocks merge into a single block $\{3, 4\}$ which is not allowed to split during later transitions. Block $\{5\}$ remains alone in its component. During transition (ii), lineages $\{1\}$ and $\{2\}$ are scattered again into two different demes by the movement of one of them, while one of the lineages $\{3, 4\}$ or $\{5\}$ changes component and the two blocks merge. Eventually, all the remaining blocks are gathered into the same deme and merge into a single block. Since elements of \mathcal{P}_5^s are defined up to a permutation of their components and since a block is not allowed to split, no other change is possible from the state reached after transition (iii).

Remark 1.1. *Movements and mergers of blocks do not alter the sample size. However, this does not guarantee that the structured genealogies are consistent in the sense given in Section 1.2 as we would expect from a reasonable genealogical process. In fact, several conditions will be imposed on the models we consider so that this property holds: see Lemma 2.2 for the consistency of the fast genealogical process, and the set of conditions (4) imposed on the geographical gatherings in Proposition 2.1. Proposition 4.1 states in particular that the latter conditions are necessary and sufficient for the genealogies to be consistent on both time scales and that when they are fulfilled, the unstructured genealogical process on the slow time scale is a Ξ -coalescent.*

Let us order the components of a given structured partition by the smallest element belonging to a block contained in the component (if it is non-empty). Empty components come last. For each $k \leq n$ and $\zeta \in \mathcal{P}_n^s$, let us write $|\zeta|_a = k$ if the a 'th component (in the order just defined) of the structured partition ζ contains k blocks, and define a subset Π_n of \mathcal{P}_n^s by

$$\Pi_n \equiv \{\zeta \in \mathcal{P}_n^s : |\zeta|_a \leq 1 \quad \forall a \in \{1, \dots, n\}\}. \quad (1)$$

Π_n is the set of all structured partitions of $[n]$ in which each deme contains at most one lineage. These sets will appear naturally in the description of the limiting processes.

Recall from the example given in Section 1.1 that the rate at which lineages are collected together in the same deme is much smaller than the rate at which lineages already occupying the same deme either coalesce or are scattered into different demes. Furthermore, as in that example, we will continue to assume that catastrophic extinction-recolonization events occur rarely, in fact, at rates that are of the same order of magnitude as the rate at which lineages occupying different demes are brought together by ordinary migration. With these points in mind, let us consider a sequence $(\mathcal{P}_s^D, s \geq 0)$ of structured genealogical processes for a finite sample from the whole population, which consists of the following kinds of events:

- within-deme coalescence and movement of lineages to empty demes at rates of order $O(1)$;
- movement of groups of lineages initially occupying different demes into the same deme, possibly followed by mergers of some of these lineages, at rates of order $O(r_D^{-1})$.

Let us rescale time by a factor of r_D so that the coalescence rate of two individuals in different demes is of order $O(1)$ as D tends to infinity. Of course, within-deme coalescence and migration now occur at increasing rates of order $O(r_D)$. This implies that, for a given sample size n , the generator G^D of the genealogical process acting on \mathcal{P}_n^s has the form

$$G^D = r_D \Psi + \Gamma + R_D,$$

where Ψ, Γ and R_D are bounded linear operators, $\langle R_D \rangle \rightarrow 0$ as $D \rightarrow \infty$, and we do not record the dependence of the operators on the sample size n . Here, if $\|\cdot\|$ stands for the supremum norm on the space of functions $f : P_n^s \rightarrow \mathbb{R}$, then $\langle R \rangle$ is defined by

$$\langle R \rangle = \sup_{f \neq 0} \frac{\|Rf\|}{\|f\|}. \quad (2)$$

Because $r_D \rightarrow \infty$, the sequence $(G^D)_{D \geq 1}$ is unbounded, even when applied to functions of the unstructured partition induced by \mathcal{P}^D , and so we do not expect the structured coalescent processes corresponding to these generators to converge pathwise. Nevertheless, our heuristic description of the fast dynamics suggests that elements of Π_n will be unaffected by the ‘fast’ events corresponding to Ψ , which will indeed be the case under the assumptions made in Section 2. Furthermore, we will show (cf. Lemma 2.1) that the process generated by Ψ on P_n^s and starting at $\zeta \in P_n^s$ a.s. reaches a random final state $\underline{\zeta}$ in Π_n in a finite number of steps. Since the rates of the events generated by Ψ grow to infinity, increasing numbers of these events take place before the first event corresponding to Γ even occurs. This motivates the description of the genealogy given above in terms of an alternation of very short scattering phases driven by Ψ and of longer collecting phases ending with the first event generated by Γ at which \mathcal{P}^D leaves Π_n . Viewing all of the transitions occurring during a given scattering phase as a single, more complex event, and exploiting the fact that these phases are vanishingly short, it is plausible that there is a genealogical process \mathcal{P} with values in Π_n such that for each fixed time $t > 0$, $\mathcal{P}_t^D \Rightarrow \mathcal{P}_t$ as $D \rightarrow \infty$. Our main result makes these heuristic arguments rigorous:

Theorem 1.1. *Let $\zeta \in P_n^s$. Under the conditions described in Section 3.1, the finite-dimensional distributions of the structured genealogical process \mathcal{P}^D starting at ζ converge to those of a Π_n -valued Markov process \mathcal{P} starting at $\underline{\zeta}$, except at time 0.*

The proof that \mathcal{P}^D converges in law to \mathcal{P} in the Skorokhod space $D_{P_n^s}[0, \infty)$ of all càdlàg paths with values in P_n^s requires tightness of the corresponding sequence of distributions. We shall show in Proposition 3.2 that this property holds if and only if the rate at which the genealogical process leaves the set Π_n tends to zero as D grows to infinity. Indeed, if this condition is not satisfied, then two or more jumps can accumulate during a scattering phase: the jump out of Π_n followed by the events needed to bring \mathcal{P}^D back into Π_n . Fortunately, the proof that the unstructured genealogical processes are tight is less demanding, since these processes do not change state when lineages move between demes. In this case, an accumulation of jumps due to the fast within-deme dynamics will be ruled out if we can show that the probability that the process \mathcal{P}^D re-enters Π_n in a single jump converges to one as D tends to infinity.

The limiting process \mathcal{P} with values in Π_n is introduced and investigated in Section 2, and we show in Proposition 2.1 that, under the assumptions of Theorem 1.1, the unstructured genealogical process induced by \mathcal{P} is the restriction to P_n of a Ξ -coalescent. We also identify the limiting process ξ for the genealogy on the fast time scale in Section 2, and state in Proposition 3.1 the convergence of $\mathcal{P}_{r_D^{-1}}^D$ to ξ as processes with values in $D_{P_n^s}[0, \infty)$. The proofs of Theorem 1.1 and Proposition 3.1 are given in Section 3, along with a discussion of the tightness of \mathcal{P}^D . Although the conditions of Theorem 1.1 are somewhat contrived, we show in Section 4 that these are necessary and sufficient for the unstructured genealogical process of a generalized island model to converge to a Ξ -coalescent on the slow time scale. In Section 5, we apply these results to a particular class of models incorporating

mass extinction events. Based on our analysis of this class, we suggest that families of Ξ -coalescents may often interpolate between Λ -coalescents and Kingman's coalescent in structured population models, and that it may be a generic property of such models that they admit simultaneous mergers whenever they admit multiple mergers.

2 Construction of the limiting genealogical processes

2.1 A generalized Island-Cannings Model

To motivate the genealogical processes considered in this paper, we begin by introducing a general model for the demography of a subdivided population which combines features of the Cannings model [Cannings, 1974] with those of the classical Island model [Wright, 1931].

Suppose that the population is subdivided into D demes, each of which contains N haploid individuals. Islands are labeled $1, \dots, D$, while individuals within each island are labeled $1, \dots, N$. At rate 1, an ND^2 -dimensional random vector $R \equiv (R_k^{i,j}, i, j \in \{1, \dots, D\}, k \in \{1, \dots, N\})$ is chosen, such that for all i, j, k , $R_k^{i,j}$ is the number of descendants of the k 'th individual in deme j which settle into deme i during the event. In keeping with the spirit of the Cannings' model, we use the term 'descendant' both to refer to the offspring of reproducing individuals as well as to individuals which were alive both before and after the event (as in Cannings' formulation of the Moran model). We impose the following conditions on the random variables $R_k^{i,j}$:

1. **Constant deme size:** With probability 1, for all $i \in [D]$ we have $\sum_{j,k} R_k^{i,j} = N$.
2. **Exchangeable dynamics:** The law of R is invariant under any permutation σ of $[D]^2 \times [N]$ such that for every $i \in [D]$, $\sigma(i, i, k)_1 = \sigma(i, i, k)_2$, i.e., σ conserves the relation *source deme* = *destination deme*. (Here, $\sigma(i, j, k)_l$ denotes the l 'th component of the permuted vector.)

Then, in each deme the current population is replaced by the N offspring coming into this deme during the event, which we label in an exchangeable manner.

Let us comment on the above conditions. The first one simply guarantees that the number of individuals in each deme is constant and equal to N . For the second condition, let us first fix i, j and a permutation τ of $[N]$, and look at the permutation σ given by $\sigma(i, j, k) = (i, j, \tau(k))$ and $\sigma(i', j', k') = (i', j', k')$ whenever $i \neq i'$ or $j \neq j'$. Then, condition 2 corresponds to the exchangeability of the contribution of the inhabitants of deme j in repopulating deme i . Second, fix i and choose a permutation τ of $[D] \setminus \{i\}$. Set $\sigma(i, j, k) = (i, \tau(j), k)$ if $j \neq i$, $\sigma(i, i, k) = (i, i, k)$ and $\sigma(i', j', k') = (i', j', k')$ whenever $i' \neq i$. In this case, condition 2 states that the demes different from deme i contribute in an exchangeable manner to the repopulation of deme i . Finally, let τ be a permutation of $[D]$ and define $\sigma(i, j, k) = (\tau(i), j, k)$ if $j \notin \{i, \tau(i)\}$, $\sigma(i, j, k) = (\tau(i), \tau(i), l)$ if $j = i$, and $\sigma(i, j, k) = (\tau(i), i, l)$ if $j = \tau(i)$. For such permutations, condition 2 asserts that the dispersal mechanism is exchangeable with respect to the destination of dispersing individuals (provided that this differs from the source deme). Overall, our assumptions aim at making the dynamics depend on the labels as weakly as possible, but we allow the repopulation mechanism of a deme to differ according to whether the new individuals are produced within this deme or come from one of the $D - 1$ other demes.

Example 1. If R is invariant under all permutations σ of $[D]^2 \times [N]$ (not just those satisfying condition 2), then the dynamics are those of a Cannings' model for a panmictic population of size DN , i.e., there is no population subdivision.

Example 2. If all demes evolve independently of each other, then $R^{i,j} \equiv 0$ whenever $j \neq i$. Condition 2 imposes that $(R^{i,i}, i \in [D])$ should be an exchangeable D -tuple of exchangeable N -tuples, a situation corresponding to a continuous-time Cannings model acting within each deme.

Example 3. Let $m \in [0, 1]$ and assume that, with probability $1 - m$, R is chosen as in Example 2. With probability m , four numbers i, j, l, k are sampled uniformly at random in $[D]^2 \times [N]^2$, and the k 'th individual in deme j produces an offspring that replaces the l 'th individual in deme i . In this case, $R^{i,i} = (1, \dots, 0, \dots, 1)$, where the unique zero is in the l 'th coordinate; $R^{i,j} = (0, \dots, 1, \dots, 0)$, where the unique 1 is in the k 'th coordinate; $R^{i,j'} = (0, \dots, 0)$ if $j' \notin \{i, j\}$ and for $i' \neq i$, $R^{i',j'} = (1, \dots, 1)$ if $i' = j'$ and $(0, \dots, 0)$ otherwise. This model gives a simple example including within-deme reproduction and individual migration. Alternatively, individuals could be exchanged between demes during a migration event, in which case a descendant of individual l in deme i (in the above notation) also replaces individual k in deme j .

Example 4. An event during which one deme goes extinct and is recolonized by the offspring of individuals coming from other demes has the following formulation: $R^{i,i} = (0, \dots, 0)$ if deme i goes extinct, $R^{l,i} = (1, \dots, 1)$ if $l \neq i$ and the repopulation of deme i satisfies the exchangeability condition 2. For instance, N individuals are chosen uniformly at random among the $N(D - 1)$ inhabitants of the other demes and contribute one offspring in the new population of deme i .

Many other kinds of events can be imagined, but these three mechanisms (reproduction, migration and extinction/recolonization) will be the building blocks of the models we shall consider in this paper. Viewed backwards in time, reproduction events as in Example 2 will correspond to the merger of several lineages if they are produced (forwards in time) by the same individual during the event considered. A migration event such as in Example 3 will correspond to the movement of one or a few lineages from their demes to other subpopulations, if these lineages happen to have their parents in the source demes. An extinction event will also typically result in the movement of lineages among demes, and could involve much larger numbers of individuals or demes than simple migration events. Note that lineages can both move and merge during the same event, if their common parent lies in a different deme.

2.2 Genealogy on the fast time scale

Let us start by constructing a structured genealogical process $(\xi_t, t \geq 0)$ such that its restriction to P_n^s describes the genealogy of n individuals on the fast time scale of individual demes. This process will incorporate mergers of lineages occupying the same deme as well as dispersal of lineages into empty demes (i.e., those not containing other ancestral lineages), but no events where geographically separated lineages end up in identical demes and possibly merge. In fact, if the rate at which such events occur is very large, then it is not difficult to see that the structure of the population effectively disappears on the fast time scale and the model collapses to that of a panmictic population. We thus rule out this kind of situations to keep a structured population.

We construct the process ξ by specifying its restriction to P_n^s . As P_n^s is a finite set, we can define a continuous-time Markov process on this space by specifying its transition rates. Because a block

represents a single ancestor, whose descendance at time 0 is made of the individuals contained in the block, we shall ask that the rates at which blocks move and merge do not depend on the number or labels of these individuals. Hence, these rates will only depend on the collection $\{k_1, \dots, k_p, 0, \dots, 0\}$ giving the numbers of blocks contained in the different components of ξ . In order to describe the possible transitions, we need the following definition.

Definition 3. Let $\hat{k} = \{k_1, \dots, k_p\}$ and $\hat{k}' = \{k'_1, \dots, k'_q\}$ be two collections of (non-zero) integers. We shall write $\hat{k} \triangleright \hat{k}'$ if $q \geq p$, $\sum_{i=1}^q k'_i \leq \sum_{j=1}^p k_j$, and we can arrange the elements of \hat{k}' so that for each $i \in \{1, \dots, p\}$, we have $1 \leq k'_i \leq k_i$ and at least one of such k'_i is strictly less than k_i .

Note that no collection \hat{k} of integers satisfies $\{1, \dots, 1\} \triangleright \hat{k}$.

For all pairs (\hat{k}, \hat{k}') such that $\hat{k} \triangleright \hat{k}'$, let $\vartheta_{\hat{k}, \hat{k}'} \in \mathbf{R}_+$. In addition, if $\zeta \in \mathbf{P}_n^s$, let $\hat{k}(\zeta)$ be the collection of integers which gives the number of blocks within each non-empty component of ζ . Define the infinitesimal rate $q_{(\xi)}(\eta|\zeta)$ of a particular transition $\zeta \rightarrow \eta$ (when $\eta \neq \zeta$ and both belong to \mathbf{P}_n^s) as:

- $q_{(\xi)}(\eta|\zeta) = \vartheta_{\hat{k}(\zeta), \hat{k}(\eta)}$, if η can be obtained from ζ by first merging some number (possibly zero) of blocks contained in the same component of ζ , and then moving some blocks to formerly empty demes with the restriction that only blocks originating from the same deme can be gathered into the same destination deme (again, we allow the number of blocks moved to be zero). In this case, we easily see that we must have $\hat{k}(\zeta) \triangleright \hat{k}(\eta)$.
- $q_{(\xi)}(\eta|\zeta) = 0$ otherwise.

In the following, we shall assume that for any $\zeta \in \mathbf{P}_n^s$ containing more than one block in at least one component, the rates satisfy the condition

$$\sum_{\eta \in \mathbf{P}_n^s} q_{(\xi)}(\eta|\zeta) > 0.$$

These conditions ensure that, whenever a deme contains more than one lineage, a scattering or a coalescence event will happen in the future with probability one. Recall the definition of Π_n given in (1). From the form of the rates given above, we see that any $\eta \in \Pi_n$ is an absorbing state for ξ . Moreover, we have the following result, saying in essence that the process ξ with values in \mathbf{P}_n^s reaches a final state in a finite number of steps, and this final state is a random variable with values in Π_n .

Lemma 2.1. Let τ_π be the stopping time defined by $\tau_\pi \equiv \inf\{t \geq 0 : \xi_t \in \Pi_n\}$. Then, τ_π is a.s. finite and for all $t \geq \tau_\pi$, $\xi_t = \xi_{\tau_\pi}$.

Proof. From our assumptions on the rates, the only absorbing states of the process ξ are the structured partitions contained in Π_n . Moreover, any transition results in a coarsening of the corresponding unstructured partition or in the movement of some lineages to different empty demes, so the number of transitions for ξ , starting at any $\xi_0 \in \mathbf{P}_n^s$ is bounded by n . Since the time between two events is exponentially distributed with a non-zero parameter (the sum of the rates of the possible transitions) as long as the process has not reached an absorbing state, the finiteness of the number of transitions undergone by ξ imposes that τ_π is a.s. finite. \square

Let us introduce the following notation, justified by the result of Lemma 2.1.

Notation 1. If $\zeta \in \mathbb{P}_n^s$, let $\underline{\zeta}$ denote a random variable with values in Π_n , whose distribution is that of the final state of the structured genealogical process ξ started at ζ .

We end this subsection with the following lemma, whose main purpose is to introduce the notion of consistency for structured genealogical processes. If $\zeta \in \mathbb{P}_k^s$ and $\tilde{\zeta} \in \mathbb{P}_{k+1}^s$ for some $k \in \mathbb{N}$, let us write $\zeta \prec \tilde{\zeta}$ if the projection of $\tilde{\zeta}$ onto \mathbb{P}_k^s (the k -tuple describing the structured partition of $1, \dots, k$) equals ζ .

Lemma 2.2. Suppose that ξ is defined on \mathbb{P}_k^s for every $k \in \mathbb{N}$. The following conditions are equivalent:

(i) For each $k \geq 1$, $\zeta, \eta \in \mathbb{P}_k^s$ and $\tilde{\zeta} \in \mathbb{P}_{k+1}^s$ such that $\zeta \prec \tilde{\zeta}$,

$$q_{(\xi)}(\eta|\zeta) = \sum_{\tilde{\eta}} q_{(\xi)}(\tilde{\eta}|\tilde{\zeta}),$$

where the sum is over all $\tilde{\eta} \in \mathbb{P}_{k+1}^s$ such that $\eta \prec \tilde{\eta}$.

(ii) The process ξ is consistent in the sense that, for all $k \geq 1$, if $\zeta \in \mathbb{P}_k^s$ and $\zeta' \in \mathbb{P}_{k+1}^s$ satisfy $\zeta \prec \zeta'$, then the law of the restriction to \mathbb{P}_k^s of the process ξ started at ζ' is the same as the law of ξ started at ζ .

In particular, if both conditions are fulfilled and if $\eta \in \Pi_k$ has r blocks, then

$$\mathbf{P}[\underline{\zeta} = \eta] = \sum_{j=1}^{r+1} \mathbf{P}[\underline{\zeta}' = \eta^{(j)}],$$

where for each $j \in \{1, \dots, r\}$, $\eta^{(j)} \in \Pi_{k+1}$ is obtained from η by adding an empty $(k+1)$ -st component to η (which turns it into an element η' of Π_{k+1}), and adding $k+1$ in the j 'th block of η' . Likewise, $\eta^{(r+1)}$ is obtained by adding the singleton $\{k+1\}$ in an empty component of η' .

Proof. Let $\xi_{(k)}$ (resp. $\xi_{(k+1)}$) denote the process ξ started at $\zeta \in \mathbb{P}_k^s$ (resp. $\zeta' \in \mathbb{P}_{k+1}^s$), and call $\xi'_{(k)}$ the projection onto \mathbb{P}_k^s of $\xi_{(k+1)}$. Since we work with finite state spaces and discrete jump processes, (ii) is equivalent to the fact that for all $\gamma, \eta \in \mathbb{P}_k^s$ the rate at which $\xi'_{(k)}$ jumps from γ to η is equal to the corresponding transition rate for $\xi_{(k)}$. By construction, the former is the sum of the rates of all the transitions from the current state of $\xi_{(k+1)}$ to a state η' such that $\eta \prec \eta'$, and so (ii) holds if and only if (i) does.

The second part of Lemma 2.2 is a direct consequence of the consistency of the process. \square

2.3 Limiting process on the slow time scale

Let us now describe the form that we would expect the genealogical process to take on the slow time scale as the number of demes tends to infinity. This process \mathscr{P} will have values in Π_n , so once again we construct it by specifying its transition rates.

Recall the two ingredients of the description of the structured genealogical processes indexed by $D < \infty$, given in Section 1.4. Coalescence and movement of blocks to formerly empty demes are the two kinds of events that constitute the fast process ξ , and we saw in Lemma 2.1 that the final state reached by ξ belongs to Π_n a.s. Therefore, we now need to describe how the resulting geographically separated lineages are gathered into identical demes and, potentially, merge during

the same event. As in the definition of ξ , the rate at which such an event occurs will only depend on the number r of demes containing at least one lineage just after the event, on the numbers k_1, \dots, k_r of blocks brought together into these components, and on the number and sizes of the groups of blocks ending up in the same demes which subsequently merge into a bigger block. Hence, we shall use the following terminology.

Definition 4. Let $k \geq 2$, and $k_1, \dots, k_r \geq 1$ such that $\sum_{i=1}^r k_i = k$ and at least one of the k_i 's is greater than 1. Let also $L_1 = \{l_{1,1}, \dots, l_{1,i_1}\}, \dots, L_r = \{l_{r,1}, \dots, l_{r,i_r}\}$ be r (unordered) sets of integers such that for $j \in \{1, \dots, r\}$, we have $\sum_{u=1}^{i_j} l_{j,u} = k_j$. We call an event in which k lineages spread in k different demes become grouped into k_1 lineages in one deme, k_2 lineages in another deme, \dots , and for all $j \in \{1, \dots, r\}$, $l_{j,1}$ lineages in deme j merge into one, $l_{j,2}$ into another, and so on (all mergers occur between lineages which landed in the same deme) a $(k; k_1, \dots, k_r; L_1, \dots, L_r)$ -geographical collision.

Remark 2.1. A geographical collision is to be understood as a particular transition. Because the order of k_1, \dots, k_r does not matter, a $(k; k_1, \dots, k_r; L_1, \dots, L_r)$ -geographical collision is also a $(k; k_{\sigma(1)}, \dots, k_{\sigma(r)}; L_{\sigma(1)}, \dots, L_{\sigma(r)})$ -geographical collision for any permutation σ of $\{1, \dots, r\}$. Thus, for a given $(k; k_1, \dots, k_r; L_1, \dots, L_r)$, the number of $(k; k_1, \dots, k_r; L_1, \dots, L_r)$ -geographical collisions is

$$A(k; k_1, \dots, k_r) \prod_{m=1}^r A(k_m; l_{m,1}, \dots, l_{m,i_m}),$$

where if k, k_1, \dots, k_r are such that $\sum_{i=1}^r k_i = k$ and b_j is the number of k_i 's equal to j , then

$$A(k; k_1, \dots, k_r) = \binom{k}{k_1, \dots, k_r} \frac{1}{\prod_{j=1}^k b_j!}. \quad (3)$$

Indeed, the binomial term gives the number of ways of choosing k_1 blocks to form a family numbered 1, k_2 other blocks to form family $n^{\circ}2$, and so on. But any permutation of the labels of families having the same size gives the same unordered structured partition, hence the normalization by the fraction in the right-hand side of (3).

Let us now define the structured genealogical process \mathcal{P} . The relation between the coefficients of \mathcal{P} and the sequence of structured genealogical processes will be given in the next section, and we simply give the form of the limiting process here. Recall that $|\zeta|_a = k$ if the a 'th component of ζ contains k blocks, and write $|\zeta|$ for the total number of blocks of $\zeta \in \mathcal{P}_n^s$, that is $|\zeta| = \sum_{a=1}^n |\zeta|_a$. Furthermore, let $\underline{\zeta}$ be a Π_n -valued random variable with the distribution specified in Notation 1.

Definition 5. For all integers and sets k, k_i and L_i satisfying the conditions of Definition 4, let $\lambda_{k; k_1, \dots, k_r; L_1, \dots, L_r}^g \geq 0$. Then, $(\mathcal{P}_t, t \geq 0)$ is the Markov process with values in Π_n which evolves as follows: when $\mathcal{P}_t = \chi \in \Pi_n$, any $(|\chi|; k_1, \dots, k_r; L_1, \dots, L_r)$ -geographical collision occurs at rate $\lambda_{|\chi|; k_1, \dots, k_r; L_1, \dots, L_r}^g$. Given that this collision has outcome $\zeta \in \mathcal{P}_n^s$, the new value of \mathcal{P} is drawn from the distribution of $\underline{\zeta}$.

We can recover the expression for the rate of any given transition in the form

$$q(\eta|\chi) = \sum_{\zeta \in \mathcal{P}_n^s} \lambda_{|\chi|; k_1, \dots, k_r; L_1, \dots, L_r}^g \zeta[\underline{\eta}],$$

where the rate $\lambda_{|\chi|;k_1,\dots,k_r;L_1,\dots,L_r}^g$ in the term of the sum labeled by a given ζ is the rate of occurrence of the only possible geographical collision turning χ into ζ , if such a collision exists. If it does not, we set the rate to 0. Consequently, the previous description does specify a Markov process on Π_n .

Observe that this description allows ‘ghost events’ in which lineages are gathered in identical demes by a geographical collision and then scattered again in different demes without coalescing, so that the actual transition is of the form $\chi \rightarrow \chi$. However, we shall need to keep track of these ghost events in the proof of convergence of the structured genealogical processes. Therefore, we shall always consider them as events which do occur at a certain rate but have no effect on \mathcal{P} .

To finish the description of our limiting process, we have the following result, which in fact describes the unstructured genealogy under some additional conditions.

Proposition 2.1. *For each $\zeta \in \Pi_n$, let us define $\zeta^u \in \mathbb{P}_n$ as the unstructured partition of n induced by ζ . Then the unstructured genealogical process $(\mathcal{P}_t^u, t \geq 0)$ induced by \mathcal{P} is a Markov process with values in \mathbb{P}_n . Suppose in addition that condition (i) of Lemma 2.2 holds and that the λ^g ’s satisfy the following consistency equations: for all $k \in \mathbb{N}$ and compatible $k_1, \dots, k_r, L_1, \dots, L_r$,*

$$\lambda_{k;k_1,\dots,k_r;L_1,\dots,L_r}^g = \sum_{u=1}^r \sum_{j=1}^{i_u+1} \lambda_{k+1;k_1,\dots,k_u+1,\dots,k_r;L_1,\dots,L_u^{(j)},\dots,L_r}^g + \lambda_{k+1;k_1,\dots,k_r,1;L_1,\dots,L_r,\{1\}}^g, \quad (4)$$

where for each $u \leq r$

$$L_u^{(j)} = \begin{cases} \{l_{u,1}, \dots, (l_{u,j} + 1), \dots, l_{u,i_u}\} & \text{if } j \leq i_u \\ \{l_{u,1}, \dots, l_{u,i_u}, 1\} & \text{if } j = i_u + 1. \end{cases}$$

(In particular, if instantaneous coalescence after the gathering of lineages is forbidden, then the λ^g ’s are associated to a Ξ -coalescent.)

Then $(\mathcal{P}_t^u, t \geq 0)$ is the restriction to \mathbb{P}_n of a Ξ -coalescent on the partitions of \mathbb{N} .

Remark 2.2. *By fixing k, k_1, \dots, k_r and summing over all compatible integer sets L_1, \dots, L_r , we see that the rates $\tilde{\lambda}_{k;k_1,\dots,k_r}^g$ at which k lineages lying in k different demes end up in a configuration where k_1 lineages are in the same deme, k_2 in another one, and so on (regardless of how many of them merge instantaneously thereafter), are associated to a Ξ -coalescent whenever condition (4) holds.*

Proof. Any component of $\gamma \in \Pi_n$ contains at most one block and all n -tuples are defined up to a permutation of their components, so the map $\Pi_n \rightarrow \mathbb{P}_n : \gamma \mapsto \gamma^u$ is a measurable bijection between Π_n and \mathbb{P}_n . Thus, \mathcal{P}^u inherits the Markov property of \mathcal{P} , and its transition rates $q^u(\eta^u | \gamma^u)$ are obviously given by $q^u(\eta^u | \gamma^u) = q(\eta | \gamma)$.

Let us turn to the second part of Proposition 2.1. By assumption, \mathcal{P}^u only coarsens as time goes on and it is easy to check that all transition rates $\rho(k; k_1, \dots, k_r)$ from a partition with k blocks to a partition obtained by merging k_1 of those blocks into one, k_2 into a second one, \dots ($k_1, \dots, k_r \in \mathbb{N}$, $\sum_{i=1}^r k_i = k$), are equal and depend only on k, k_1, \dots, k_r (the order of k_1, \dots, k_r does not matter). Therefore, we need only check the consistency condition given in Schweinsberg [2000] to identify \mathcal{P}^u as the restriction to the partitions of $[n]$ of a Ξ -coalescent. As the rates do not depend on n , let us rather work in Π_k with $\gamma = (\{\{1\}\}, \dots, \{\{k\}\})$ and $\eta = (\{\{1, \dots, k_1\}\}, \{\{k_1 + 1, \dots, k_1 + k_2\}\}, \dots, \{\{k_1 + \dots + k_{r-1} + 1, \dots, k\}\}, \emptyset, \dots, \emptyset)$, and check that

$$\rho(k; k_1, \dots, k_r) = \sum_{i=1}^r \rho(k + 1; k_1, \dots, k_i + 1, \dots, k_r) + \rho(k + 1; k_1, \dots, k_r, 1).$$

Since the λ^g 's satisfy (4), we have

$$\begin{aligned}
\rho(k; k_1, \dots, k_r) &= q(\eta | \gamma) \\
&= \sum_{\zeta \in \mathbb{P}_k^s} \lambda_{k; l_1, \dots, l_s; L_1, \dots, L_s}^g \underline{\zeta}[\eta] \\
&= \sum_{\zeta \in \mathbb{P}_k^s} \sum_{v=1}^s \sum_{j=1}^{i_v+1} \lambda_{k+1; l_1, \dots, l_v+1, \dots, l_s; L_1, \dots, L_v^{(j)}, \dots, L_s}^g \underline{\zeta}[\eta] + \sum_{\zeta \in \mathbb{P}_k^s} \lambda_{k+1; l_1, \dots, l_s, 1; L_1, \dots, L_s, \{1\}}^g \underline{\zeta}[\eta].
\end{aligned} \tag{5}$$

We wish to compare this rate to the rates corresponding to $k+1$ blocks. To this end, let us define $\zeta_{(v,j)} \in \mathbb{P}_{k+1}^s$ for all $\zeta \in \mathbb{P}_k^s$ with l non-empty components and $v \in \{1, \dots, l+1\}$, $j \in \{1, \dots, i_v+1\}$ (i_v being the number of blocks in the v 'th non-empty component of ζ) by turning ζ into a $(k+1)$ -tuple and adding individual $k+1$ in the j 'th block of the v 'th component of the new vector ($v = l+1$ means that we add the block $\{k+1\}$ in the extra component, and likewise $j = i_v+1$ means that we add the block $\{k+1\}$ in the v 'th component of the new vector). For example, with the previous notation γ ,

$$\gamma_{(1,2)} = (\{\{1\}, \{k+1\}\}, \dots, \{\{k\}\}, \emptyset) \quad \text{and} \quad \gamma_{(k+1,1)} = (\{\{1\}\}, \dots, \{\{k\}\}, \{\{k+1\}\}).$$

Define also $\gamma^{(j)} \in \Pi_{k+1}$, for all $\gamma \in \Pi_k$ with r blocks and $j \in \{1, \dots, r+1\}$, by turning γ into a $(k+1)$ -tuple and adding individual $k+1$ in the block of the j 'th component of the new vector. Once again, $j = k+1$ means that we add a block $\{k+1\}$ in the extra component. For instance,

$$\eta^{(1)} = (\{\{1, \dots, k_1, k+1\}\}, \{\{k_1+1, \dots, k_1+k_2\}\}, \dots, \{\{k_1+\dots+k_{r-1}+1, \dots, k\}\}, \emptyset, \dots, \emptyset)$$

and

$$\eta^{(k+1)} = (\{\{1, \dots, k_1\}\}, \{\{k_1+1, \dots, k_1+k_2\}\}, \dots, \{\{k_1+\dots+k_{r-1}+1, \dots, k\}\}, \{\{k+1\}\}, \emptyset, \dots, \emptyset).$$

With this notation, we see that

$$\sum_{i=1}^r \rho(k+1; k_1, \dots, k_i+1, \dots, k_r) + \rho(k+1; k_1, \dots, k_r, 1) = \sum_{i=1}^{r+1} q(\eta^{(i)} | \gamma_{(k+1,1)}). \tag{6}$$

For all $\zeta' \in \mathbb{P}_{k+1}^s$, there exists a unique triplet (ζ, v, j) where $\zeta \in \mathbb{P}_k^s$ has l non-empty components, $v \in \{1, \dots, l+1\}$ and $j \in \{1, \dots, i_v+1\}$ such that $\zeta' = \zeta_{(v,j)}$. Indeed, ζ is given by the partition of $\{1, \dots, k\}$ induced by ζ' , v is the component containing $k+1$ and j is the block of that component in which $k+1$ lies. Therefore, the right-hand side of (6) is equal to

$$\sum_{i=1}^{r+1} \sum_{\zeta \in \mathbb{P}_k^s} \sum_{v=1}^s \sum_{j=1}^{i_v+1} \lambda_{k+1; l_1, \dots, l_v+1, \dots, l_s; L_1, \dots, L_v^{(j)}, \dots, L_s}^g \underline{\zeta}_{(v,j)}[\eta^{(i)}] + \sum_{i=1}^{r+1} \sum_{\zeta \in \mathbb{P}_k^s} \lambda_{k+1; l_1, \dots, l_s, 1; L_1, \dots, L_s, \{1\}}^g \underline{\zeta}_{(s+1,1)}[\eta^{(i)}], \tag{7}$$

where s and the coefficients $\lambda_{k+1; l_1, \dots, l_v+1, \dots, l_s; L_1, \dots, L_v^{(j)}, \dots, L_s}^g$ correspond to the particular ζ indexing the term of the sum. Let us look at a particular ζ in the second sum. The block $\{k+1\}$ remains a singleton just after the geographical collision, so it is not affected by a following genealogical event

and $\zeta_{(s+1,1)}[\eta^{(i)}] = 0$ for all $i \in \{1, \dots, r\}$. Lemma 2.2 hence implies that $\zeta_{(s+1,1)}[\eta^{(r+1)}] = \underline{\zeta}[\eta]$, and the second term of (7) is equal to

$$\sum_{\zeta \in \mathbb{P}_k^s} \lambda_{k+1; l_1, \dots, l_s, 1; L_1, \dots, L_s, \{1\}}^g \underline{\zeta}[\eta].$$

Let us look at a particular ζ in the first sum, now. When $v \leq s$, the corresponding geographical collision brings $k+1$ in a block of the v 'th component of ζ . By the second part of Lemma 2.2, the probability that the final state of all the blocks different from $k+1$ is given by η is equal to the sum over all corresponding final states of these blocks and $k+1$. But taking the sum over i in $\sum_{i=1}^{s+1} \zeta_{(v,j)}[\eta^{(i)}]$ boils down to considering all such final states, since $\zeta_{(v,j)}[\eta^{(i)}] = 0$ if the individuals in the i 'th block of η were not in the v 'th component of ζ before their rearrangement by the genealogical process (recall that, under the action of ζ , lineages can merge only if they start in the same deme). Therefore, we obtain that, for all $\zeta \in \mathbb{P}_k^s$ and compatible v, j ,

$$\sum_{i=1}^{r+1} \zeta_{(v,j)}[\eta^{(i)}] = \underline{\zeta}[\eta].$$

Coming back to expressions (6) and (7), we obtain

$$\begin{aligned} & \sum_{i=1}^r \rho(k+1; k_1, \dots, k_i+1, \dots, k_r) + \rho(k+1; k_1, \dots, k_r, 1) \\ &= \sum_{\zeta \in \mathbb{P}_k^s} \sum_{v=1}^s \sum_{j=1}^{i_v+1} \lambda_{k+1; l_1, \dots, l_v+1, \dots, l_s; L_1, \dots, L_v^{(j)}, \dots, L_s}^g \underline{\zeta}[\eta] + \sum_{\zeta \in \mathbb{P}_k^s} \lambda_{k+1; l_1, \dots, l_s, 1; L_1, \dots, L_s, \{1\}}^g \underline{\zeta}[\eta] \\ &= \rho(k; k_1, \dots, k_r), \end{aligned}$$

where the last equality follows from (5). This completes the proof of Proposition 2.1. \square

3 Convergence of the structured genealogical processes

Now that we have constructed the potential limits for our sequence of structured genealogical processes on the fast and slow time scales, let us state precisely what conditions we impose and in which sense $\mathcal{P}_{r_D}^D$ and \mathcal{P}^D converge.

3.1 Description of the conditions

Let $n \geq 1$ be the sample size and define two types of events:

- Type 1: some lineages contained in the same demes merge and some move (potentially in groups) to empty islands. The number of lineages involved in either step can be zero (meaning that only coalescence or only scattering has occurred), and lineages starting from different demes are not gathered into the same deme by the event.

- Type 2: k lineages move, but at least one of them lands in a non-empty deme or at least two dispersing lineages not coming from the same deme are gathered. During that event, k_1 lineages end up in the same deme, k_2 lineages in another, and so on. This is immediately followed by the coalescence of some lineages lying in identical demes (the number of such mergers can be zero, meaning that the lineages have only moved).

By our assumptions on the genealogical processes, these two types describe all kinds of events which can happen to the structured genealogical process \mathcal{P}^D , for each D . For conciseness, we shall call an event of type i an i -event. Assume now that, when \mathcal{P}^D has value $\zeta \in \mathbb{P}_n^s$ and $\eta \in \mathbb{P}_n^s$ is a possible new value compatible with the type of the event (o 's hold as D goes to infinity):

1. The rate of occurrence of a particular 1-event $\zeta \rightarrow \eta$ can be written

$$r_D \vartheta_{\hat{k}(\zeta), \hat{k}(\eta)} + v^{(n)}(\zeta, \eta) + o(1) \quad \text{as } D \rightarrow \infty,$$

where for each n , $v^{(n)}(\cdot, \cdot)$ is a bounded function on $(\mathbb{P}_n^s)^2$ and $r_D \rightarrow \infty$ as $D \rightarrow \infty$.

2. Consider a 2-event involving k lineages, for which there exist $k_1, \dots, k_r \geq 1$ such that $\sum_{i=1}^r k_i = |\zeta|$ and there exist r sets of integers $L_1 = \{l_{1,1}, \dots, l_{1,i_1}\}$, \dots , $L_r = \{l_{r,1}, \dots, l_{r,i_r}\}$ such that for all $j \in \{1, \dots, r\}$ we have $\sum_{u=1}^{i_j} l_{j,u} = k_j$, satisfying: in the new structured partition, k_1 lineages end up in one deme, k_2 in another deme, \dots , and for all $j \in \{1, \dots, r\}$, $l_{j,1}$ lineages in deme j merge into one, l_{j,i_2} into another one, and so on (once again, all mergers occur between lineages lying in the same deme). Then the rate of occurrence of any such event is of the form

$$l_k^{(n)}(\zeta, \eta) + o(1),$$

where for each n and all $k \leq n$, $l_k^{(n)}$ is a bounded function on $\mathbb{P}_n^s \times \mathbb{P}_n^s$, and in particular if $\zeta \in \Pi_n$,

$$l_k^{(n)}(\zeta, \eta) = \lambda_{|\zeta|; k_1, \dots, k_r; L_1, \dots, L_r}^g.$$

Here again, the order of k_1, \dots, k_r does not matter.

3. The ϑ 's correspond to a structured genealogical process ξ as described in the last section, and the λ^g 's satisfy the consistency equations (4).

Morally, the coalescence of lineages occupying common demes and the scattering of such lineages into empty demes occur more and more rapidly as D tends to infinity, whereas events collecting lineages into common demes occur at bounded rates. Other events are less and less frequent, so that in the limit we obtain a separation of time scales between the instantaneous structured genealogical process and the slow collecting phase of the limiting unstructured genealogical process. Notice that 1-events do not affect a structured partition contained in Π_n .

Let $G^{n,D}$ denote the generator of the genealogical process of a sample of n individuals when the number of demes is D . For each D , the domain $\mathcal{D}(G^{n,D})$ of $G^{n,D}$ contains the measurable symmetric functions of n variables (by symmetric, we mean invariant under all permutations of the variables). From the last remark, we see that for all $f \in \mathcal{D}(G^{n,D})$, the parts of $G^{n,D}f$ corresponding to 1-events vanish on Π_n . Furthermore, we can define linear operators Ψ^n , Γ^n and R_D^n such that $G^{n,D}$ has the following form:

$$G^{n,D} = r_D \Psi^n + \Gamma^n + R_D^n.$$

More precisely, for every function f as above and each $\zeta \in \mathbb{P}_n^s$, we have

$$\Psi^n f(\zeta) = \sum_{\eta \in \mathbb{P}_n^s} \vartheta_{\hat{k}(\zeta), \hat{k}(\eta)} (f(\eta) - f(\zeta)) \quad \text{and} \quad \Gamma^n f(\zeta) = \sum_{\eta \in \mathbb{P}_n^s} \{v^{(n)}(\zeta, \eta) + l_k^{(n)}(\zeta, \eta)\} (f(\eta) - f(\zeta)),$$

and by the nonnegativity of their coefficients, these two operators can each be viewed as generating a jump process independent of D . In particular, we can define the structured genealogical process ξ on \mathbb{P}_n^s as the process generated by Ψ^n . The remaining terms $o(1)$ in Assumptions 1 and 2 constitute the coefficients of the (not necessarily positive) operator R_D^n , and so if we again use the operator norm introduced in (2), the finiteness of the number of possible transitions guarantees that $\langle R_D^n \rangle = o(1)$ as $D \rightarrow \infty$.

3.2 Convergence of the structured genealogical processes

The main result of this section is the convergence of the finite-dimensional distributions of the \mathbb{P}_n^s -valued structured genealogical processes \mathcal{P}^D to the corresponding ones of \mathcal{P} , except at time $t = 0$. The difficulty stems from the fact that the sequence of generators $G^{n,D}$ is unbounded because of the fast genealogical events driven by Ψ^n . The proof consists in essence in showing that the dynamics of the genealogical processes become very close to the description of the dynamics of \mathcal{P} , in that for D large enough, once a Γ^n -event (i.e., a geographical collision) occurs, enough Ψ^n -events happen in a very short period of time to bring the structured partition back into Π_n . During that short period, the probability that a Γ^n - or an R_D^n -event occurs is vanishingly small so that at the time when \mathcal{P}^D re-enters Π_n , with a high probability it has the distribution of the final state of ξ started at the structured partition created by the geographical collision. Overall, R_D^n -events are more and more infrequent and do not occur in the limit.

Before stating the results of this section, let us define the probability measures of interest. We take for granted the fact that the processes ξ and \mathcal{P}^D for each $D \in \mathbb{N}$ and all $n \in \mathbb{N}$ can be constructed on the same probability space $(\Omega, \mathbb{P}, \mathcal{F})$. For all $\zeta \in \mathbb{P}_n^s$, we thus denote the probability measure under which these processes start at ζ by \mathbf{P}_ζ . Likewise, let $(\Omega', \mathbb{P}, \mathcal{F}')$ be the probability space on which the processes \mathcal{P} and χ (see Definition 6) are defined for all $n \in \mathbb{N}$. \mathbb{P}_η denotes the probability measure under which these processes start at $\eta \in \Pi_n$.

With this notation, Theorem 1.1 can be restated as:

Theorem 1.1'. *Suppose that the conditions stated in Section 3.1 hold, and let $\zeta \in \mathbb{P}_n^s$. Then, the structured genealogical processes \mathcal{P}^D started at ζ converge to the process \mathcal{P} started at $\underline{\zeta}$ as D tends to infinity, in the sense that for all $0 < t_1 < \dots < t_p$,*

$$\mathbf{P}_\zeta(\mathcal{P}_{t_1}^D, \dots, \mathcal{P}_{t_p}^D) \Rightarrow \mathbb{P}_{\underline{\zeta}}(\mathcal{P}_{t_1}, \dots, \mathcal{P}_{t_p}) \quad \text{as } D \rightarrow \infty,$$

where $\mathbf{P}_\zeta(X)$ stands for the law of the random variable X under \mathbf{P}_ζ and $\mathbb{P}_{\underline{\zeta}}(X)$ is defined similarly.

We also have the following result.

Proposition 3.1. *Assume again that the conditions of Section 3.1 hold. Then the sequence of $D_{\mathbb{P}_n^s} [0, \infty)$ -valued processes $\{\mathcal{P}_{r_D^{-1}t}^D, t \geq 0\}$ converges in distribution to the structured genealogical process ξ introduced in Section 2.2.*

The proof of Proposition 3.1 is a direct consequence of the uniform convergence of the generator of $\mathcal{P}_{r_D^{-1}}^D$ (namely $r_D^{-1}G^{n,D}$) to the generator of ξ and the finiteness of the state space. A coupling with ξ shows that the first time at which both processes differ when started from the same value tends to infinity in probability, which is the main argument to obtain the desired convergence. The proof being immediate, we turn instead to the proof of Theorem 1.1.

Let us first introduce the following notation, for each $D \in \mathbb{N}$:

$$\sigma_1^D \equiv \inf\{t \geq 0 : \mathcal{P}_t^D \in \Pi_n\}, \quad \tau_1^D \equiv \inf\{t > \sigma_1^D : \text{a 2-event occurs at } t\},$$

and for all $i \geq 2$,

$$\sigma_i^D \equiv \inf\{t \geq \tau_{i-1}^D : \mathcal{P}_t^D \in \Pi_n\}, \quad \tau_i^D \equiv \inf\{t > \sigma_i^D : \text{a 2-event occurs at } t\}, \quad (8)$$

with the convention that $\inf \emptyset = +\infty$ and if σ_i^D or $\tau_i^D = +\infty$, then the following random times are all equal to $+\infty$. Note that if a 2-event occurs, its outcome may still be in Π_n (if all lineages gathered in identical demes merge into one lineage in each of these demes). In that case, $\sigma_{i+1}^D = \tau_i^D$. Let us also denote the ranked epochs of events occurring to the process \mathcal{P} by σ_i , $i \geq 1$, including what we previously called the ‘ghost events’, with the conventions that $\sigma_1 = 0$ and $\sigma_k = +\infty$ for $k \geq j+1$ if there are no more events after the j ’th transition.

Proof of Theorem 1.1. We start by proving the convergence of the one-dimensional distributions, then establish the convergence of the finite dimensional distributions by induction on their dimension. Since the sample size is fixed, we drop the superscript n in our notation.

As a first step, let us state the following definition and two lemmas, which will be useful in the course of the proof. For the sake of clarity, the proofs of the lemmas are postponed until after the proof of Theorem 1.1.

Definition 6. Let $(\chi_t, t \in [0, T])$ denote a Π_n -valued Markov process generated by Γ^n , where T is defined as

$$T \equiv \inf\{t \geq 0 : \chi_t \notin \Pi_n\}.$$

Then, for all $\eta \in \Pi_n$, $\chi(\eta)$ is defined as a \mathbb{P}_n^s -random variable distributed like the outcome of the first geographical collision when χ starts at η (this event is always defined if the λ^s ’s satisfy (4) and η has at least two blocks, since the coefficients $\tilde{\lambda}^s$ are the rates of a Ξ -coalescent as mentioned in Remark 2.2).

Lemma 3.1. Let $i \geq 1$. Then for all bounded measurable functions f on $\mathbf{R}_+ \times \mathbb{P}_n^s$, we have

$$\begin{aligned} \lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\sigma_i^D, \mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{\{\sigma_i^D < \infty\}}] &= \mathbb{E}_\zeta [f(\sigma_i, \mathcal{P}_{\sigma_i}) \mathbb{I}_{\{\sigma_i < \infty\}}], \\ \lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\tau_i^D, \mathcal{P}_{\tau_i^D}^D) \mathbb{I}_{\{\tau_i^D < \infty\}}] &= \mathbb{E}_\zeta [f(\sigma_{i+1}, \chi(\mathcal{P}_{\sigma_i})) \mathbb{I}_{\{\sigma_{i+1} < \infty\}}]. \end{aligned}$$

In particular, by taking $f(t, \eta) = \mathbb{I}_{\{t \leq s\}}$ for all $s > 0$, we obtain that the law under \mathbf{P}_ζ of the $[0, +\infty]$ -valued random variable σ_i^D (resp. τ_i^D) converges to the law under \mathbb{P}_ζ of σ_i (resp. σ_{i+1}).

Lemma 3.2. Let $t \in (0, \infty)$ and let $i \in \mathbb{N}$ be such that $\mathbb{P}_\zeta[\sigma_i < \infty] > 0$. By Lemma 3.1, we also have for D large enough $\mathbf{P}_\zeta[\sigma_i^D < \infty] > 0$. Let f be a real-valued function on \mathbb{P}_n^s . Then

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \mid \sigma_i^D < \infty] = \mathbb{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t) \mid \sigma_i < \infty].$$

Fix $t > 0$, let f be a real-valued function on \mathbb{P}_n^s and denote the supremum norm of f by $\|f\|$. We have for each D and all $N \in \mathbb{N}$:

$$\begin{aligned}
& \left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D)] - \mathbf{E}_\zeta [f(\mathcal{P}_t)] \right| \\
&= \left| \mathbf{E}_\zeta \left[\sum_{i=1}^{\infty} f(\mathcal{P}_t^D) \mathbb{I}_{[\tau_{i-1}^D, \sigma_i^D)}(t) + \sum_{i=1}^{\infty} f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \right] - \mathbf{E}_\zeta \left[\sum_{i=1}^{\infty} f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t) \right] \right| \\
&\leq \sum_{i=1}^N \left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t)] - \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t)] \right| \\
&\quad + \sum_{i=1}^N \left| \mathbf{E}_\zeta [|f(\mathcal{P}_t^D)| \mathbb{I}_{[\tau_{i-1}^D, \sigma_i^D)}(t)] + \left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{\{t \geq \tau_N^D\}}] \right| + \left| \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{\{t \geq \sigma_{N+1}\}}] \right| \right|,
\end{aligned} \tag{9}$$

where $\tau_0 \equiv 0$. Let $\epsilon > 0$. The random variables σ_i are the jump times of \mathcal{P} , the rates of which are bounded above by a constant $b \geq 0$. Thus, for each $N \geq 1$, σ_N is bounded below by the sum of N independent exponentials with parameter b , and so there exists $N \geq 1$ such that

$$\mathbb{P}_\zeta [\sigma_{N+1} < t] < \frac{\epsilon}{4\|f\|}.$$

In addition, $\tau_N^D \Rightarrow \sigma_{N+1}$ by Lemma 3.1, so there exists a D_0 such that for $D \geq D_0$,

$$\mathbf{P}_\zeta [\tau_{N+1}^D < \infty] < \frac{\epsilon}{4\|f\|}.$$

Consequently, for $D \geq D_0$ we have

$$\left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{\{t \geq \tau_N^D\}}] \right| + \left| \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{\{t \geq \sigma_{N+1}\}}] \right| \leq \|f\| \left(\mathbf{P}_\zeta [\tau_N^D \leq t] + \mathbb{P}_\zeta [\sigma_{N+1} \leq t] \right) < \frac{\epsilon}{2}. \tag{10}$$

Let $i \in \{1, \dots, N\}$. We have

$$\mathbf{E}_\zeta [|f(\mathcal{P}_t^D)| \mathbb{I}_{[\tau_{i-1}^D, \sigma_i^D)}(t)] \leq \|f\| \mathbf{P}_\zeta [\tau_{i-1}^D \leq t < \sigma_i^D] = \|f\| \left(\mathbf{P}_\zeta [\tau_{i-1}^D \leq t] - \mathbf{P}_\zeta [\sigma_i^D \leq t] \right).$$

By Lemma 3.1, both τ_{i-1}^D and σ_i^D converge in law towards σ_i (whose distribution function is continuous on \mathbf{R}_+), so the right-hand side of the last inequality tends to 0 when $D \rightarrow \infty$. Hence, there exists a D_1 such that for all $D \geq D_1$,

$$\sum_{i=1}^N \mathbf{E}_\zeta [|f(\mathcal{P}_t^D)| \mathbb{I}_{[\tau_{i-1}^D, \sigma_i^D)}(t)] \leq \frac{\epsilon}{4}. \tag{11}$$

Once again, let $i \in \{1, \dots, N\}$. If $\mathbb{P}_\zeta [\sigma_i \leq t] = 0$, then $\mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t)] = 0$ and

$$\left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t)] \right| \leq \|f\| \mathbf{P}_\zeta [\sigma_i^D \leq t] \rightarrow 0$$

as D tends to infinity, by Lemma 3.1 and the continuity of the distribution function of σ_i in t . If $\mathbb{P}_\zeta [\sigma_i \leq t] > 0$, we also have $\mathbf{P}_\zeta [\sigma_i^D \leq t] > 0$ for D large enough, so we can write

$$\begin{aligned}
\mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t)] &= \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \mid \sigma_i^D < \infty] \mathbf{P}_\zeta [\sigma_i^D < \infty] \\
&\rightarrow \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t) \mid \sigma_i < \infty] \mathbb{P}_\zeta [\sigma_i < \infty] \\
&= \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t)],
\end{aligned}$$

where the convergence on the second line stems from Lemma 3.2 and the convergence in distribution of σ_i^D towards σ_i . Consequently, there exists D_2 such that for all $D \geq D_2$,

$$\sum_{i=1}^N \left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t)] - \mathbf{E}_\zeta [f(\mathcal{P}_t) \mathbb{I}_{[\sigma_i, \sigma_{i+1})}(t)] \right| \leq \frac{\epsilon}{4}. \quad (12)$$

Combining to (9), (10), (11) and (12), we obtain for all $D \geq \max\{D_0, D_1, D_2\}$

$$\left| \mathbf{E}_\zeta [f(\mathcal{P}_t^D)] - \mathbf{E}_\zeta [f(\mathcal{P}_t)] \right| \leq \epsilon.$$

We can hence conclude that

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\mathcal{P}_t^D)] = \mathbf{E}_\zeta [f(\mathcal{P}_t)],$$

which completes the proof of the convergence of the one-dimensional distributions of \mathcal{P}^D under \mathbf{P}_ζ to the corresponding ones of \mathcal{P} under \mathbb{P}_ζ .

Let us now turn to the convergence of the finite-dimensional distributions. We prove by induction on p that, for all $0 < t_1 < \dots < t_p$, $\mathbf{P}_\zeta(\mathcal{P}_{t_1}^D, \dots, \mathcal{P}_{t_p}^D) \Rightarrow \mathbb{P}_\zeta(\mathcal{P}_{t_1}, \dots, \mathcal{P}_{t_p})$ as $D \rightarrow \infty$. By the preceding step, the case $p = 1$ is already established. Let $p \geq 2$, and suppose that the convergence holds for the $(p-1)$ -dimensional distributions. Let $0 < t_1 < \dots < t_p$, and let f_1, \dots, f_p be real-valued functions on \mathbb{P}_n^s . We denote the σ -field generated by $\{\mathcal{P}_s^D, s \in [0, t]\}$ by \mathcal{F}_t^D . Then,

$$\begin{aligned} \mathbf{E}_\zeta \left[\prod_{i=1}^p f_i(\mathcal{P}_{t_i}^D) \right] &= \mathbf{E}_\zeta \left[\mathbf{E} \left[\prod_{i=1}^p f_i(\mathcal{P}_{t_i}^D) \middle| \mathcal{F}_{t_{p-1}}^D \right] \right] \\ &= \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) \mathbf{E}_{\mathcal{P}_{t_{p-1}}^D} [f_p(\tilde{\mathcal{P}}_{t_p - t_{p-1}}^D)] \right] \quad \text{by the Markov property} \\ &= \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) \left(\sum_{\eta \in \mathbb{P}_n^s} p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) f_p(\eta) \right) \right], \end{aligned}$$

where here and in the following \tilde{X} denotes an independent version of the random variable X , the second expectation is taken with regards to \tilde{X} , and $p^D(\cdot, \cdot, s)$ is the transition kernel of \mathcal{P}^D corresponding to time s . Continuing the preceding equalities, we obtain

$$\begin{aligned} \mathbf{E}_\zeta \left[\prod_{i=1}^p f_i(\mathcal{P}_{t_i}^D) \right] &= \sum_{\eta \in \mathbb{P}_n^s} f_p(\eta) \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \right] \\ &= \sum_{\eta \in \mathbb{P}_n^s} f_p(\eta) \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \notin \Pi_n\}} \right] \quad (13) \end{aligned}$$

$$+ \sum_{\eta \in \mathbb{P}_n^s} f_p(\eta) \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \in \Pi_n\}} \right]. \quad (14)$$

For all $\eta \in \mathbb{P}_n^s$,

$$\left| \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \notin \Pi_n\}} \right] \right| \leq \left(\prod_{i=1}^{p-1} \|f_i\| \right) \mathbf{P}_\zeta [\mathcal{P}_{t_{p-1}}^D \notin \Pi_n] \rightarrow 0 \quad (15)$$

by the convergence of $\mathcal{P}_{t_{p-1}}^D$ to $\mathcal{P}_{t_{p-1}}$ in distribution and the finiteness of \mathbb{P}_n^s . As the sum in (13) is finite, (15) implies that this sum tends to 0 when D grows to infinity. Moreover, the convergence in law of $\mathcal{P}_{t_p - t_{p-1}}^D$ to $\mathcal{P}_{t_p - t_{p-1}}$, the finiteness of \mathbb{P}_n^s and the fact that $\underline{\gamma} = \gamma$ a.s. if $\gamma \in \Pi_n$ enable us to write

$$\max_{\gamma \in \Pi_n} \max_{\eta \in \mathbb{P}_n^s} |p^D(\gamma, \eta, t_p - t_{p-1}) - p(\gamma, \eta, t_p - t_{p-1})| \rightarrow 0 \quad \text{as } D \rightarrow \infty, \quad (16)$$

where $p(\gamma, \eta, t_p - t_{p-1})$ is the transition kernel of \mathcal{P} corresponding to time $t_p - t_{p-1}$, extended to $\eta \notin \Pi_n$ by $p(\gamma, \eta, t_p - t_{p-1}) = 0$. Now, we have for all $\eta \in \mathbb{P}_n^s$

$$\begin{aligned} \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \in \Pi_n\}} \right] \\ = \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) (p^D(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) - p(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1})) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \in \Pi_n\}} \right] \end{aligned} \quad (17)$$

$$+ \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \in \Pi_n\}} \right] \quad (18)$$

The expression in (17) tends to 0 by (16) and dominated convergence. As for the quantity in (18), for each $\eta \in \mathbb{P}_n^s$ the function $\gamma \mapsto p(\gamma, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\gamma \in \Pi_n\}}$ (vanishing on $\mathbb{P}_n^s \setminus \Pi_n$) is necessarily continuous and bounded on the finite set \mathbb{P}_n^s , so by the induction hypothesis for $p - 1$, we have

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}^D) p(\mathcal{P}_{t_{p-1}}^D, \eta, t_p - t_{p-1}) \mathbb{I}_{\{\mathcal{P}_{t_{p-1}}^D \in \Pi_n\}} \right] = \mathbb{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}) p(\mathcal{P}_{t_{p-1}}, \eta, t_p - t_{p-1}) \right].$$

The two latter results, together with (14), (15), the finiteness of the sums and the Markov property applied to \mathcal{P} lead to

$$\begin{aligned} \lim_{D \rightarrow \infty} \mathbf{E}_\zeta \left[\prod_{i=1}^p f_i(\mathcal{P}_{t_i}^D) \right] &= \sum_{\eta \in \mathbb{P}_n^s} f_p(\eta) \mathbb{E}_\zeta \left[\prod_{i=1}^{p-1} f_i(\mathcal{P}_{t_i}) p(\mathcal{P}_{t_{p-1}}, \eta, t_p - t_{p-1}) \right] \\ &= \mathbb{E}_\zeta \left[\prod_{i=1}^p f_i(\mathcal{P}_{t_i}) \right]. \end{aligned}$$

As any real-valued function on $(\mathbb{P}_n^s)^p$ can be obtained as a uniform limit of product functions, the convergence of the p -dimensional distributions is proven. The proof of Theorem 1.1 is complete by the induction principle. \square

Proof of Lemma 3.1. Let us start by proving that σ_1^D converges in probability to 0. If $\zeta \in \Pi_n$, then $\sigma_1^D = 0$ a.s. for all D so the convergence trivially holds. If $\zeta \notin \Pi_n$, then $\sigma_1^D > 0$ a.s. and with the notation introduced previously, we have for each function f on \mathbb{P}_n^s

$$G^D f(\zeta) = r_D \Psi f(\zeta) + \Gamma f(\zeta) + R_D f(\zeta),$$

where $\Psi f(\zeta) \neq 0$ (in fact, this holds for any $\eta \notin \Pi_n$, and consequently for all values of \mathcal{P}_t^D , $t \in [0, \sigma_1^D)$). Let us write $r_D c_\Psi(\zeta)$ (resp. $c_\Gamma(\zeta)$, $c_{R_D}(\zeta)$) the total rate of the non-trivial events generated

by $r_D\Psi$ (resp. Γ, R_D) when $G^D f$ is applied to ζ . As events are discrete for each D , we can write for $s > 0$

$$\begin{aligned} & \mathbf{P}_\zeta [\sigma_1^D > s] \\ & \leq \mathbf{P}_\zeta [\text{at most } n \Psi\text{-events and then a } \Gamma\text{- or } R_D\text{-event occur in } [0, s] \text{ and } \mathcal{P}_u^D \notin \Pi_n \forall u \in [0, s]] \\ & \quad + \mathbf{P}_\zeta [\text{at most } n \Psi\text{-events and no } \Gamma\text{- or } R_D\text{-events occur in } [0, s], \text{ and } \mathcal{P}_u^D \notin \Pi_n \forall u \in [0, s]] \\ & \quad + \mathbf{P}_\zeta [\text{more than } n \Psi\text{-events occur before the first } \Gamma\text{- or } R_D\text{-event}]. \end{aligned} \quad (19)$$

Since the events generated by Ψ correspond to the structured genealogical process $(\xi_t, t \geq 0)$ started at ζ as long as no Γ - or R_D -events occurred, by the bound on the number of transitions of ξ (n , see the previous section), the third term on the right-hand side of (19) vanishes. Moreover, the probability that the next event generated by G^D is a Γ or an R_D -event when the current value of \mathcal{P}^D is $\eta \notin \Pi_n$ is given by

$$\frac{c_\Gamma(\eta) + c_{R_D}(\eta)}{c_\Gamma(\eta) + c_{R_D}(\eta) + r_D c_\Psi(\eta)} \rightarrow 0, \quad D \rightarrow \infty,$$

since $c_\Psi(\eta) > 0$ for such an η , and this is precisely the kind of situation required to be in the configuration given by the first term of (19). So by bounding this term by the maximum over $\eta \notin \Pi_n$ of the probabilities calculated just before, we obtain that the first term of (19) tends to 0 as D grows to infinity. To finish, for each D and all $k \in \{1, \dots, n\}$ let us call U_k^D the random time of the k 'th event occurring to \mathcal{P}^D , with the convention that $U_k^D = +\infty$ if there are less than k such events. If k events occur (i.e., $U_k^D < \infty$) and \mathcal{P}^D stays out of Π_n , then U_{k+1} is stochastically bounded by the sum of $k+1$ i.i.d. exponential variables with parameter $r_D \min_{\eta \notin \Pi_n} c_\Psi(\eta)$, whose distribution becomes concentrated close to 0 as D grows since $\min_{\eta \notin \Pi_n} c_\Psi(\eta) > 0$. Consequently,

$$\begin{aligned} & \mathbf{P}_\zeta [\text{exactly } k \Psi\text{-events and no } \Gamma\text{- or } R_D\text{-events occur in } [0, s], \text{ and } \mathcal{P}_u^D \notin \Pi_n \forall u \in [0, s]] \\ & \leq \mathbf{P}_\zeta [U_{k+1}^D > s, U_k^D < \infty \text{ and } \mathcal{P}_u^D \notin \Pi_n \forall u \in [0, s]] \rightarrow 0. \end{aligned}$$

As the second term in (19) is bounded by the sum over $k \in \{0, \dots, n\}$ of the preceding quantities, it converges to zero. Hence, $\mathbf{P}_\zeta[\sigma_1^D > s] \rightarrow 0$ for all $s > 0$ and $\sigma_1 \rightarrow 0$ in probability.

Now, let f be a function on \mathbb{P}_n^s . For each $s > 0$, we have

$$\mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D) \mathbb{I}_{\{\sigma_1^D < s\}}] = \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D)] - \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D) \mathbb{I}_{\{\sigma_1^D \geq s\}}]. \quad (20)$$

By the convergence in probability of σ_1^D to 0 and the fact that f is bounded, the second term in the right-hand side of (20) vanishes as D grows to infinity. Furthermore, we have

$$\begin{aligned} \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D)] &= \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D); \text{ only } \Psi\text{-events before } \sigma_1^D] \\ & \quad + \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D); \text{ at least one } \Gamma\text{- or } R_D\text{-events before } \sigma_1^D]. \end{aligned} \quad (21)$$

The second term in (21) is bounded by $\|f\| \mathbf{P}_\zeta [\text{at least one } \Gamma\text{- or } R_D\text{-events before } \sigma_1^D]$ which tends to 0 by the preceding calculations, giving as a by-product that $\mathbf{P}_\zeta [\text{only } \Psi\text{-events before } \sigma_1^D] > 0$ for D large enough. Moreover, when only Ψ -events occurred between 0 and σ_1^D , then the evolution of \mathcal{P}^D between these two times is driven by the

structured genealogical process ξ started at ζ , so $\mathcal{P}_{\sigma_1^D}^D$ has the same distribution as $\underline{\zeta}$. Thus,

$$\begin{aligned} & \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D) ; \text{ only } \Psi\text{-events before } \sigma_1^D] \\ &= \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D) | \text{ only } \Psi\text{-events before } \sigma_1^D] \mathbf{P}_\zeta [\text{ only } \Psi\text{-events before } \sigma_1^D] \\ &= \mathbf{E} [f(\underline{\zeta})] \mathbf{P}_\zeta [\text{ only } \Psi\text{-events before } \sigma_1^D] \\ &\rightarrow \mathbf{E} [f(\underline{\zeta})]. \end{aligned}$$

Together with (20) and (21), we obtain that

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_1^D}^D) \mathbb{I}_{\{\sigma_1^D < s\}}] = \mathbf{E} [f(\underline{\zeta})] = \mathbf{E}_{\underline{\zeta}} [f(\mathcal{P}_0) \mathbb{I}_{\{0 < s\}}].$$

A monotone class argument of enables us to conclude the same result for any bounded measurable function f on $\mathbf{R}_+ \times \mathbf{P}_n^s$.

Let us now investigate the convergence of τ_1^D . Recall that if $\eta \in \Pi_n$ and $f \in \mathcal{D}(G^D)$, then

$$G^D f(\eta) = \Gamma f(\eta) + R_D f(\eta).$$

If $s > 0$, by the strong Markov property applied to \mathcal{P}^D at time σ_1^D we have

$$\mathbf{P}_\zeta [\tau_1^D > s] = \mathbf{E}_\zeta [\mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} [\tilde{\tau}_1^D > s - \sigma_1^D] \mathbb{I}_{\{s > \sigma_1^D\}}] + \mathbf{E}_\zeta [\mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} [\tilde{\tau}_1^D > s - \sigma_1^D] \mathbb{I}_{\{s \leq \sigma_1^D < \infty\}}]. \quad (22)$$

The second term in (22) is equal to $\mathbf{P}_\zeta [s \leq \sigma_1^D < \infty]$ which tends to 0 when D grows to infinity. If a Γ -event occurs when the current value of \mathcal{P}^D lies in Π_n , it is necessarily a 2-event, hence the first term is equal to

$$\begin{aligned} & \mathbf{E}_\zeta [\mathbb{I}_{\{s > \sigma_1^D\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} [\text{no } \Gamma\text{- or } R_D\text{-events between } 0 \text{ and } s - \sigma_1^D]] \\ &+ \mathbf{E}_\zeta [\mathbb{I}_{\{s > \sigma_1^D\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} [\text{no } \Gamma\text{-events and at least one } R_D\text{-event between } 0 \text{ and } s - \sigma_1^D; \tilde{\tau}_1^D > s - \sigma_1^D]]. \end{aligned}$$

But for all $\eta \in \Pi_n$,

$$\begin{aligned} & \mathbf{P}_\eta [\text{ no } \Gamma\text{-events and at least one } R_D\text{-event between } 0 \text{ and } s - \sigma_1^D; \tilde{\tau}_1^D > s - \sigma_1^D] \\ &\leq \mathbf{P}_\eta [\text{no } \Gamma\text{-events and at least one } R_D\text{-event between } 0 \text{ and } s] \\ &\leq 1 - \exp(-s \max_{\gamma \in \mathbf{P}_n^s} c_{R_D}(\gamma)) \rightarrow 0, \end{aligned}$$

so by dominated convergence,

$$\mathbf{E}_\zeta [\mathbb{I}_{\{s > \sigma_1^D\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} [\text{no } \Gamma\text{-event and at least one } R_D\text{-event between } 0 \text{ and } s - \sigma_1^D; \tilde{\tau}_1^D > s - \sigma_1^D]] \rightarrow 0.$$

Consequently,

$$\begin{aligned} \mathbf{P}_\zeta [\tau_1^D > s] &= \mathbf{E}_\zeta [\mathbb{I}_{\{s > \sigma_1^D\}} \exp - \left\{ (c_\Gamma(\mathcal{P}_{\sigma_1^D}^D) + c_{R_D}(\mathcal{P}_{\sigma_1^D}^D))(s - \sigma_1^D) \right\}] \\ &\rightarrow \mathbf{E} [e^{-s c_\Gamma(\underline{\zeta})}] = \mathbb{P}_{\underline{\zeta}} [\sigma_2 > s] \end{aligned}$$

by the preceding convergence result for $(\sigma_1^D, \mathcal{P}_{\sigma_1^D}^D)$ and the uniform convergence of c_{R_D} towards 0. We can thus conclude that the law of τ_1^D under \mathbf{P}_ζ converges to the law of σ_2 under \mathbb{P}_ζ .

Now, by the strong Markov property applied to \mathcal{P}^D at time σ_1^D , we have

$$\begin{aligned} & \mathbf{E}_\zeta \left[\mathbb{I}_{\{\tau_1^D < s\}} f(\mathcal{P}_{\tau_1^D}^D) \mathbb{I}_{\{\tau_1^D < \infty\}} \right] \\ &= \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \infty\}} \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[\mathbb{I}_{\{\tilde{\tau}_1^D < s - \sigma_1^D\}} f(\mathcal{P}_{\tilde{\tau}_1^D}^D); \text{ the first event is an } R_D\text{-event} \right] \right] \\ & \quad + \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \infty\}} \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[\mathbb{I}_{\{\tilde{\tau}_1^D < s - \sigma_1^D\}} f(\mathcal{P}_{\tilde{\tau}_1^D}^D); \text{ the first event is a } \Gamma\text{-event} \right] \right]. \end{aligned} \quad (23)$$

The absolute value of the first term in the right-hand side of (23) is bounded by

$$\|f\| \max_{\eta \in \Pi_n} \mathbf{P}_\eta [\text{a first event occurs and is an } R_D\text{-event}] \rightarrow 0.$$

Moreover, if $\mathcal{P}_0^D = \eta \in \Pi_n$ and the first event is a Γ -event, then $\tilde{\tau}_1^D$ is the time of that first event and $\mathcal{P}_{\tilde{\tau}_1^D}^D$ its outcome. Therefore, both are independent and $\mathcal{P}_{\tilde{\tau}_1^D}^D$ is distributed like $\chi(\eta)$, so the second term in (23) is equal to

$$\begin{aligned} & \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \infty\}} \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[\mathbb{I}_{\{\tilde{\tau}_1^D < s - \sigma_1^D\}} f(\chi(\mathcal{P}_0^D)) \right] \right] + o(1) \\ &= \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \infty\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D < s - \sigma_1^D \right] \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[f(\chi(\mathcal{P}_0^D)) \right] \right] + o(1). \end{aligned}$$

Let us write

$$\mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D < s - \sigma_1^D \right] = \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D < s \right] - \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D \in [s - \sigma_1^D, s] \right]$$

and fix $\epsilon > 0$. For any $\delta > 0$, we have

$$\begin{aligned} & \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \infty\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D \in [s - \sigma_1^D, s] \right] \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[f(\chi(\mathcal{P}_0^D)) \right] \right] \\ & \leq \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \delta\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D \in [s - \delta, s] \right] \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[|f(\chi(\mathcal{P}_0^D))| \right] \right] + \|f\| \mathbf{P}_\zeta \left[\sigma_1^D \in [\delta, \infty) \right]. \end{aligned}$$

By the convergence in probability of σ_1^D to 0, there exists $D_0 \geq 1$ such that for all $D \geq D_0$,

$$\mathbf{P}_\zeta \left[\sigma_1^D \in [\delta, \infty) \right] < \frac{\epsilon}{3\|f\|}.$$

Let $\eta \in \Pi_n$. By the continuity of the distribution function of σ_2 , there exists $\delta_0 > 0$ such that

$$\mathbf{P}_\eta \left[\tilde{\sigma}_2 \in [s - \delta_0, s] \right] < \frac{\epsilon}{3\|f\|}.$$

In addition, $\tilde{\tau}_1^D$ converges in distribution to σ_2 , hence there exists $D_1 \geq 1$ such that for all $D \geq D_1$,

$$\left| \mathbf{P}_\eta \left[\tilde{\tau}_1^D \in [s - \delta_0, s] \right] - \mathbf{P}_\eta \left[\tilde{\sigma}_2 \in [s - \delta_0, s] \right] \right| < \frac{\epsilon}{3\|f\|}.$$

Since Π_n is a finite set, we can conclude that for $\delta > 0$ small enough, and D large enough, we have

$$\begin{aligned} & \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \delta\}} \mathbf{P}_{\mathcal{P}_{\sigma_1^D}^D} \left[\tilde{\tau}_1^D \in [s - \delta, s] \right] \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[|f(\chi(\mathcal{P}_0^D))| \right] \right] + \|f\| \mathbf{P}_\zeta \left[\sigma_1^D \in [\delta, \infty) \right] \\ & \leq \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1^D < \delta\}} \max_{\eta \in \Pi_n} \mathbf{P}_\eta \left[\tilde{\tau}_1^D \in [s - \delta, s] \right] \mathbf{E}_{\mathcal{P}_{\sigma_1^D}^D} \left[|f(\chi(\mathcal{P}_0^D))| \right] \right] + \frac{\epsilon}{3} \\ & \leq \epsilon. \end{aligned}$$

Now, $\eta \mapsto \mathbf{P}_\eta[\tilde{\tau}_1^D < s]$ converges uniformly in $\eta \in \Pi_n$ to $\eta \mapsto \mathbb{P}_\eta[\tilde{\sigma}_2 < s]$ and

$$(s, \eta) \mapsto \mathbb{I}_{\{s < \infty\}} \mathbb{I}_{\{\eta \in \Pi_n\}} \mathbb{P}_\eta[\tilde{\sigma}_2 < s] \mathbb{E}_\eta[f(\chi(\tilde{\mathcal{P}}))]]$$

is a bounded measurable function, so by the convergence in distribution of $(\sigma_1^D, \mathcal{P}_{\sigma_1^D}^D)$ proven above, for D large enough we have

$$\begin{aligned} & \left| \mathbf{E}_\zeta \left[\mathbb{I}_{\{\tau_1^D < s\}} f(\mathcal{P}_{\tau_1^D}^D) \mathbb{I}_{\{\tau_1^D < \infty\}} \right] - \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_2 < s\}} f(\chi(\mathcal{P}_{\sigma_1})) \mathbb{I}_{\{\sigma_2 < \infty\}} \right] \right| \\ &= \left| \mathbf{E}_\zeta \left[\mathbb{I}_{\{\tau_1^D < s\}} f(\mathcal{P}_{\tau_1^D}^D) \mathbb{I}_{\{\tau_1^D < \infty\}} \right] - \mathbf{E}_\zeta \left[\mathbb{I}_{\{\sigma_1 < \infty\}} \mathbb{P}_{\mathcal{P}_{\sigma_1}}[\tilde{\sigma}_2 < s] \mathbb{E}_{\mathcal{P}_{\sigma_1}}[f(\chi(\tilde{\mathcal{P}}))] \right] \right| \\ &< 3\epsilon. \end{aligned}$$

Letting ϵ tend to zero yields the desired result (once again by invoking monotone classes) and completes the step $i = 1$ of the proof of Lemma 3.1.

Suppose that the desired properties hold for $i - 1$. Let f be a bounded continuous function on $\mathbf{R}_+ \times \mathbf{P}_n^s$. Since $\mathbb{I}_{\{\sigma_i^D < \infty\}} = \mathbb{I}_{\{\sigma_i^D < \infty\}} \mathbb{I}_{\{\tau_{i-1}^D < \infty\}}$, the strong Markov property applied to \mathcal{P}^D at time τ_{i-1}^D gives

$$\mathbf{E}_\zeta[f(\sigma_i^D, \mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{\{\sigma_i^D < \infty\}}] = \mathbf{E}_\zeta[\mathbb{I}_{\{\tau_{i-1}^D < \infty\}} \mathbf{E}_{\mathcal{P}_{\tau_{i-1}^D}^D}[f(\tau_{i-1}^D + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}]]]$$

But, for all $\eta \notin \Pi_n$, if X denotes a random variable whose distribution under \mathbf{P}_η is that of $\underline{\eta}$ (e.g. ξ_{τ_n} in the notation of Proposition 2.1), then

$$\begin{aligned} \left| \mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] - \mathbf{E}_\eta[f(t, X)] \right| &\leq \left| \mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] - \mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, X) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] \right| \\ &\quad + \left| \mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, X) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] - \mathbf{E}_\eta[f(t, X)] \right|. \end{aligned}$$

Since $\tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D$ has the same distribution as $\underline{\eta}$ under \mathbf{P}_η if only Ψ -events occurred between 0 and $\tilde{\sigma}_1^D$, the first term is equal to

$$\begin{aligned} & \left| \mathbf{E}_\eta \left[\mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}} (f(t + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) - f(t + \tilde{\sigma}_1^D, X)) \right] \right|; \text{ not only } \Psi\text{-events between 0 and } \tilde{\sigma}_1^D \\ & \leq 2\|f\| \max_{\eta \notin \Pi_n} \mathbf{P}_\eta[\tilde{\sigma}_1^D < \infty, \text{ not only } \Psi\text{-events between 0 and } \tilde{\sigma}_1^D] \rightarrow 0 \end{aligned}$$

by the calculations done in the proof of the convergence of σ_1^D . Moreover,

$$\mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, X) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] - \mathbf{E}_\eta[f(t, X)] \rightarrow 0$$

uniformly in η by the convergence in probability of $\tilde{\sigma}_1^D$ towards 0 and the finiteness of the number of states that X can take. Therefore,

$$\mathbf{E}_\eta[f(t + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] \rightarrow \mathbf{E}_\eta[f(t, X)] = \mathbb{E}_{\underline{\eta}}[f(t, \mathcal{P}_0)]$$

uniformly in (t, η) . This uniform convergence (which trivially holds also for $\eta \in \Pi_n$ since $\underline{\eta} = \eta$ and $\sigma_1^D = 0$ a.s.), together with the induction hypothesis for $i - 1$ yields

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta \left[\mathbb{I}_{\{\tau_{i-1}^D < \infty\}} \mathbf{E}_{\mathcal{P}_{\tau_{i-1}^D}^D} [f(\tau_{i-1}^D + \tilde{\sigma}_1^D, \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^D) \mathbb{I}_{\{\tilde{\sigma}_1^D < \infty\}}] \right] = \mathbb{E}_\zeta \left[\mathbb{I}_{\{\sigma_i < \infty\}} \mathbb{E}_{\chi(\mathcal{P}_{\sigma_{i-1}})} [f(\sigma_i, X)] \right].$$

But, from the description of the evolution of \mathcal{P} in terms of the geographical events followed by the instantaneous action of the structured genealogical process ξ , we see that the random variable $\chi(\mathcal{P}_{\sigma_{i-1}})$ is distributed precisely like \mathcal{P}_{σ_i} (if $\sigma_i < \infty$). Consequently,

$$\lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\sigma_i^D, \mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{\{\sigma_i^D < \infty\}}] = \mathbf{E}_\zeta [\mathbb{I}_{\{\sigma_i < \infty\}} f(\sigma_i, \mathcal{P}_{\sigma_i})].$$

The same technique applies to $(\tau_i^D, \mathcal{P}_{\tau_i^D}^D)$, where this time we use the strong Markov property at time σ_i^D and the following convergence result:

$$\mathbf{E}_\eta [f(t + \tau_1^D, \mathcal{P}_{\tau_1^D}^D) \mathbb{I}_{\{\tau_1^D < \infty\}}] \rightarrow \mathbf{E}_\eta [f(t + \sigma_2, \chi(Y)) \mathbb{I}_{\{\sigma_2 < \infty\}}]$$

uniformly in $(t, \eta) \in \mathbf{R}_+ \times \Pi_n$, where under \mathbf{P}_η , Y is a.s. equal to η .

□

Proof of Lemma 3.2. If an event occurs in the (random) interval $[\sigma_i^D, \tau_i^D)$, the first such event can be neither a Ψ -event since $\mathcal{P}_{\sigma_i^D}^D \in \Pi_n$, nor a Γ -event since \mathcal{P}^D would then undergo a 2-event before time τ_i^D , contradicting the definition of τ_i^D , so it must be an R_D -event. Consequently, if we write

$$\begin{aligned} \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \mid \sigma_i^D < \infty] &= \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t); \text{ nothing happens in } [\sigma_i^D, t] \mid \sigma_i^D < \infty] \\ &\quad + \mathbf{E}_\zeta [f(\mathcal{P}_t^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t); \text{ something occurs in } [\sigma_i^D, t] \mid \sigma_i^D < \infty], \end{aligned} \quad (24)$$

then the absolute value of the second term of the right-hand side of (24) is bounded by

$$\|f\| \mathbf{P}_\zeta [\sigma_i^D \leq t \text{ and an } R_D\text{-event occurs in } [\sigma_i^D, t] \mid \sigma_i^D < \infty] \leq \|f\| (1 - \exp(-t \max_\eta c_{R_D}(\eta))) \rightarrow 0,$$

where in the exponential the maximum is over $\eta \in \mathbf{P}_n^s$ and recall that $c_{R_D}(\eta)$ is the total rate at which R_D -events occur when the current value of \mathcal{P}^D is η .

The first term of (24) is equal to

$$\begin{aligned} \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t); \text{ nothing happens in } [\sigma_i^D, t] \mid \sigma_i^D < \infty] \\ = \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \mid \sigma_i^D < \infty] - \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t); \text{ something happens in } [\sigma_i^D, t] \mid \sigma_i^D < \infty] \end{aligned}$$

As before,

$$\mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t); \text{ something happens in } [\sigma_i^D, t] \mid \sigma_i^D < \infty] \leq \|f\| (1 - \exp(-t \max_\eta c_{R_D}(\eta))) \rightarrow 0$$

and furthermore

$$\mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{[\sigma_i^D, \tau_i^D)}(t) \mid \sigma_i^D < \infty] = \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{\{\sigma_i^D \leq t\}} \mid \sigma_i^D < \infty] - \mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i^D}^D) \mathbb{I}_{\{\tau_i^D \leq t\}} \mid \sigma_i^D < \infty]. \quad (25)$$

On the one hand, by Lemma 3.1 and the fact that $\mathbf{P}_\zeta [\sigma_i^D < \infty] \rightarrow \mathbb{P}_\zeta [\sigma_i < \infty] > 0$, the first term in (25) converges as D tends to infinity to

$$\mathbf{E}_\zeta [f(\mathcal{P}_{\sigma_i}) \mathbb{I}_{\{\sigma_i \leq t\}} \mid \sigma_i < \infty].$$

On the other hand, by the strong Markov property applied to \mathscr{P}^D at time σ_i^D , the second term in (25) is equal to

$$\mathbf{E}_\zeta [f(\mathscr{P}_{\sigma_i^D}^D) \mathbf{P}_{\mathscr{P}_{\sigma_i^D}^D} [\tilde{\tau}_1^D \leq t] \mid \sigma_i^D < \infty].$$

The function $\eta \mapsto \mathbf{P}_\eta [\tilde{\tau}_1^D \leq t]$ converges uniformly in $\eta \in \Pi_n$ to $\eta \mapsto \mathbb{P}_\eta [\tilde{\sigma}_2 \leq t]$, so by Lemma 3.1 we obtain

$$\begin{aligned} \lim_{D \rightarrow \infty} \mathbf{E}_\zeta [f(\mathscr{P}_{\sigma_i^D}^D) \mathbf{P}_{\mathscr{P}_{\sigma_i^D}^D} [\tilde{\tau}_1^D \leq t] \mid \sigma_i^D < \infty] &= \mathbb{E}_\zeta [f(\mathscr{P}_{\sigma_i}) \mathbb{P}_{\mathscr{P}_{\sigma_i}} [\tilde{\sigma}_2 \leq t] \mid \sigma_i < \infty] \\ &= \mathbb{E}_\zeta [f(\mathscr{P}_{\sigma_i}) \mathbb{I}_{\{\sigma_{i+1} \leq t\}} \mid \sigma_i < \infty] \end{aligned}$$

by the strong Markov property applied this time to \mathscr{P} at time σ_i . Combining the above, we obtain the desired result. □

The results obtained in this section are similar in spirit to perturbation theorems such as Theorem 1.7.6 in Ethier and Kurtz [1986]. Indeed, in our case the existence of a projector p corresponding to Ψ and the convergence of the semigroup required (see condition (7.12) and Remark 1.7.5 in Ethier and Kurtz, 1986, p.39) easily follows from Lemma 2.1 and the finiteness of \mathbb{P}_n^s . Furthermore, the existence of a limit for $r_D^{-1}G^D$ is obvious from the form of G^D . However, condition (7.17) of Theorem 1.7.6 requires the existence of a subspace E of functions on \mathbb{P}_n^s such that for every $f \in E$, there exist functions g, f_1, f_2, \dots satisfying

$$\|f - f_D\| \rightarrow 0 \quad \text{and} \quad \|g - G^D f_D\| \rightarrow 0 \quad \text{as } D \rightarrow \infty.$$

The condition on $(f_D)_{D \geq 1}$ and the finiteness of \mathbb{P}_n^s yield

$$G^D f_D = r_D \Psi f + o(r_D),$$

implying that a corresponding function g can exist only if $\Psi f \equiv 0$. Although $\Psi f(\zeta) = 0$ if $\zeta \in \Pi_n$, this condition would also require that $f(\zeta) = 0$ whenever $\zeta \notin \Pi_n$. Hence, to fit into Ethier and Kurtz' framework, an obvious candidate for E would be

$$E = \{f : f(\zeta) = 0 \text{ for all } \zeta \in \mathbb{P}_n^s \setminus \Pi_n\},$$

where we then define a bounded linear transformation $\varphi_n : \mathbb{P}_n^s \rightarrow \Pi_n$ such that $\varphi_n(\eta) = \eta$ for every $\eta \in \Pi_n$. We may then apply Theorem 1.7.6 of Ethier and Kurtz [1986] and obtain convergence of the semigroup corresponding to (or equivalently here of the finite dimensional distributions of) $\varphi_n(\mathscr{P}^D)$ to that of \mathscr{P} . However, it is unclear how to define φ_n on the set $\mathbb{P}_n^s \setminus \Pi_n$, that is to specify how to project \mathbb{P}_n^s down onto its subset Π_n , in such a way that the operator $\{(f \circ \varphi_n, (\Gamma^n \circ p)(f \circ \varphi_n)), f : \mathbb{P}_n^s \rightarrow \mathbb{P}_n^s\}$ generates a Markov process. Unfortunately, unless this condition is satisfied, Theorem 1.7.6 cannot be used to deduce the convergence result given in our Theorem 1.1.

3.3 Tightness

The convergence of the finite-dimensional distributions relies on the fact that the time required for the process to re-enter Π_n following a geographical collision is vanishingly small as D tends to

infinity. On the other hand, multiple changes to the configuration of the genealogy can occur during this short period with high probability, so that the conditions for \mathscr{P}^D to converge as processes in $D_{\mathbb{P}_n^s}([0, \infty))$ are much more delicate.

Recall the definition of the stopping times σ_i^D and τ_i^D given in (8). Suppose that the probability that a 2-event results in a configuration not in Π_n vanishes as $D \rightarrow 0$, or equivalently that

$$\lim_{D \rightarrow \infty} \mathbf{P}_\zeta[\tau_1^D < \infty, \mathscr{P}_{\tau_1^D}^D \notin \Pi_2] = 0, \quad (26)$$

where $\zeta = (\{\{1\}\}, \{\{2\}\})$ and the equivalence stems from the consistency equations (4). Then, we easily see that the first time τ after σ_1^D such that $\mathscr{P}^D \notin \Pi_n$ converges to $+\infty$ in probability. Since

$$G^D f(\eta) = \Gamma f(\eta) + o(1) \quad \text{as } D \rightarrow \infty$$

if $\eta \in \Pi_n$, we readily obtain that for any $a > 0$, the sequence of processes $(\{\mathscr{P}_t^D, t \geq a\}, D \geq 1)$ is tight (recall that σ_1^D converges in probability towards 0). Let us now show that if condition (26) does not hold, the sequence \mathscr{P}^D is not tight. It will be easier to work with a metric on \mathbb{P}_n^s , the associated topology still being the discrete topology.

Proposition 3.2. *Assume that (26) does not hold. Let d be a discrete metric on \mathbb{P}_n^s , and suppose that $\zeta \in \mathbb{P}_n^s$ is such that $\mathbb{P}_\zeta[\sigma_2 < \infty] > 0$. Then the sequence of processes \mathscr{P}^D under \mathbf{P}_ζ is not tight in $D_{\mathbb{P}_n^s}([0, \infty))$ endowed with the Skorokhod topology corresponding to d .*

Proof. First, recall the definition of the modulus of continuity w' given in Ethier and Kurtz [1986], p.122: for $X \in D_{\mathbb{P}_n^s}([0, \infty))$, $\delta > 0$ and $T > 0$,

$$w'(X, \delta, T) \equiv \inf_{\{t_i\}} \max_i \sup_{s, t \in [t_{i-1}, t_i]} d(X_s, X_t), \quad (27)$$

where the infimum is over all finite sets of times of the form $0 = t_0 < t_1 < \dots < t_{n-1} < T \leq t_n$ such that $\min_{1 \leq i \leq n} (t_i - t_{i-1}) > \delta$ and $n \geq 1$.

Suppose that the sequence \mathscr{P}^D is tight. \mathbb{P}_n^s is a finite set, so the discrete topology on (\mathbb{P}_n^s, d) turns it into a complete and separable metric space, therefore \mathscr{P}^D is also relatively compact. By Corollary 3.7.4 of Ethier and Kurtz [1986], this implies that for every $\gamma \in \mathbb{P}_n^s$, all $\eta > 0$ and $T > 0$, there exists $\delta > 0$ such that

$$\limsup_{D \rightarrow \infty} \mathbf{P}_\gamma[w'(\mathscr{P}^D, \delta, T) \geq \eta] \leq \eta. \quad (28)$$

Besides, the finiteness of \mathbb{P}_n^s guarantees the existence of $\epsilon > 0$ such that, if $\gamma \neq \gamma' \in \mathbb{P}_n^s$, then $d(\gamma, \gamma') > \epsilon$.

Let $T = 1$, $\eta \in (0, \epsilon)$ and $\delta \in (0, 1)$. We have

$$\begin{aligned} \mathbf{P}_\zeta[w'(\mathscr{P}^D, \delta, 1) \geq \eta] &= \mathbf{P}_\zeta\left[w'(\mathscr{P}^D, \delta, 1) \geq \eta \mid \tau_1^D \geq \frac{1}{2}\right] \mathbf{P}_\zeta\left[\tau_1^D \geq \frac{1}{2}\right] \\ &\quad + \mathbf{P}_\zeta\left[w'(\mathscr{P}^D, \delta, 1) \geq \eta \mid \tau_1^D < \frac{1}{2}\right] \mathbf{P}_\zeta\left[\tau_1^D < \frac{1}{2}\right]. \end{aligned} \quad (29)$$

On the one hand, σ_1^D converges to 0 in probability and $\tau_1^D \Rightarrow \sigma_2$, so by Slutsky's lemma (see Lemma 2.8 in van der Vaart, 1998) $\tau_1^D - \sigma_1^D \Rightarrow \sigma_2$, which is an exponential random variable with positive

parameter, so we have

$$\begin{aligned}
\mathbf{P}_\zeta \left[\tau_1^D < \frac{1}{2} \right] &\geq \mathbf{P}_\zeta \left[\sigma_1^D < \frac{1}{3} \text{ and } \tau_1^D - \sigma_1^D \leq \frac{1}{6} \right] \\
&= \mathbf{P}_\zeta \left[\tau_1^D - \sigma_1^D \leq \frac{1}{6} \right] - \mathbf{P}_\zeta \left[\sigma_1^D \geq \frac{1}{3} \text{ and } \tau_1^D - \sigma_1^D \leq \frac{1}{6} \right] \\
&\rightarrow \mathbb{P}_\zeta \left[\sigma_2 \leq \frac{1}{6} \right] \equiv C > 0
\end{aligned}$$

since the last term in the second line vanishes by the convergence in probability of σ_1^D to 0. On the other hand,

$$\begin{aligned}
\mathbf{P}_\zeta \left[w'(\mathcal{P}^D, \delta, 1) \geq \eta \mid \tau_1^D < \frac{1}{2} \right] &\geq \mathbf{P}_\zeta \left[w'(\mathcal{P}^D, \delta, 1) \geq \eta \mid \tau_1^D < \frac{1}{2}, \sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \\
&\quad \times \mathbf{P}_\zeta \left[\sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \mid \tau_1^D < \frac{1}{2} \right]. \tag{30}
\end{aligned}$$

By the convergence in probability of σ_1^D to 0, uniformly in $\eta \in \mathbb{P}_n^s$, and the strong Markov property applied to \mathcal{P}^D at time τ_1^D , we obtain that $\sigma_2^D - \tau_1^D$ converges in probability to 0. Furthermore, on the event that no R_D -events occurred between the times σ_1^D and τ_1^D (the probability of which is growing to one), τ_1^D is the epoch of the first event after σ_1^D and $\mathcal{P}_{\tau_1^D}^D$ its outcome so, by the strong Markov property, τ_1^D and $\mathcal{P}_{\tau_1^D}^D$ are independent conditionally on $\mathcal{F}_{\sigma_1^D}^D$. Since (26) does not hold, we can write

$$\liminf_{D \rightarrow \infty} \mathbf{P}_\zeta \left[\sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \mid \tau_1^D < \frac{1}{2} \right] \geq \liminf_{D \rightarrow \infty} \mathbf{P}_\zeta \left[\mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] > 0.$$

Now, if $\tau_1^D < \frac{1}{2}$, $\mathcal{P}_{\tau_1^D}^D \notin \Pi_n$ and $\sigma_2^D - \tau_1^D < \frac{\delta}{2}$, then by definition of ϵ ,

$$d(\mathcal{P}_{\tau_1^D}^D, \mathcal{P}_{\tau_1^D}^D) > \epsilon \quad \text{and} \quad d(\mathcal{P}_{\tau_1^D}^D, \mathcal{P}_{\sigma_2^D}^D) > \epsilon,$$

and by assumption $\sigma_2^D - \tau_1^D < \frac{\delta}{2}$, so $w'(\mathcal{P}^D, \delta, 1) \geq \epsilon \geq \eta$. Consequently,

$$\liminf_{D \rightarrow \infty} \mathbf{P}_\zeta \left[w'(\mathcal{P}^D, \delta, 1) \geq \eta \mid \tau_1^D < \frac{1}{2} \right] > 0.$$

Therefore, we see from (29) that, for all $\delta \in (0, 1)$,

$$\liminf_{D \rightarrow \infty} \mathbf{P}_\zeta \left[w'(\mathcal{P}^D, \delta, 1) \geq \eta \right] > C' > \eta$$

for any $\eta \in (0, \epsilon \wedge C')$. This yields a contradiction with (28). \square

>From the last proof, we see that what prevents the sequence of structured genealogical processes from being tight is that at each geographical collision, at least two jumps accumulate: the geographical collision itself and one or more transitions generated by ξ to bring \mathcal{P}^D back into Π_n .

Yet the unstructured genealogical process, which is not a Markov process for $D < \infty$, is not modified by movements of blocks. Thus, if the number of jumps needed by \mathcal{P}^D to re-enter Π_n after a geographical collision were at most one with a probability growing to 1, we would expect tightness to hold for $\mathcal{P}^{D,u}$ (recall that ζ^u denotes the unstructured partition generated by ζ). The next proposition in fact gives an equivalence between the behaviour of the latter probability and tightness of $\{\mathcal{P}^{D,u}, D \geq 1\}$.

Proposition 3.3. For each $D \in \mathbb{N}$, let U_1^D be the random time defined by

$$U_1^D \equiv \inf \{t > 0 : \mathcal{P}_{t-}^D \neq \mathcal{P}_t^D\},$$

with the convention that $\inf \emptyset = +\infty$. Note that, if $\mathcal{P}_0^D \notin \Pi_n$, then $U_1^D \leq \sigma_1^D$. Let also $\chi(\Pi_n)$ denote the image of Π_n by the first geographical collision (when it exists), that is

$$\chi(\Pi_n) \equiv \{\gamma \in \mathbb{P}_n^s : \exists \zeta \in \Pi_n, \mathbb{P}[\chi(\zeta) = \gamma] > 0\}.$$

Suppose that for all $\gamma \notin \Pi_n$, $\mathbf{P}[\gamma^u \neq \gamma^u] > 0$ (meaning that the process ξ started at γ has at least one coalescence with positive probability).

Then the following are equivalent:

(i) For all $\gamma \in \chi(\Pi_n) \setminus \Pi_n$, $\lim_{D \rightarrow \infty} \mathbf{P}_\gamma[U_1^D = \sigma_1^D] = 1$.

(ii) For all $\zeta \in \mathbb{P}_n^s$ and $a > 0$, the sequence of $D_{\mathbb{P}_n}([a, \infty))$ -valued random variables $\mathcal{P}^{D,u}$, started at ζ^u at time 0, is tight.

Furthermore, if $\zeta \in \Pi_n \cup \chi(\Pi_n)$, then condition (i) is equivalent to the tightness in $D_{\mathbb{P}_n}([0, \infty))$ of $\mathcal{P}^{D,u}$ started at ζ^u .

As a consequence of Theorem 1.1, if conditions (i) and (ii) hold, then for all $\zeta \in \mathbb{P}_n^s$ and $a > 0$, the law of $(\mathcal{P}_t^{D,u}, t \geq a)$ under \mathbf{P}_ζ converges to the law under \mathbb{P}_{ζ^u} of $(\mathcal{P}_t^u, t \geq a)$. Furthermore, if $\zeta \in \Pi_n$, then the convergence holds for $a = 0$.

Remark 3.1. Assuming that for all $\gamma \notin \Pi_n$, $\mathbf{P}[\gamma^u \neq \gamma^u] > 0$ is actually not required, but not supposing it makes the proof unnecessarily more involved.

Proof. Once again we work with a metric d on \mathbb{P}_n , so that $D_{\mathbb{P}_n}([0, \infty))$ is a complete and separable metric space and the sequence $(\mathcal{P}^{D,u})_{D \geq 1}$ is tight if and only if it is relatively compact. We call $\epsilon > 0$ the minimum distance between two different partitions. Let us first show that if condition (i) is not fulfilled, then neither is condition (ii). The following proof is highly reminiscent to the proof of Proposition 3.2, so let us adopt directly the same notation. In particular, we work with $T = 1$ and ζ such that $\mathbb{P}_\zeta[\sigma_2 < \infty] > 0$.

For each $a > 0$, let us write w'_a the modulus of continuity of a process corresponding to times $t \geq a$, defined as in (27) with the condition on the finite sets $\{t_i\}$ replaced by $a = t_0 < \dots < T \leq t_n$. Fix $a \in (0, 1/3)$, and let $\eta \in (0, \epsilon)$ and $\delta \in (0, 1)$. The same calculation as in the proof of Proposition 3.2 holds by replacing the event $\{w'(\mathcal{P}^D, \delta, 1) \geq \eta\}$ by $\{w'_a(\mathcal{P}^{D,u}, \delta, 1) \geq \eta\}$ and $\mathbf{P}_\zeta[\tau_1^D < 1/2]$ by $\mathbf{P}_\zeta[1/3 \leq \tau_1^D < 1/2]$. Hence, by (30) and the argument directly following it, we just need to prove that

$$\mathbf{P}_\zeta \left[w'_a(\mathcal{P}^{D,u}, \delta, 1) \geq \eta \mid \frac{1}{3} \leq \tau_1^D < \frac{1}{2}, \sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \quad (31)$$

is bounded below by a positive constant for D large enough. If we define V_1^D by

$$V_1^D \equiv \inf \{t > \tau_1^D : \mathcal{P}_{t-}^D \neq \mathcal{P}_t^D\},$$

then the expression in (31) is equal to

$$\begin{aligned} & \mathbf{P}_\zeta \left[w'_a(\mathcal{P}^{D,u}, \delta, 1) \geq \eta ; \mathcal{P}_{\tau_1^D}^{D,u} = \mathcal{P}_{V_1^D}^{D,u} \text{ or } \mathcal{P}_{V_1^D}^{D,u} = \mathcal{P}_{\sigma_2^D}^{D,u} \mid \frac{1}{3} \leq \tau_1^D < \frac{1}{2}, \sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \\ & + \mathbf{P}_\zeta \left[w'_a(\mathcal{P}^{D,u}, \delta, 1) \geq \eta ; \mathcal{P}_{\tau_1^D}^{D,u} \neq \mathcal{P}_{V_1^D}^{D,u} ; \mathcal{P}_{V_1^D}^{D,u} \neq \mathcal{P}_{\sigma_2^D}^{D,u} \mid \frac{1}{3} \leq \tau_1^D < \frac{1}{2}, \sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \end{aligned} \quad (32)$$

The first term in (32) is nonnegative, and if we are in the conditions given by the second term, then

$$d(\mathcal{P}_{\tau_1^D}^{D,u}, \mathcal{P}_{V_1^D}^{D,u}) \geq \epsilon, \quad d(\mathcal{P}_{V_1^D}^{D,u}, \mathcal{P}_{\sigma_2^D}^{D,u}) \geq \epsilon \quad \text{and} \quad \sigma_2^D - \tau_1^D < \frac{\delta}{2},$$

implying that $w'_a(\mathcal{P}^D, \delta, 1) \geq \epsilon > \eta$. Therefore, the second term in (32) is equal to

$$\begin{aligned} & \mathbf{P}_\zeta \left[\mathcal{P}_{\tau_1^D}^{D,u} \neq \mathcal{P}_{V_1^D}^{D,u} ; \mathcal{P}_{V_1^D}^{D,u} \neq \mathcal{P}_{\sigma_2^D}^{D,u} \mid \frac{1}{3} \leq \tau_1^D < \frac{1}{2}, \sigma_2^D - \tau_1^D < \frac{\delta}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \\ &= \mathbf{P}_\zeta \left[\mathcal{P}_{\tau_1^D}^{D,u} \neq \mathcal{P}_{V_1^D}^{D,u} ; \mathcal{P}_{V_1^D}^{D,u} \neq \mathcal{P}_{\sigma_2^D}^{D,u} \mid \frac{1}{3} \leq \tau_1^D < \frac{1}{2}, \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] (1 + o(1)). \end{aligned}$$

Now, by the strong Markov property applied to \mathcal{P}^D at time τ_1^D , we have

$$\begin{aligned} & \mathbf{P}_\zeta \left[\mathcal{P}_{\tau_1^D}^{D,u} \neq \mathcal{P}_{V_1^D}^{D,u} ; \mathcal{P}_{V_1^D}^{D,u} \neq \mathcal{P}_{\sigma_2^D}^{D,u} ; \frac{1}{3} \leq \tau_1^D < \frac{1}{2} ; \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] \tag{33} \\ &= \mathbf{E}_\zeta \left[\mathbf{P}_{\mathcal{P}_{\tau_1^D}^D} \left[\mathcal{P}_{\tau_1^D}^{D,u} \neq \tilde{\mathcal{P}}_{\tilde{U}_1^D}^{D,u} ; \tilde{\mathcal{P}}_{\tilde{U}_1^D}^{D,u} \neq \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^{D,u}, \right] \mathbb{I}_{\{1/3 \leq \tau_1^D < 1/2\}} \mathbb{I}_{\{\mathcal{P}_{\tau_1^D}^D \notin \Pi_n\}} \right]. \end{aligned}$$

Since we assumed that condition (i) did not hold, there exists $\eta \in \chi(\Pi_n) \setminus \Pi_n$ such that $\mathbf{P}_\eta[\tilde{U}_1^D < \tilde{\sigma}_1^D] \geq C_1$ for a constant $C_1 > 0$ and D large enough. As $\eta \in \chi(\Pi_n)$, we can choose ζ such that $\mathbb{P}[\chi(\underline{\zeta}) = \eta] > 0$ (and $\mathbb{P}_\zeta[\sigma_2 < \infty] > 0$). Now, since we assumed that $\mathbf{P}[\underline{\gamma}^u \neq \gamma^u] > 0$ for all $\gamma \notin \Pi_n$, the probability that a coalescence event occurs before a scattering event in the structured genealogical process ξ started at any value not in Π_n is greater than a constant C_2 . Therefore, we can write

$$\mathbf{P}_\eta[\eta^u \neq \tilde{\mathcal{P}}_{\tilde{U}_1^D}^{D,u} ; \tilde{\mathcal{P}}_{\tilde{U}_1^D}^{D,u} \neq \tilde{\mathcal{P}}_{\tilde{\sigma}_1^D}^{D,u}] > C'_1$$

for a constant $C'_1 > 0$. By the distribution of the epochs of the geographical collisions, the convergence in law of $(\tau_1^D, \mathcal{P}_{\tau_1^D}^D)$ to $(\sigma_2, \chi(\underline{\zeta}))$ (c.f. Lemma 3.1) and the fact that $\eta \notin \Pi_n$, we have for ζ chosen as above

$$\mathbf{P}_\zeta \left[\mathcal{P}_{\tau_1^D}^D = \eta ; \frac{1}{3} \leq \tau_1^D < \frac{1}{2} ; \mathcal{P}_{\tau_1^D}^D \notin \Pi_n \right] > C_3$$

for a constant $C_3 > 0$ and D large enough, so the expression in the right-hand side of (33) is bounded below by $C'_1 C_3$, and so is (31). Hence, (ii) \Rightarrow (i).

Suppose now that condition (i) is fulfilled. Condition (a) of Corollary 3.7.4 in Ethier and Kurtz [1986] trivially holds, so we only need to check condition (b) on the modulus of continuity. Fix $\zeta \in \mathbb{P}_n^s$ and $a > 0$, and let $T > a$ and $\eta > 0$. Firstly, by the convergence in probability of σ_1^D to 0, there exists $D_1 \in \mathbb{N}$ such that for all $D \geq D_1$, $\mathbf{P}_\zeta[\sigma_1^D \geq a] < \frac{\eta}{5}$. Secondly, we have

$$\mathbf{P}_\zeta \left[\text{at least one } R_D\text{-event in } [0, T] \right] \leq 1 - \exp \left(- T \max_{\xi \in \mathbb{P}_n^s} c_{R_D}(\xi) \right) \rightarrow 0, \quad D \rightarrow \infty,$$

so there exists $D_2 \geq 1$ such that for all $D \geq D_2$, the previous quantity is less than $\frac{\eta}{5}$. Thirdly, by the same argument as in the beginning of the proof of Theorem 1.1, there exists $N \in \mathbb{N}$ such that $\mathbb{P}_\zeta[\sigma_N \leq T] < \frac{\eta}{5}$. Hence, by Lemma 3.1, there exists $D_3 \geq 1$ such that for all $D \geq D_3$, $\mathbf{P}_\zeta[\sigma_N^D \leq T] < \frac{\eta}{5}$.

Consequently, we can write for each $D \geq \max\{D_1, D_2, D_3\}$ and all $\delta > 0$

$$\begin{aligned} \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta] &\leq \mathbf{P}_\zeta[\sigma_1^D \geq a] + \mathbf{P}_\zeta[\sigma_N^D \leq T] + \mathbf{P}_\zeta[\text{at least one } R_D\text{-event in } [0, T]] \\ &\quad + \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta; \sigma_1^D < a; \sigma_N^D > T; \text{no } R_D\text{-events in } [0, T]] \\ &< \frac{3\eta}{5} + \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta; \sigma_1^D < a; \sigma_N^D > T; \text{no } R_D\text{-events in } [0, T]]. \end{aligned}$$

Furthermore, there exists $\delta > 0$ such that $\mathbb{P}_\gamma[\sigma_2 < 3\delta] < \frac{\eta}{5N}$ for all $\gamma \in \Pi_n$. Now, for all $i \in \{1, \dots, N\}$, by the strong Markov property applied to \mathscr{P}^D at time τ_{i-1}^D and the convergence of $\mathbf{P}_\gamma[\tau_1^D < 3\delta]$ to $\mathbb{P}_\gamma[\sigma_2 < 3\delta]$, uniformly in γ , we have

$$\mathbf{P}_\zeta[\tau_{i-1}^D < \infty; \tau_i^D - \tau_{i-1}^D < 3\delta] = \mathbf{E}_\zeta[\mathbb{I}_{\{\tau_{i-1}^D < \infty\}} \mathbf{P}_{\mathscr{P}_{\tau_{i-1}^D}^D}[\tilde{\tau}_1^D < 3\delta]] \leq \frac{\eta}{5N}$$

for D large enough. Therefore,

$$\begin{aligned} \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta; \sigma_1^D < a; \sigma_N^D \leq T; \text{no } R_D\text{-event in } [0, T]] \\ \leq \sum_{i=1}^N \mathbf{P}_\zeta[\tau_{i-1}^D < \infty; \tau_i^D - \tau_{i-1}^D < 3\delta] \\ + \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta; \sigma_1^D < a; \sigma_N^D \leq T; \text{no } R_D\text{-event in } [0, T]; \tau_i^D - \tau_{i-1}^D \geq 3\delta \text{ for all } i \leq N \\ \text{s.t. } \tau_{i-1}^D < \infty] \end{aligned} \quad (34)$$

and the first sum is less than $\frac{\eta}{5}$. To finish, let V_i^D denote the epoch of the next event after τ_i^D if $\mathscr{P}_{\tau_i^D}^D \notin \Pi_n$ (if it exists, $V_i^D = +\infty$ otherwise), and set $V_i^D = \tau_i^D = \sigma_{i+1}^D$ if $\mathscr{P}_{\tau_i^D}^D \in \Pi_n$. Since we assume that condition (i) holds, for all $i \in \{1, \dots, N\}$ we have by the strong Markov property applied at time τ_i^D and the fact that the distribution of $\mathscr{P}_{\tau_i^D}^D$ concentrates on $\chi(\Pi_n)$ as D grows to infinity by Lemma 3.1,

$$\mathbf{P}_\zeta[\tau_i^D < \infty; V_i^D < \sigma_{i+1}^D] \rightarrow 0, \quad D \rightarrow \infty,$$

so the last term in (34) is less than

$$\begin{aligned} \sum_{i=1}^N \mathbf{P}_\zeta[\tau_i^D < \infty; V_i^D < \sigma_{i+1}^D] \\ + \mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta; \sigma_1^D < a; \sigma_N^D > T; \text{no } R_D\text{-event in } [0, T]; \tau_i^D - \tau_{i-1}^D \geq 3\delta \text{ and} \\ V_i^D = \sigma_{i+1}^D \text{ for all } i \leq N \text{ s.t. } \tau_{i-1}^D < \infty], \end{aligned}$$

where the first sum is less than $\frac{\eta}{5}$ for D large enough. But on that last event, σ_1^D is less than a and no R_D -events occur so τ_1^D is the epoch of the event directly after σ_1^D , then all geographical collisions are at least 3δ away from each other and the σ_i^D 's are the only times in between at which an event occurs, so necessarily $w'_a(\mathscr{P}^D, \delta, T) = 0$. Assembling all the pieces, we obtain that

$$\mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta] < \eta,$$

completing the proof of (i) \Rightarrow (ii).

If $\zeta \in \chi(\Pi_n) \cup \Pi_n$, then we only need to show that (i) implies the tightness of $(\mathscr{P}^{D,u})_{D \geq 1}$ on $[0, \infty)$. Let us directly use the same notation as in the last proof. In the last paragraph, we proved that with

a high probability, there is no accumulations of jumps between the random time τ_1^D and T . Also, we can make $\mathbf{P}_\zeta[\tau_1^D \leq 2a]$ as small as we want by adjusting a and taking D large enough, and the probability that at least one R_D -event occurs is vanishingly small, so we are left with proving that, if δ is such that $\mathbf{P}_\zeta[w'_a(\mathscr{P}^{D,u}, \delta, T) \geq \eta] < \eta$, $\tau_1^D > 2a$ and no R_D -events occur between 0 and T , then $\mathbf{P}_\zeta[w'(\mathscr{P}^{D,u}, \delta', a) \geq \eta] < \eta$, for some $\delta' \in (0, \delta)$. If $\zeta \in \Pi_n$, $\tau_1^D > 2a$ and no R_D -events occur, then τ_1^D is the epoch of the first event occurring to \mathscr{P}^D so $w'(\mathscr{P}^{D,u}, \delta', a) = 0$ for all $\delta' \in (0, \delta \wedge a)$. If $\zeta \in \chi(\Pi_n)$ and the other conditions hold, then by condition (i) we have

$$\mathbf{P}_\zeta[U_1^D = \sigma_1^D] \rightarrow 1, \quad D \rightarrow \infty,$$

and furthermore $\mathbf{P}_\zeta[\sigma_1^D < a] \rightarrow 1$, so with a probability tending to one as D grows to infinity, one event occurs between 0 and a , then nothing happens between a and $2a$ (there is no R_D -events, so the next event after σ_1^D must occur at time $\tau_1^D > 2a$) and the condition on the modulus of continuity is fulfilled after time a so, for any $\delta' \in (0, \delta \wedge a)$, we do have

$$\mathbf{P}_\zeta[w'(\mathscr{P}^{D,u}, \delta', a) \geq \eta] < \eta.$$

This completes the proof of the case $\zeta \in \chi(\Pi_n) \cup \Pi_n$.

Now, by Theorem 3.7.8 in Ethier and Kurtz [1986], the two ingredients to obtain the convergence of the processes $(\mathscr{P}^D)_{D \geq 1}$ are tightness, given by the first part of Proposition 3.3 for any $a > 0$, and convergence of the finite-dimensional distributions, given by Theorem 1.1 and the bijective correspondence between Π_n and \mathbb{P}_n . For $\zeta \in \Pi_n$ and $a = 0$, tightness still holds by virtue of the last paragraph, and an easy modification (namely allowing $t = 0$ in the proof of the convergence of the one-dimensional distributions) of the proof of Theorem 1.1 in that case, where $\underline{\zeta} = \zeta$ and $\sigma_1^D = 0$ a.s., gives the convergence of the finite-dimensional distributions of \mathscr{P}^D , including at time $t = 0$. \square

Let us briefly comment on the condition $\mathbf{P}_\zeta[U_1^D = \sigma_1^D] \rightarrow 1$. If the fast within-deme coalescence is given by a Ξ -coalescent (including Kingman's coalescent) occurring in one deme at a time, the condition is fulfilled if and only if at most two lineages can be collected into the same deme during a single event. Indeed, in that case the next step of the genealogical process is either to scatter these two lineages into two different demes or to merge them into one lineage, the outcome of which is always in Π_n . If more than 2 lineages are gathered in the same deme and do not merge during the geographical collision, then with a positive probability only two of them are involved in the next genealogical event and at least two rapid steps are needed for \mathscr{P}^D to re-enter Π_n . The same conclusion holds if two pairs of lineages are gathered in two demes (meaning 2 lineages per deme), since the genealogical process acts in one deme at a time by assumption.

4 Collapse of structured genealogical processes

The next proposition states that the only reasonable structured genealogies which collapse to an unstructured genealogy (given by a Ξ -coalescent) when the number of demes tends to infinity are the genealogies that we have described before, subject to certain conditions.

Note that if we want the lineages to be exchangeable in the limit, the limiting process needs to take its values in $\bigcup_{n \geq 1} \Pi_n$. Indeed, since the rates of intra- and inter-demes mergers greatly differ, we should observe only inter-demes events on the slow time scale. This requires that each deme contains at most one lineage at any given time in the limit.

Proposition 4.1. Let $(\mathcal{P}_t^D, t \geq 0)_{D \geq 1}$ be a sequence of structured genealogical processes with values in $\bigcup_{n \geq 1} \mathcal{P}_n^s$. Then the following are equivalent

1. There exists a sequence r_D such that $r_D \rightarrow +\infty$ as $D \rightarrow \infty$ and two structured genealogical processes, $(\xi_t, t \geq 0)$ (resp. $(\mathcal{P}_t, t \geq 0)$) with values in $\bigcup_{n \geq 1} \mathcal{P}_n^s$ (resp. $\bigcup_{n \geq 1} \Pi_n$) satisfying
 - (a) for each $n \in \mathbb{N}$, the sequence of structured genealogical processes $(\mathcal{P}_{r_D^{-1}t}^D, t \geq 0)_{D \geq 1}$ on the fast time scale, with initial value in \mathcal{P}_n^s , converges to ξ as a process in $D_{\mathcal{P}_n^s}[0, \infty)$. In addition, ξ is consistent in the sense of Lemma 2.2;
 - (b) the sequence $(\mathcal{P}_t^D, t \geq 1)_{D \geq 1}$ on the slow time scale converges towards \mathcal{P} in that the finite-dimensional distributions (except possibly at time 0) converge as in Theorem 1.1 for every sample size n ;
 - (c) there exists a Ξ -coalescent $(R_t, t \geq 1)$ such that for all $n \geq 1$, the unstructured genealogical process \mathcal{P}^u induced by $\mathcal{P}|_{\Pi_n}$ has the law of the restriction of R to \mathcal{P}_n .
2. The rates associated to \mathcal{P}^D satisfy conditions (1), (2) and (3) of Section 3.1, and condition (i) of Lemma 2.2 holds.

We shall see in the proof that the consistency of ξ is a key ingredient to obtain the desired equivalence. In fact, if we did not impose it, it would certainly be possible to construct particular examples in which the unstructured genealogy on the slow time scale is also a Ξ -coalescent, but the genealogies within a deme are not consistent. We would need to impose ‘good’ values for the corresponding rates. We rather chose here to emphasize more biologically relevant models, for which the within-deme genealogical process is also consistent and which can be described as part of an entire class of models rather than special cases.

Proof. The implication $2 \Rightarrow 1$ is a consequence of Theorem 1.1, Proposition 3.1 and Proposition 2.1. Let us prove that $1 \Rightarrow 2$. From the definition of a structured genealogical process, blocks can only move and coalesce. Furthermore \mathcal{P}^D stays in \mathcal{P}_n^s whenever its initial value lies in this set, so we just need to fix $n \geq 0$ and look at the corresponding rates of scattering, gathering and coalescence. From the description of the limiting processes ξ and \mathcal{P} , the rates of \mathcal{P}^D must be of the form

$$r_D \rho_D^{(1)}(\eta|\zeta) + \rho_D^{(2)}(\eta|\zeta) + o(1),$$

where for $i \in \{1, 2\}$, $\rho_D^{(i)}(\eta|\zeta) \rightarrow \rho^{(i)}(\eta|\zeta)$ as D tends to infinity. (To simplify notation, we shall write $\rho_D^{(i)}(\eta|\zeta) \equiv \rho^{(i)}(\eta|\zeta)$.) Thus, $\rho^{(i)}(\eta|\zeta)$ are the rates associated to the generator Ψ of the process ξ . Let us check that all cited conditions necessarily hold:

- If $\zeta \rightarrow \eta$ is a 1-event, then by adding an $(n + 1)$ -st individual in one of the existing blocks (therefore changing the sizes of the blocks but not their number), we see that the consistency of ξ imposes that the part of the rate corresponding to the fast time scale depends neither on n , nor on the sizes of the blocks. By exchangeability of the demes, this rate is thus characterized by the number of lineages present in each deme before and after the transition, the order of these numbers being irrelevant. Therefore, condition (1) holds. By Lemma 2.2, the consistency of ξ implies that condition (i) of Lemma 2.2 is also satisfied.

- Once again by consistency of ξ , the rate of a 2-event must be of order 1. Indeed, it may otherwise lead to an additional 1-event for the restriction of the process with the $(n + 1)$ -st lineage (if this additional lineage lands in a non-empty deme or in the same deme as another moving lineage coming from a different subpopulation, and the other dispersing lineages land in different demes), or involve at least two lineages alone in their demes on the fast time scale. If such an event was allowed, then by exchangeability of the islands the fast dynamic could act on a structured partition in Π_n and merge two lineages starting from different demes. Again by exchangeability, any pair of lineages could merge on the fast time scale and so the outcome of ξ would be a single lineage with probability one, a trivial situation which is of no interest here. Now, since we want to keep exchangeability of the lineages in the unstructured genealogy (on the slow time scale), the rates of 2-events should depend only on the number of lineages and their geographical distribution (and possibly on n). But if $\zeta \in \Pi_n$, all lineages are in different demes, so the corresponding rates are necessarily of the form given in condition (2). If the rates were to depend on n , then as the rates of the fast genealogical process which follows directly (for D large enough, as in the proof of Theorem 1.1) are independent of n , the overall transition from $\eta \in \Pi_n$ to the value of \mathcal{P}^D when it reenters Π_n would eventually give different rates for \mathcal{P} acting on Π_n and for the restriction to Π_n of \mathcal{P} acting on Π_{n+1} (recall the convergence of τ_{i-1}^D and σ_i^D towards σ_i to see that the transitions of \mathcal{P} actually can be described as in Section 3.2). This would contradict the fact that the process \mathcal{P}^u corresponds to a Ξ -coalescent. Finally, we obtain that condition (2) must hold.
- The last argument imposes also that geographical collisions involving k lineages occur at a rate which is the sum of all corresponding geographical events involving $k + 1$ lineages, which is exactly writing the consistency equations (4) of condition (3).

Finally, we obtain that $2 \Rightarrow 1$. □

5 Example

We now turn our attention to a particular class of metapopulation models which combine a (finite) Λ -coalescent within demes with migration between demes and sporadic mass extinction events. We will use the results derived in the preceding sections to characterize the form that the genealogy takes in the infinitely many demes limit. This, in turn, will allow us to illustrate how the statistics of the population-wide Ξ -coalescent depend on the interplay between extinction/recolonization events and the local demographic processes occurring within demes. While these models are quite contrived - in particular, we have simply imposed the condition that a small number of demes is responsible for repopulating vacant demes following a mass extinction - they will allow us to explicitly calculate some quantities of interest.

We first describe how the population evolves forwards-in-time. Suppose that for each D , each deme contains exactly N individuals. Fix $K \in \mathbb{N}$, and let $\Lambda^d(dx)$ and $\Lambda^g(dy)$ be two probability measures on $[0, 1]$ with no atom at 0. Then reproduction, migration, and extinction/recolonization events occur according to the following rules.

- Each individual in each deme reproduces at rate D according to the following scheme. If an individual in deme i reproduces, then a number x is sampled from $[0, 1]$ according to the

probability distribution $\Lambda^d(dx)$, and then each occupant of that deme dies with probability x and is replaced by an offspring of the reproducing individual. In terms of the notation of Section 2.1, such an event has the following representation when k is the label of the reproducing individual. First, $R^{j,j'} = (0, \dots, 0)$ for all pairs of integers $j \neq j' \in [D]$ and $R^{j,j} = (1, \dots, 1)$ if $j \in [D] \setminus \{i\}$. $R^{i,i}$ is a random vector obtained by choosing a number x according to $\Lambda^d(dx)$, a number m according to a binomial distribution with parameters (N, x) , and finally a set $\mathcal{O} \subset [N]$ of offspring of the reproducing individual by sampling m labels in $[N]$ uniformly without replacement. Then, $R_k^{i,i} = m$, $R_{k'}^{i,i} = 0$ for all $k' \in \mathcal{O} \setminus \{k\}$, and $R_l^{i,i} = 1$ for all $l \notin \mathcal{O} \cup \{k\}$.

- At rate Dm_1 , each individual gives birth to a single migrant offspring which then moves to any one of the D demes, chosen uniformly at random, and replaces one of the N individuals within that deme, also uniformly at random. In this case, if j is the label of the deme containing the parent and k is its label, then a pair (i, l) is sampled uniformly in $[D] \times [N]$ and the vectors R are as described in Example 3 of Section 2.1.
- Mass extinction events occur at rate e . When such an event occurs, a number y is sampled from $[0, 1]$ according to the probability distribution $\Lambda^g(dy)$. Then, each deme goes extinct with probability y , independently of all the others, and is unaffected by the extinction otherwise. Simultaneously, K of the D demes are chosen uniformly at random to be source demes, and the deceased occupants of the extinct island are replaced by offspring produced by individuals living in the source demes according to the following scheme. The parent of each individual recolonizing a deme left vacant by the mass extinction is chosen uniformly at random and with replacement from among the NK inhabitants of the source demes. If a source deme is chosen from among the extinct ones, then the parents of the offspring emerging from that deme are the individuals that occupied the deme immediately prior to the extinction. To describe such an event using the notation of Section 2.1, suppose that a number y is chosen according to $\Lambda^g(dy)$, a number m is sampled according to a $\text{Binom}(D, y)$ -distribution and a (random) set $\mathcal{O}_{\text{ext}} \subset [D]$ is constructed by sampling uniformly without replacement m deme labels. Independently, another set \mathcal{O}_{rec} of K recolonizing demes is also chosen by uniform sampling. Then, for all $i \notin \mathcal{O}_{\text{ext}}$ we have $R^{i,i} = (1, \dots, 1)$ and each deme $j \in \mathcal{O}_{\text{ext}} \setminus \mathcal{O}_{\text{rec}}$ satisfies $R^{i,j} = (0, \dots, 0)$ for all $i \in [D]$. The vectors $R^{i,j}$ with $j \in \mathcal{O}_{\text{rec}}$ and $i \in \mathcal{O}_{\text{ext}} \cup \mathcal{O}_{\text{rec}}$ are not easily formulated explicitly (in particular, their description depends on whether the recolonizing demes also go extinct during the event), but it is clear that the evolution of the population satisfies the two conditions required in Section 2.1.

Suppose that n individuals are sampled from the population at time 0, and let us consider the evolution (backwards-in-time) of the structured coalescent process \mathcal{P}^D in \mathbb{P}_n^s . From the description of the model forwards-in-time, the events affecting the genealogy occur at the following rates:

1. If a deme contains b lineages, then each k -tuple of lineages in this deme (for $k \leq b$) merges into one lineage in the same deme at rate

$$D\lambda_{b;k,1,\dots,1}^d = DN \int_0^1 \Lambda^d(dx) x^k (1-x)^{b-k}.$$

Furthermore, any merger event occurs in one deme at a time.

2. Each lineage migrates (alone) at rate Dm_1 . Indeed, the total rate at which migrant offspring are produced forwards-in-time is $ND \times Dm_1$, but the probability that such a migrant belongs to the lineage under consideration is $(ND)^{-1}$ (recall that the deme and the label of the individual replaced by the migrant are chosen uniformly at random). Consequently, the probability that a migrating lineage lands in a non-empty deme is D^{-1} times the number of demes occupied by the other lineages of \mathcal{P}_{t-}^D . When such an event occurs, the probability that the migrating lineage also merges with an ancestral lineage present in the source deme is N^{-1} times the number of distinct ancestral lineages present in that deme.
3. Extinction events generate geographical collisions at rate $O(1)$. Because the K recolonizing demes are chosen uniformly from among the D islands, recolonization by a deme containing at least one lineage of the genealogical process occurs with a probability of order $O(D^{-1})$, and so these events are negligible in the limit. Suppose that $\mathcal{P}_{t-}^D \in \Pi_n$. Let $k \leq |\mathcal{P}_{t-}^D|$, $r \leq K$, and let k_1, \dots, k_r be integers greater than 1 and summing to k . For each $i \in \{1, \dots, r\}$, let $L_i = \{l_{i1}, \dots, l_{ij_i}\}$ be a collection of j_i integers summing to k_i . Then each $(|\mathcal{P}_{t-}^D|; k_1, \dots, k_r, 1, \dots, 1; L_1, \dots, L_r, \{1\}, \dots, \{1\})$ -geographical collision occurs at rate

$$\begin{aligned}
& e \int_0^1 \Lambda^g(dy) \sum_{s=0}^{|\mathcal{P}_{t-}^D| - k} \mathbb{I}_{\{s \leq K-r\}} \binom{|\mathcal{P}_{t-}^D| - k}{s} y^{k+s} (1-y)^{|\mathcal{P}_{t-}^D| - k - s} \frac{K!}{(K-r-s)!} \frac{1}{K^{k+s}} \\
& \quad \times \prod_{i=1}^r \left\{ \frac{N!}{(N-j_i)!} \frac{1}{N^{k_i}} \right\} + O\left(\frac{1}{D}\right) \tag{35} \\
& \equiv \tilde{\lambda}_{|\mathcal{P}_{t-}^D|; k_1, \dots, k_r, 1, \dots, 1; L_1, \dots, L_r, \{1\}, \dots, \{1\}}^g + o\left(\frac{1}{D}\right).
\end{aligned}$$

The rate expression that appears in Eq. (35) can be interpreted in the following way. As well as the k ancestral lineages that are known to be affected by the disturbance (this is specified by the type of event), an additional s lineages may be caught up in the extinction event and moved to demes where they remain isolated (hence producing no changes in the structured genealogy). In (35), the first part in each term of the sum corresponds to the number of choices for these s additional lineages, followed by the probability that only these $k + s$ lineages are affected. The condition $r + s \leq K$ is imposed by the fact that the r groups of lineages geographically gathered and the s lineages affected but remaining alone in their demes must then belong to $r + s$ distinct recolonizing demes. The middle part of the term specifies the probability that the affected lineages are grouped in the desired way: regardless of the labels of the recolonizing demes, if the latter contain no lineages of the sample just before the extinction then $\frac{K!}{(K-r-s)!}$ is the number of (unordered) ways of choosing $r + s$ of them to receive the affected lineages, while K^{-k-s} is the probability that each of the $k + s$ lineages moves to the prescribed recolonizing deme. Finally, the last product is obtained in a similar manner by allocating as many distinct ancestors as required to the groups of lineages gathered into the same demes. As explained above, the $O(D^{-1})$ remainder term accounts for the probability that at least one of the finitely-many recolonizing demes contains a lineage of \mathcal{P}_{t-}^D .

Let us say that a **simple collision** occurs when a single lineage moves into a non-empty deme, and possibly merges with one of the lineages present in this deme. To verify that the convergence results from the previous sections apply to the example, it will be convenient to introduce the following quantities, defined for all $\zeta, \eta \in \mathbb{P}_n^s$:

$$\phi_c(\zeta, \eta) = \begin{cases} 1 & \text{if } \zeta \rightarrow \eta \text{ is a simple collision with coalescence,} \\ 0 & \text{otherwise,} \end{cases}$$

and likewise

$$\phi_{nc}(\zeta, \eta) = \begin{cases} 1 & \text{if } \zeta \rightarrow \eta \text{ is a simple collision without coalescence,} \\ 0 & \text{otherwise.} \end{cases}$$

By ‘with coalescence’ (resp. ‘without coalescence’), we mean that the migrating lineage merges (resp. does not merge) with a lineage in the source deme during the same event.

Let us consider a particular 1-event. If this event involves a single lineage moving to an empty deme, it may be caused either by a migration event of the kind described in item 2 above (which occurs at rate $Dm_1(1 - k/D)$ if k is the number of demes occupied by the other lineages at the time of the event), or by a mass extinction event (whose rate is of order $O(1)$ according to item 3). Consequently, the overall rate of any 1-event is of the form $Dm_1 + O(1)$. Groups of more than one lineage can also move simultaneously, but only through an extinction event and so at a rate of order $O(1)$. If the event involves an intra-deme merger, then its rate is easily written in the form given in Section 3.1 with $r_D = D$; see item 1. A 2-event $\zeta \rightarrow \eta$ occurs at a rate of order $O(1)$, and in particular if $\zeta \in \Pi_n$, then this rate is given by

$$\tilde{\lambda}^g(\zeta, \eta) + 2m_1 \left\{ \phi_c(\zeta, \eta) \frac{1}{N} + \phi_{nc}(\zeta, \eta) \frac{N-1}{N} \right\} + O\left(\frac{1}{D}\right) \equiv \lambda^g(\zeta, \eta) + O\left(\frac{1}{D}\right),$$

where $\tilde{\lambda}^g(\zeta, \eta)$ is the rate of the unique extinction event which turns ζ into η . In this expression, the term in brackets is nonzero only if the event is a simple collision involving two lineages that have been collected in the same deme through migration. Such collisions occur at rate $2m_1$, and then the two lineages either coalesce, with probability N^{-1} , or remain distinct, with probability $1 - N^{-1}$. Finally, we must check that the λ^g 's satisfy (4), and that the rates on the fast time scale satisfy condition (i) of Lemma 2.2. The latter condition follows from the description of the rates and the consistency of Λ -coalescents, and the validity of the former condition can be deduced from the fact that lineages choose independently of each other whether they are involved in the event, and which of the NK individual they take as a parent. We leave the straightforward but tedious calculations to the interested reader.

All conditions of Theorem 1.1 and Proposition 2.1 hold. Thus, we can conclude that the finite dimensional distributions of \mathcal{P}^D converge to those of a structured genealogical process \mathcal{P} with values in Π_n , and that the unstructured process \mathcal{P}^u is a Ξ -coalescent with values in \mathbb{P}_n . Let us describe \mathcal{P}^u as precisely as we can. To apply the results of Section 2.3, we need to know the distribution of the final state of the ‘fast’ process ξ that was introduced in Section 2.2. Starting from a structured partition where all blocks are contained in the same component (i.e., all lineages lie initially in the same deme), this distribution coincides with the sampling distribution of the infinitely many alleles model of the generalized Fleming-Viot process dual to the Λ -coalescent with finite measure $x^2 \Lambda^d(dx)$ acting within this deme. Indeed, on the fast time scale, ancestral lineages belonging to a common deme migrate out to distinct, empty islands, a process analogous to mutation to unique types with a ‘mutation’ rate equal to m_1 . Recursion formulae are given in Möhle [2006] which can be used to compute the probability $p(\mathbf{n})$ of unordered allele configurations $\mathbf{n} = \{n_1, \dots, n_k\}$ in the infinitely many alleles model when the genealogy is given by a Λ - or a Ξ -coalescent. In our case, the

formula of interest is (with $p(1) = 1$):

$$p(\mathbf{n}) = \frac{nm_1}{g_n + nm_1} \sum_{j=1}^k \mathbb{I}_{\{n_j=1\}} \frac{1}{k} p(\tilde{\mathbf{n}}_j) + \sum_{i=1}^{n-1} \frac{g_{n,n-i}}{g_n + nm_1} \sum_{j=1}^k \mathbb{I}_{\{n_j>i\}} \frac{n_j - i}{n - i} p(\mathbf{n} - i\mathbf{e}_j),$$

where $n \equiv \sum_{j=1}^k n_j \geq 2$, $\tilde{\mathbf{n}}_j \equiv (n_1, \dots, n_{j-1}, n_{j+1}, \dots, n_k)$, \mathbf{e}_j denotes the j 'th unit vector in \mathbf{R}^k and g_{nk} (resp. g_n) is the rate at which the number of lineages decreases from n to k (resp. the total rate at which the number of lineages changes when n lineages are alive), given by

$$g_{nk} = \binom{n}{k-1} \int_0^1 \Lambda^d(dx) x^{n-k+1} (1-x)^{k-1}$$

and

$$g_n = \sum_{k=1}^{n-1} g_{nk} = \int_0^1 \Lambda^d(dx) (1 - (1-x)^{n-1} (1-x+nx)).$$

These expressions are related to the distribution of $\underline{\zeta}$ by the following formula:

$$\mathbf{P}[\underline{\zeta} = (\{B_1\}, \dots, \{B_k\}, \emptyset, \dots, \emptyset)] = p(|B_1|, \dots, |B_k|),$$

where $\zeta = (\{\{1\}, \dots, \{n\}\}, \emptyset, \dots, \emptyset)$ and $|B_i|$ denotes the number of elements in the block B_i . Indeed, because the dynamics on the fast time scale of lineages occupying different demes are independent, the final state of the fast genealogical process is the concatenation of all the final states of the groups of lineages starting in the same deme. Hence, the preceding results are sufficient to describe $\underline{\zeta}$ for any $\zeta \in \mathcal{P}_n^s$. Unfortunately, with this level of generality, there does not appear to be a simple description of the measure Ξ associated to \mathcal{P}^u , but the rate associated to its Kingman part (that is its mass at $\mathbf{0}$) is given by:

$$2m_1 \frac{1}{N} + 2m_1 \frac{N-1}{N} p(2) = 2 \frac{m_1}{N} \left\{ 1 + (N-1) \frac{\int_0^1 \Lambda^d(dx) x^2}{\int_0^1 \Lambda^d(dx) x^2 + 2m_1} \right\}. \quad (36)$$

The first term in (36) corresponds to a simple collision with coalescence, and the second term to a simple collision without coalescence; the probability that the lineages then coalesce before one of them migrates is given by $p(2)$.

One case which can be characterized more thoroughly is when dispersal between demes only occurs during extinction-recolonization events ($m_1 = 0$). For example, this might be a reasonable approximation to make when modeling a population in which migrants are at a substantial competitive disadvantage relative to residents, so that dispersal is only successful into demes in which the resident population has gone extinct. In this case, the Kingman component of the genealogy disappears (see (36)). Furthermore, viewed backwards in time, lineages gathered into common demes by mass extinction events cannot migrate away before the rapid within-deme coalescent reaches a common ancestor, and so any such group of lineages merges instantaneously into a single lineage. The shape of the resulting global coalescent therefore is determined only by the way in which mass extinction events gather lineages together. Recall the expression for the rates of geographical collisions given in (35), and let us examine how K , the number of demes contributing colonists in the wake of a mass extinction, affects the shape of the genealogy.

If $K = 1$, all lineages affected by a mass extinction event have parents within the same deme. The resulting genealogy is a Λ -coalescent, and the rate at which k ancestral lineages merge when m are present is equal to the rate at which exactly k lineages are caught up in an extinction event when m demes contain one lineage, that is

$$e \int_0^1 \Lambda^g(dy) y^k (1-y)^{m-k}.$$

On the other hand, if we let K tend to infinity, then each term in the sum in (35) is asymptotically equivalent to $\frac{K!}{(K-r-s)!} K^{-k-s} \sim K^{r-k}$, up to a constant (recall that the sample size n is finite and bounds the number of lineages at any times). Consequently, binary geographical collisions ($k = k_1 = 2$, $r = 1$, $j_1 \in \{1, 2\}$) occur at a rate of order $O(K^{-1})$, whereas the rate of a collision involving at least 3 lineages is of order at most $O(K^{-2})$. Hence, for fixed sample size n , the probability that only binary mergers occur in the sample genealogy approaches 1 as K tends to infinity, and the rate of each binary merger (multiplied by K) converges to

$$e \int_0^1 \Lambda^g(dy) y^2, \tag{37}$$

where the term y^2 is obtained by observing that the condition $s \leq K - 1$ in (35) is always fulfilled for n fixed and K large enough, and that $\sum_{s=0}^{|\mathcal{P}_t^D|-2} (|\mathcal{P}_t^D|-2) y^{2+s} (1-y)^{|\mathcal{P}_t^D|-2-s} = y^2$. Once the lineages are gathered into the same deme, they can only coalesce and they do so instantaneously on the slow time scale as $D \rightarrow \infty$. It follows that if time is rescaled by a factor of DK , then the rate of a binary merger converges to that of Kingman's coalescent run at the rate shown in (37). Moreover, under this time rescaling, the rates of the finitely many possible multiple merger events converge to 0 as K grows to infinity, and so the limiting (as $D \rightarrow \infty$) unstructured genealogical process \mathcal{P}^u corresponding to an evolution with K recolonizing demes converges to Kingman's coalescent as a process in $D_{P_n}[0, \infty)$ as K tends to infinity. (Note, however, that this does not imply that one can interchange the limits $D \rightarrow \infty$ and $K \rightarrow \infty$.) Finally, if K is finite but greater than 1, then geographical collisions involving more than two lineages occur at a non-negligible rate, and so the resulting unstructured genealogy is a more general Ξ -coalescent.

This example shows that a large class of coalescent processes can arise in the infinitely many demes limit of a subdivided population with sporadic mass extinctions. Depending on both the migration and the extinction rates, as well as on the number of demes contributing to population recovery following a mass extinction, the limiting genealogical process can range from Kingman's coalescent ($K = \infty$), as derived by Wakeley [2004], to a Λ -coalescent ($K = 1$, $m_1 = 0$), with a family of Ξ -coalescents interpolating between these two extremes. In this particular class of models, multiple mergers of ancestral lineages are more likely to occur when all three parameters, K , N and m_1 , are small, so that mass extinctions have a non-negligible probability of gathering lineages into a common deme where they undergo a series of rapid mergers before being scattered again by migration. This observation suggests that it is a generic property of structured population models that if the limiting coalescent admits any multiple mergers, then it also admits simultaneous mergers.

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References

- C. Cannings. The Latent Roots of Certain Markov Chains Arising in Genetics: A New Approach, I. Haploid Models. *Adv. Appl. Probab.*, 6:260–290, 1974. MR0343949
- J.T. Cox. Coalescing random walks and voter model consensus times on the torus in \mathbb{Z}^d . *Ann. Probab.*, 17:1333–1366, 1989. MR1048930
- J.T. Cox and R. Durrett. The stepping stone model: New formulas expose old myths. *Ann. Appl. Probab.*, 12:1348–1377, 2002. MR1936596
- B. Eldon and J. Wakeley. Coalescent Processes When the Distribution of Offspring Number Among Individuals is Highly Skewed. *Genetics*, 172:2621–2633, 2006.
- S.N. Ethier and T.G. Kurtz. *Markov processes: characterization and convergence*. Wiley, 1986. MR0838085
- S.N. Ethier and T. Nagylaki. Diffusion approximation of Markov chains with two time scales and applications to population genetics. *Adv. Appl. Probab.*, 12:14–49, 1980. MR0552945
- R. Fisher. *The Genetical Theory of Natural Selection*. Clarendon, Oxford, 1930.
- A. Greven, V. Limic and A. Winter. Coalescent processes arising in a study of diffusive clustering. *Preprint*, 2007.
- J.F.C. Kingman. The coalescent. *Stoch. Proc. Appl.*, 13:235–248, 1982. MR0671034
- M. Möhle. Ancestral Processes in Population Genetics - the Coalescent. *J. Theoret. Biol.*, 204:629–638, 2000.
- M. Möhle. On sampling distributions for coalescent processes with simultaneous multiple collisions. *Bernoulli*, 12:35–53, 2006. MR2202319
- M. Möhle and S. Sagitov. A Classification of Coalescent Processes for Haploid Exchangeable Population Models. *Ann. Probab.*, 29:1547–1562, 2001. MR1880231
- M. Nordborg. *Coalescent theory*, Chapter 7 in *Handbook of Statistical Genetics*. Wiley, Chichester, UK, 2001.
- M. Nordborg and S.M. Krone. *Separation of time scales and convergence to the coalescent in structured populations*. In *Modern Developments in Theoretical Population Genetics: The Legacy of Gustave Malécot*. Oxford University Press, Oxford, 2002.
- M. Notohara. The coalescent and the genealogical process in geographically structured populations. *J. Math. Biol.*, 29:59–75, 1990. MR1083665
- J. Pitman. Coalescents with Multiple Collisions. *Ann. Probab.*, 27:1870–1902, 1999. MR1742892
- S. Sagitov. The general coalescent with asynchronous mergers of ancestral lines. *J. Appl. Probab.*, 36:1116–1125, 1999. MR1742154

- O. Sargsyan and J. Wakeley. A coalescent process with simultaneous multiple mergers for approximating the gene genealogies of many marine organisms. *Theor. Popul. Biol.*, 74:104–114, 2008.
- J. Schweinsberg. Coalescents with simultaneous multiple collisions. *Electr. J. Probab.*, 5:1–50, 2000. MR1781024
- J. Schweinsberg. Coalescent processes obtained from supercritical Galton-Watson processes. *Stochastic Process. Appl.*, 106:107–139, 2003. MR1983046
- W.P. Sousa. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15:353–391, 1984.
- A.W. van der Vaart. *Asymptotic Statistics*. Cambridge University Press, 1998. MR1652247
- J. Wakeley. Segregating sites in Wright’s island model. *Theor. Popul. Biol.*, 53:166–175, 1998.
- J. Wakeley. Nonequilibrium Migration in Human History. *Genetics*, 153:1863–1871, 1999.
- J. Wakeley. Metapopulation models for historical inference. *Mol. Ecol.*, 13:865–875, 2004.
- J. Wakeley and N. Aliacar. Gene Genealogies in a Metapopulation. *Genetics*, 159:893–905, 2001.
- H.M. Wilkinson-Herbots. Genealogy and subpopulation differentiation under various models of population structure. *J. Math. Biol.*, 37:535–585, 1998. MR1664797
- S. Wright. Evolution in Mendelian populations. *Genetics*, 16:97–159, 1931.
- I. Zähle, J.T. Cox and R. Durrett. The stepping stone model II:Genealogies and the infinite sites model. *Ann. Appl. Probab.*, 15:671–699, 2005. MR2114986