

The influence of explicit local dynamics on range expansions driven by long-range dispersal

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Range expansions are common in natural populations. They can take such forms as an invasive species spreading into a new habitat or a virus spreading from host to host during a pandemic. When the expanding species is capable of dispersing offspring over long distances, population growth is driven by rare but consequential long-range dispersal events that seed satellite colonies far from the densely occupied core of the population. These satellites accelerate growth by accessing unoccupied territory, and also act as reservoirs for maintaining neutral genetic variation present in the originating population, which would ordinarily be lost to drift. Prior theoretical studies of dispersal-driven expansions have shown that the sequential establishment of satellites causes initial genetic diversity to be either lost or maintained to a level determined by the breadth of the distribution of dispersal distances. If the tail of the distribution falls off faster than a critical threshold, diversity is steadily eroded over time; by contrast, broader distributions with a slower falloff allow some initial diversity to be maintained for arbitrarily long times. However, these studies used lattice-based models and assumed an instantaneous saturation of the local carrying capacity after the arrival of a founder. Real-world populations expand in continuous space with complex local dynamics, which potentially allow multiple pioneers to arrive and establish within the same local region. Here, we evaluate the impact of local dynamics on the population growth and the evolution of neutral diversity using a computational model of range expansions with long-range dispersal in continuous space, with explicit local dynamics that can be controlled by altering the mix of local and long-range dispersal events. We found that many qualitative features of population growth and neutral genetic diversity observed in lattice-based models are preserved under more complex local dynamics, but quantitative aspects such as the rate of population growth, the level of maintained diversity, and the rate of decay of diversity all depend strongly on the local dynamics. Besides identifying situations in which modeling the explicit local population dynamics becomes necessary to understand the population structure of jump-driven range expansions, our results show that local dynamics affects different features of the population in distinct ways, and can be more or less consequential depending on the degree and form of long-range dispersal as well as the scale at which the population structure is measured.

I. INTRODUCTION

Range expansion—the act of a population expanding into new territory—is common in biological populations. Range expansions occur naturally and randomly all the time, often as the result of a species’ natural movement, such as by animals moving into new territory or maple helicopters carrying seeds away from their parent tree. Researchers have documented range expansions in a wide variety of organisms, such as plants [1], birds [2], sea creatures [3, 4], and terrestrial animals [5, 6], even humans [7]. Range expansions are increasingly forced by global warming as the changing climate makes traditional habitats inhospitable, while potentially opening up new hospitable regions [8].

Range expansions leave distinctive signatures in the patterns of genetic diversity of a population that can mimic the effects of natural selection [9]. Individuals at the frontier of an expanding population make a large contribution to the subsequent expansion wave, even if their frontier position was solely due to chance; as a result, genetic variants they carry can acquire high fre-

quencies in the population in a phenomenon termed gene surfing [10, 11]. Independent surfing events in separate sections of the expansion front cause the population to segregate into genetically distinct sectors, promoting an illusion of local adaptation from purely neutral mutations [12–15]. Modeling the combined effect of spatial structure and stochasticity on neutral genetic diversity is key to understanding the biological origins of established genetic patterns, and to the successful prediction of future genetic diversity in pandemics and ecological expansions.

The influence of random chance on genetic diversity during range expansions can be amplified by long-range dispersal [16]. Many species have evolved ingenious ways of dispersing offspring over long distances with help from natural forces and from other organisms [17]. Plants rely on the dispersal of seeds and pollen by wind, waves, and animals [18]. Glacier ice worms can travel hundreds of miles, likely carried by migratory birds [19]. Modern pandemics are driven by microorganisms hitchhiking on air travelers to find new uninfected populations [20]. Even if long-range dispersal events are rare, they have an outsized influence on the expansion because they enable pioneers to seed satellite colonies in uninhabited areas. If a pioneer happens to land in a place with abundant resources and little to no competition, its descendants may flourish. The pioneer’s genes will then propagate and any

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53 genetic variants they carry will reach high frequencies in
54 the vicinity of the satellite [21–25] even in the absence of
55 a selective advantage; random chance alone has caused
56 the pioneer’s genes to become prominent by means of a
57 founder effect, leading to a *suppression* of local diversity
58 within satellites. However, long-range dispersal also *fa-*
59 *vors* neutral diversity at larger scales, by ensuring that
60 individuals well within the expanding population have a
61 chance of contributing to growth. The evolution of over-
62 all diversity during the range expansion is governed by
63 the trade-off between the two effects, and can depend sen-
64 sitively on the degree of long-range dispersal experienced
65 by the population [26, 27].

66 Modeling the general characteristics of range expan-
67 sions requires two minimal ingredients: a probability dis-
68 tribution of dispersal distances $J(r)$, also called the *jump*
69 *kernel*, from which dispersal events are randomly drawn;
70 and a method of local density regulation to model the
71 existence of a finite carrying capacity. When long-range
72 jumps are present, the tail of the jump kernel, i.e. its
73 behavior at long distances, critically influences the fate
74 of the population at long times. Fundamental differences
75 from short-range dispersal are observed when the jump
76 kernel is “fat-tailed”; i.e. it decays slower than exponen-
77 tially with increasing distance. Fat-tailed jump kernels
78 lead to expansions that accelerate as they progress, unlike
79 the constant-speed expansions that occur when dispersal
80 is exclusively short-range [28].

81 A commonly used fat-tailed kernel is the power-law
82 jump kernel $J(r) \sim 1/r^{\mu+1}$. Besides providing a good
83 description of the dispersal behavior of many species [29],
84 power-law kernels are a useful tool for analyzing and clas-
85 sifying the breadth of potential population outcomes due
86 to long-range dispersal [16]. The exponent μ is a key fac-
87 tor governing the long-time characteristics of the growth
88 and the dispersal patterns, whereas other details of $J(r)$
89 such as its short-distance functional behavior are less rel-
90 evant [16]. A broad range of expansion behaviors is en-
91 compassed by varying the kernel exponent (limited to
92 $\mu > 0$ to ensure a normalizable distance distribution).
93 At high μ , the jump kernel decays quickly with increas-
94 ing distance, and a colony expands at a constant rate as
95 if there were exclusively short-range dispersal. As $\mu \rightarrow 0$,
96 spatial structure becomes irrelevant and a colony grows
97 as if it were in a well-mixed liquid environment. The
98 intermediate range of kernel values connects these two
99 extremes in a tunable manner.

100 Recent work has catalogued the distinctive features
101 of population growth dynamics [16] and spatial genomic
102 patterns [27] that can be achieved upon varying the ker-
103 nel exponent in range expansions driven by power-law
104 growth kernels (a detailed summary is provided in Sec-
105 tion II). These studies have identified a critical value
106 of the kernel exponent μ below which the population
107 grows nearly as fast as a well-mixed population, and a
108 significant fraction of the neutral variation in the orig-
109 inating population is preserved for arbitrary long times
110 due to serial reintroduction of variants from the core of

111 the expanding population. For kernel exponents close
112 to but above the critical threshold, population growth
113 is slowed down dramatically and neutral diversity is
114 steadily eroded. However, at even higher values of μ , the
115 behavior approaches that of short-ranged jump kernels,
116 where the population advances as a front moving outward
117 at constant speed. In this situation, a small fraction of
118 the diversity in the originating population persists due
119 to the formation of sectors [12, 30].

120 Less well understood is the influence of the second key
121 feature of spatial population models: the density regula-
122 tion mechanism. Modeling growing populations in a spa-
123 tial continuum presents challenges to both the forward-
124 in-time [31] and backward-in-time [32, 33] approaches,
125 due to the necessity of systematically imposing a local re-
126 gion of influence within which each individual can impact
127 the growth of its neighbors. Local density regulation is
128 commonly implemented by dividing up space into a regu-
129 lar grid of well-mixed subpopulations called demes, each
130 of which has a fixed carrying capacity. Migration events,
131 drawn from the jump kernel, transport individuals across
132 demes. Deme-based models and their variants are widely
133 used in population genetics [34], including for the study
134 of range expansions [9, 30]. However, models that rely
135 on a lattice of demes have their limitations. By design,
136 they do not capture spatial structure and stochasticity
137 at scales smaller than the effective deme size. Impos-
138 ing an artificial grid of demes also introduces artifacts
139 to the population structure, which can in some instances
140 get *worse* upon increasing the grid resolution to better
141 approximate a continuum [35].

142 Additionally, using deme-based models forces re-
143 searchers to make decisions about the specifics of deme
144 saturation and population management. The follow-
145 ing selection of recent work exemplifies various possible
146 strategies. Some may choose to have demes that instan-
147 taneously change from being empty to full upon the ar-
148 rival of the first migrant [16, 27], while others may let
149 the deme population grow logistically at a predetermined
150 rate [36, 37] or let the growth be determined by random
151 migration events that bring in individuals from other
152 demes [38]. Death can occur in various ways, such as by
153 attempting to disperse into an already full deme [16, 27]
154 or by being randomly resampled out of an overfull deme’s
155 population [38]. If the density regulation unit is the deme
156 population as a whole rather than the individuals in the
157 deme, death may not explicitly occur to any individuals,
158 but the deme population size changes from one time step
159 to the next [36, 37]. Since most computational studies
160 involving long-range dispersal, including the quoted prior
161 results [16, 21–25, 27, 36, 37, 39], have relied on deme-
162 based approximations, the applicability of their conclu-
163 sions to continuum-space population growth remains an
164 open question.

165 The aforementioned results on the population dynam-
166 ics and neutral evolution of range expansions driven by
167 power-law kernels [16, 27] were derived using a lattice of
168 demes with an additional simplifying assumption: upon

169 arrival at an empty deme, the pioneer immediately sat-
170 urates the deme, excluding any other migrants from es-
171 tablishing themselves. Not only does this assumption ex-
172 clude any effects of local dynamics on population growth,
173 it also enforces a local *founder takes all* effect where
174 only one migrant is allowed to contribute to the genetic
175 makeup of a density regulation region. Instant local sat-
176 uration is justified when long-range jumps are rare and
177 most offspring land within a short distance of their par-
178 ents; then, the local logistic growth within a deme oc-
179 curs extremely fast compared to the typical time to ar-
180 rival of another migrant from a different deme, and can
181 be treated as instantaneous. However, the instant satu-
182 ration and founder-takes-all assumptions can be invalid
183 when the time scales of local and long-range dispersal
184 are comparable, in which case a local region might receive
185 and send out several migrants while it is being saturated.
186 The influence of the breakdown of fast local saturation on
187 the population dynamics and the spatial genomic struc-
188 tures left behind by long-range dispersal is unknown.

189 In this work, we address these gaps in our knowledge
190 of range expansions driven by long-range dispersal by
191 performing and analyzing continuum space, individual-
192 based simulations of range expansions driven by power-
193 law kernels. Our simulations were implemented in the
194 population genetics program SLiM [40], and do not use
195 a grid of demes or assume instant saturation of the local
196 carrying capacity by the first arrival. Instead, individ-
197 uals occupy positions in continuum space and their sur-
198 vival depends on the number of other individuals present
199 within a defined region of influence at the time of their
200 birth. When possible, we compared the outputs to the
201 predictions from models based on lattices of demes of
202 the population growth rate [16] and the evolution of neu-
203 tral genetic diversity [27]—we term these prior models
204 “lattice-based” predictions. We found that our results
205 often agreed with the lattice-based predictions, giving
206 conditional support to prior results based on models that
207 only focus on the founders. However, when individuals
208 can share resources with many others, we found that fo-
209 cusing exclusively on the founders misses important dy-
210 namics between coexisting or competing alleles. In those
211 cases, it becomes necessary to also consider individ-
212 uals who arrive after the pioneer. We identify parameter
213 regimes where using the lattice-based models is justified,
214 and show that they depend on the specific kernel expo-
215 nent.

216 II. BACKGROUND

217 We first summarize prior results [16, 27] on range
218 expansion dynamics for populations experiencing long-
219 range dispersal with fat-tailed kernels, which were ob-
220 tained using lattice models conforming to the founder-
221 takes-all assumption at the deme level. Ref. 16 used
222 a lattice model to quantify how a colony expands into
223 unoccupied space when offspring are dispersed accord-

224 ing to a power law jump kernel that decays according
225 to $J(r) \sim 1/r^{\mu+1}$. The authors showed that the power-
226 law tail captures the qualitative features of the long-term
227 population growth, and that the short-range behavior of
228 the jump kernel has a negligible impact on the long term
229 population growth. The model of Ref. 16 (hereafter “the
230 lattice model”) divides d -dimensional space into a lattice
231 of habitats or “demes”. Occupied demes generate off-
232 spring according to a Poisson process; offspring attempt
233 to migrate to a new deme randomly chosen by drawing
234 a dispersal distance from $J(r)$ and a random direction
235 relative to the originating deme. Instant local satura-
236 tion is assumed and is enforced in the model by allowing
237 only two states to each deme: occupied, or empty. A
238 migration attempt to an empty deme is successful, and
239 immediately turns the state of that deme to occupied.
240 A migration attempt to an occupied deme is unsuccess-
241 ful, and the offspring dies. These assumptions guarantee
242 a founder-takes-all effect at the local level. Henceforth,
243 when we refer to the lattice model, it is implied that
244 instant local saturation and local founder-takes-all are
245 enforced. Much of our current understanding of jump-
246 driven range expansions derives from the lattice model,
247 as summarized below.

248 A. Population growth and time-doubling hierarchy

249 Analysis of the lattice model [16] showed that at all
250 times t , a core region of the colony can be identified that
251 is centered at the originating population of the range ex-
252 pansion and within which most demes are occupied. The
253 size of this core region is proportional to the total pop-
254 ulation size $M(t)$ of occupied demes in the expansion.
255 The long-time asymptotic behavior of the radius of the
256 core region $\ell(t) \propto [M(t)]^{1/d}$ depends on the “heaviness”
257 of the tail of the jump kernel, which is set by the kernel
258 exponent μ . There are two distinct growth possibilities,
259 separated by the value $\mu = d + 1$: the colony expands
260 at a constant rate for $\mu > d + 1$ and it expands faster
261 than linearly when $\mu < d + 1$ [16]. The faster-than-linear
262 growth regime is driven by long jumps whose character-
263 istic size continues to increase as the core expands: this
264 “jump-driven” growth regime, in which pioneers have a
265 large impact on growth, will be the focus of this pa-
266 per. Within the jump-driven regime, a second special
267 value $\mu = d$ separates two distinct asymptotic behav-
268 iors of the core growth at long times ($t \rightarrow \infty$): when
269 $d < \mu < d + 1$, the core grows asymptotically as a power
270 law which is faster-than-linear in time ($\ell(t) \propto t^{\frac{1}{\mu-d}}$), in
271 contrast to stretched-exponential growth when $\mu < d$
272 ($\ell(t) \propto \exp(B_\mu t^\eta)$, where B_μ and η themselves depend
273 on μ and d).

274 A key result of Ref. 16 was that expansions in the
275 jump-driven regime are governed by a hierarchical time-
276 doubling structure, as depicted in Fig. 1. The core of
277 the colony expands by “absorbing” satellite colonies that
278 were seeded at an earlier time by a rare but consequen-

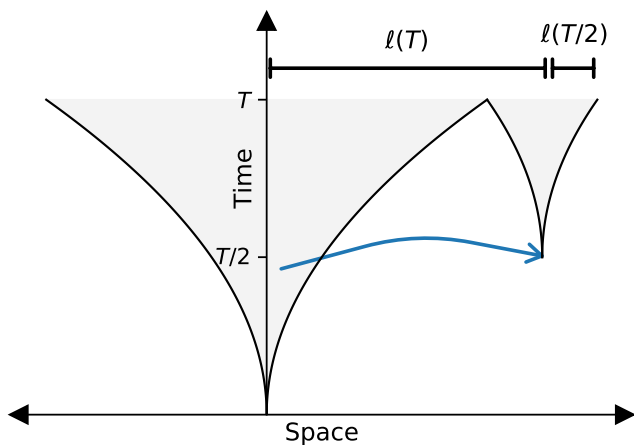


FIG. 1. Schematic diagram of the time doubling hierarchy discovered by Ref. 16. Shaded parts of the plot represent regions of space that are occupied at a given time. The core of the colony (central funnel) grows by absorbing satellites that were seeded at an earlier time by long-range dispersal. A typical satellite being absorbed into the core at time T (smaller funnel at right) was seeded at time of order $T/2$ by an offspring who dispersed a distance of roughly $\ell(T)$ from its parent in the core of the colony; it has grown to a size of order $\ell(T/2)$ when it merges with, and becomes part of, the core.

279 tial long jump. A typical satellite being absorbed into the
 280 core at time t was seeded approximately at time $t/2$ by
 281 an offspring who dispersed roughly a distance $\ell(t)$ from
 282 its parent in the core of the colony. Mathematically, this
 283 self-consistency condition can be expressed as

$$\ell(t)^{d+\mu} \sim t\ell(t/2)^{2d}, \quad (1)$$

284 where the tilde signifies agreement of the leading func-
 285 tional dependence of either side of the relation on the
 286 time variable, without including time-independent pref-
 287 actors or terms whose fractional contributions vanish at
 288 long times. The time-doubling hierarchy and Eq. (1)
 289 form the basis for deriving the asymptotic functional
 290 forms of $\ell(t)$ summarized above; unlike those asymptotic
 291 forms that are valid only at very long times $t \rightarrow \infty$, the
 292 self-consistency condition holds as long as the population
 293 is large enough that an appreciable number of long-range
 294 jumps have occurred [16]. Equation (1) forms a basis for
 295 more accurate functional forms of the outbreak growth
 296 dynamics [16], and also leads to quantitative insights into
 297 the evolution of genetic diversity when multiple variants
 298 are present in a population experiencing long-range dis-
 299 persal [27, 39]. Note that the time-doubling hierarchy
 300 only relies on the assumption of instant local saturation,
 301 and does not require that space be discretized into a reg-
 302 ular lattice of demes.

B. Persistence of initial neutral variation

303
 304 A striking consequence of range expansions is that the
 305 combination of stochasticity and spatial structure can
 306 leave behind patterns of neutral genetic variation that are
 307 typically associated with selection, such as sweep-like en-
 308 richment of individual alleles [10], diversity gradients [11],
 309 and segregation of variants into distinct regions [12].
 310 Simplified models of neutral evolution in spatially struc-
 311 tured populations enable us to understand such patterns
 312 and to distinguish them from the outcomes of selective
 313 events. One aspect of neutral variation that is closely
 314 tied to the mode of dispersal is the persistence of initial
 315 genetic diversity in the originating population during its
 316 expansion into new territory [21, 26]. When dispersal is
 317 exclusively short-ranged, only individuals near the edge
 318 of the range expansion contribute to future variation; in
 319 the absence of new mutations, much of the initial di-
 320 versity can be lost over time due to successive founder
 321 events at the edge. Long-range dispersal enables regions
 322 far within the population to contribute to the expansion,
 323 which maintains their alleles in the growing population
 324 and favors diversity. However, founder effects are not
 325 eliminated: each long-range jump seeds a satellite out-
 326 break in which all offspring share the allelic identity of
 327 the seeding pioneer, acting as a genetic bottleneck which
 328 eliminates diversity locally in the absence of mutations.
 329 The fate of the initial neutral variation as the expansion
 330 progresses is determined by the balance between these
 331 contrasting effects.

332 The evolution of initial neutral diversity in jump-
 333 driven range expansions was analyzed in Ref. 27, us-
 334 ing a lattice model in which neutral variation was intro-
 335 duced in the starting population, and no new mutations
 336 appeared during the expansions. The existence of the
 337 time-doubling hierarchy, Eq. (1), was used to identify an
 338 effective population of homogeneous satellites whose evo-
 339 lution captures the balance between diversification and
 340 coarsening for a given jump kernel exponent. As with the
 341 behavior of the core radius growth, the amount of initial
 342 diversity preserved after a range expansion was shown to
 343 suffer different fates depending on the value of the kernel
 344 exponent relative to the spatial dimension. When $\mu < d$,
 345 the diversifying influence of long jumps dominates; note
 346 the large number of satellites well separated from the
 347 core in Fig. 2g–i. The seeding of many satellites by long-
 348 range dispersal events from the core enables the popu-
 349 lation to preserve a finite amount of its initial heterozy-
 350 gosity at long times. By contrast, when $d < \mu < d + 1$,
 351 the local coarsening of diversity due to bottlenecks be-
 352 comes more significant; note the small number of large
 353 monoclonal satellites in Fig. 2d–f. The heterozygosity
 354 decays inexorably towards zero as the range expansion
 355 progresses, albeit at a slow rate. As μ approaches d , the
 356 heterozygosity approaches a finite value but the conver-
 357 gence to this value becomes extremely slow and cannot
 358 be observed over practical simulation times. Notably, for
 359 $\mu > d + 1$, some diversity is also preserved at long times



FIG. 2. Snapshots of simulated range expansions at different population sizes M . These simulations began with 100 individuals equally split between two neutral alleles, labeled as either purple or yellow in these plots. **a-c.**) Diversity is preserved by the formation of monoallelic sectors for $\mu > d + 1$. **d-f.**) The small number of satellite outbreaks act as bottlenecks, eroding diversity for $d < \mu < d + 1$. **g-i.**) Long-range jumps transport alleles from the core to the exterior of the colony, preserving diversity for $\mu < d$. Additional parameters are $K = 10$ and $p = 0$.

360 due to the formation of sectors in outward range expan- 384
 361 sions, as shown in Fig. 2a-c [12, 30]. Jump kernels of 385
 362 intermediate breadth ($d < \mu < d + 1$) therefore support
 363 lower neutral diversity than broader ($\mu \leq d$) and nar-
 364 rower ($\mu \geq d + 1$) kernels.

365 In summary, Ref. 27 established that long-range dis- 386
 366 persal can preserve some of the genetic diversity from the 387
 367 originating population at long times, but only for jump 388
 368 kernels broader than a dimension-dependent threshold. 389
 369 Narrower kernels cause diversity to erode over the course 390
 370 of the expansion due to successive founder events, which 391
 371 can erase even the limited heterozygosity preserved due 392
 372 to the formation of sectors in range expansions with ex- 393
 373 clusively short-ranged dispersal. However, these features 394
 374 were observed in lattice models which assumed instant lo- 395
 375 cal dynamics and founder-takes-all at the deme level; the 396
 376 influence of slow local saturation on the evolution of het- 397
 377 erozygosity could not be gauged. In this study, we aim to 398
 378 establish whether insights derived from lattice models of 399
 379 range expansions still apply in a continuous-space model 400
 380 for which the lattice model assumptions can be violated 401
 381 to a controllable degree, and to quantify the effect of ex- 402
 382 plicit local dynamics on neutral genetic variation as the 403
 383 expansion progresses. We next introduce our simulation 404

model which we use to investigate these questions.

III. METHODS

386 In order to study jump-driven range expansions which 387
 388 rely on neither a lattice nor the assumption of instant lo- 389
 390 cal dynamics, we used the evolutionary simulation soft- 391
 392 ware SLiM [40] to simulate range expansions on a 2D 393
 394 continuous landscape without restricting ourselves to a 394
 395 lattice of demes. Individuals produce offspring at a con- 395
 396 stant rate, and offspring attempt to establish themselves 396
 397 by dispersing in a random direction with dispersal dis- 397
 398 tances drawn from a jump kernel incorporating short- 398
 399 ranged and long-ranged dispersal which we define below 399
 400 (Eq. (3)). To focus on the effects of the spreading pro- 400
 401 cess and enable direct comparison with previous work 401
 402 (see Section II), our model includes two simplifying as- 402
 403 sumptions. First, each individual has an allelic identity 403
 404 which is passed on exactly to offspring with no possi- 404
 bility of new mutations; this enables us to evaluate the
 persistence of initial neutral variation purely due to dis-
 persal and spatial structure during spreading. Second,
 once offspring are successfully established, they do not

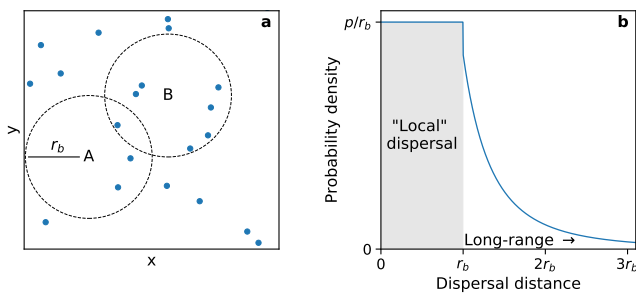


FIG. 3. An outline of the simulation procedure. **a.)** A snapshot of a population during a range expansion. The dots represent individuals in the population. Suppose the local carrying capacity is 5. An individual born at position A would only count three others in its local region (dashed circle centered at A), so it would survive. An individual born at position B would count seven others within its local region. That is too many for the individual to successfully compete against, so it would die. **b.)** An example jump kernel. There is a probability p of dispersing within the “local” (shaded) region, that is, within distance r_b . The jump kernel decays according to the power law $J(r) \sim 1/r^{\mu+1}$ beyond the local region.

405 move, die, or renew themselves. This assumption al-
 406 lows us to hone in on the dynamics of establishment
 407 and expansion, without confounding effects or compu-
 408 tational expense from reshuffling and replenishment of
 409 regions that have already been saturated. Immortality
 410 and immobility post-establishment provide a reasonable
 411 approximation for trees that produce massive numbers of
 412 seeds over scores of growing seasons, or perennial plants
 413 that replenish themselves in place once established. Even
 414 in populations for which these assumptions do not hold,
 415 the patterns left behind by the initial expansion can still
 416 be representative of long-time trends despite the subse-
 417 quent gene flow due to replenishment and reshuffling of
 418 individuals [14, 15].

419 In the absence of demes with a fixed carrying capacity,
 420 a different mechanism to regulate population growth is
 421 needed. We assume that the environment has uniformly-
 422 distributed resources which can support a uniform carry-
 423 ing capacity per unit area, quantified by a maximum
 424 population density ρ . We introduce an interaction dis-
 425 tance r_b which demarcates a disc-shaped region within
 426 which an individual competes with others for resources
 427 (Fig. 3a). The population density and interaction dis-
 428 tance can be combined to define a local carrying capacity
 429 K via

$$K = \rho\pi r_b^2. \quad (2)$$

430 When an individual is born, it undertakes a random dis-
 431 persal event and counts the number of individuals within
 432 the interaction region surrounding its new location. If
 433 there are at least K other individuals in the interaction
 434 region, the duplication event is unsuccessful and the new
 435 individual dies. If there are fewer than K other individ-
 436 als, the new individual establishes successfully in its new
 437 location and survives for the remainder of the simulation.

438 The local interaction region in our continuous-space
 439 simulation resembles the geographic subdivision unit (the
 440 deme) used in lattice-based models. The concept of in-
 441 stantaneous local saturation, or a local founder-takes-
 442 all effect, would therefore correspond to an individual
 443 quickly filling its interaction region with its offspring be-
 444 fore it (or its descendants) attempted any long-range
 445 dispersal events. In order to smoothly depart from the as-
 446 sumptions of the lattice model, it would be useful to con-
 447 trol the fraction of dispersal events which are “local”, i.e.
 448 within the interaction region, as opposed to long-range.
 449 To do so, we used a two-part jump kernel that allows us
 450 to explicitly specify the probabilities of local versus long-
 451 range dispersal, as sketched in Fig. 3b. In full, the jump
 452 kernel is as follows:

$$J(r) = \begin{cases} p/r_b & r \leq r_b \\ \frac{(1-p)}{r_b^{-\mu}} \mu r^{-(\mu+1)} & r > r_b \end{cases} \quad (3)$$

453 where p is the probability of dispersing within the local
 454 region. The short-range part of the jump kernel is cho-
 455 sen to be featureless, with the only notable property be-
 456 ing that the integrated probability $\int_0^{r_b} J(r) dr = p$. The
 457 long-range part of the jump kernel matches the power-law
 458 kernel used in the prior works discussed [16, 27, 39] and
 459 the prefactor ensures the normalization $\int_{r_b}^{\infty} J(r) dr =$
 460 $1 - p$. Jump distances are randomly drawn from this
 461 distribution using inverse transform sampling (detailed
 462 procedure in SI Section VI A).

463 A few comments about our choice of jump kernel,
 464 Eq. (3), are in order. Our aim is not to exactly reproduce
 465 a biologically measured jump distribution at all lengths,
 466 but rather to capture the two main features of interest
 467 in a simplified kernel—a tunable balance between short-
 468 and long-range dispersal determined by the parameter p ,
 469 and a fat-tailed kernel with a specified power-law falloff
 470 controlled by the exponent μ . For simplicity, we chose
 471 the short-range part of the jump kernel to be constant
 472 with distance r ; other forms are expected to lead to sim-
 473 ilar results provided the integrated probability of jump
 474 lengths between 0 and r_b evaluates to p . The chosen
 475 form also implicitly assumes that the same length scale
 476 r_b governs the interaction distance for the density regu-
 477 lation and the dispersal behavior. We could have built
 478 a model with an additional length parameter dictating
 479 the spatial features of the dispersal kernel, but at the
 480 cost of added complexity and a larger parameter space.
 481 Our simplified choice allows us to dial in a specific bal-
 482 ance between local and long-range dispersal by adjusting
 483 the parameter p alone, which enables direct comparisons
 484 of different simulations where the kernel exponent, local
 485 carrying capacity, and size of the density regulation re-
 486 gion are kept unchanged. Since the exact shape of the
 487 jump kernel at short distances is not biologically realis-
 488 tic (for instance, it has a discontinuity at $r = r_b$), we
 489 do not use our model to draw any conclusions about the
 490 spatial distribution of individuals on scales smaller than
 491 the interaction distance.

We now specify appropriate units for length and time in our simulations. Since the individuals and the environment are both featureless, and the same length scale r_b governs both the density regulation and the dispersal, the interaction distance is the natural length unit in our model. In our simulations, we set r_b to one, so that all distances reported from simulations are in units of r_b . Time units are chosen such that each individual generates offspring via a Poisson process with a duplication rate of one; i.e. time is reported in units of the average generation time for an individual. Note that not all offspring survive, because of the density regulation mechanism.

Once the length and time units have been fixed, the consequential parameters are the kernel exponent μ , the probability of local dispersal p , and the local carrying capacity K (which determines the local density ρ via Eq. (2)). Simulations begin with $10K$ individuals whose x and y positions are random draws from a Gaussian distribution with mean zero and standard deviation $2r_b$. Everyone in the population gets a chance to produce offspring every time step, which disperse according to the jump kernel with relevant p and μ and then either survive or don't depending on the population density where they happen to land. Simulations end once the population size exceeds a predetermined threshold, usually four orders of magnitude larger than the initial population size. See SI Section VIA for more details on the simulation procedure.

We next identify characteristic time scales in the problem which will enable us to choose parameters which violate the instant local dynamics and local founder-takes-all assumptions. (For an expanded discussion with potential improvements, see SI Section VIB). First let us consider the characteristic saturation time scale for a single interaction region (which takes the place of a deme in our model). While the full saturation dynamics is complicated because of the influence of offspring from nearby interaction regions, we can make a simplified estimate of the saturation time by considering only the descendants of the pioneer individual which undergo local dispersal. Assuming that all these descendants land in the same interaction region, we have an effective division rate of p (in our units) for the local population. In this simplified model, the interaction region fills up according to a logistic function with growth rate p , for which the saturation dynamics are set by the characteristic time scale $\tau_s \equiv 1/p$. (The actual saturation time for a deme with a discrete population has an additional logarithmic dependence on the carrying capacity, see SI Section VIC; we ignore this weaker dependence compared to the dominant $1/p$ dependence in the present discussion of characteristic time scales.) The saturation time scale must be compared to the typical time for the interaction region to send out long-range jumps. The highest possible rate occurs when the region has saturated to population K and sends out long-range jumps at a rate $K(1-p)$. Therefore, we identify $\tau_j \equiv 1/(K(1-p))$ as the characteristic time scale separating long-range jumps out of an

interaction region. Note that the local saturation time scale is independent of K , whereas the rate of long-range jumps out of an interaction region does depend on K .

The instantaneous local dynamics assumed in the lattice model is approached when the local saturation time is much smaller than the typical time between long-range jumps; i.e. $\tau_s \ll \tau_j$. Using the above estimates for the characteristic times, we find the criterion

$$\frac{p}{1-p} \gg K \quad (4)$$

for fast local dynamics. This criterion is always satisfied as $p \rightarrow 1$. When K is large, p must be at least $1 - 1/K$ for Eq. (4) to be satisfied: for appreciable local carrying capacities, the fraction of local dispersal events must be very close to one for the criterion to hold. If an individual competes with a large number of other individuals in its neighborhood for resources, Eq. (4) is satisfied only if the vast majority of dispersal events are local and long-range jumps are exceedingly rare. Our estimate emphasizes the need for simulations with explicit local dynamics to investigate the broad range of parameters where the lattice model assumptions do not hold during jump-driven range expansions.

The criterion $\tau_s \ll \tau_j$ ensures that new migrants originate from fully saturated regions. To satisfy the second assumption of the lattice model—the local founder-takes-all effect—we additionally require that the characteristic time between the arrival of the first migrant and a potential second migrant by long-range dispersal, which we call τ_2 , is much larger than the local saturation time scale τ_s . Unlike τ_s and τ_j , however, we do not have direct control over τ_2 ; the latter time scale will depend not only on the model parameters but also on the location of the region being colonized. For example, the expected time to second arrival will be different for a region near the core of a colony compared with a region far from the core that was recently seeded by long-range dispersal. Nevertheless, we expect that τ_2 is closely related to the time scale τ_j associated with sequential long-range jumps out of any given region: if long-range dispersal from all regions is exceedingly rare (τ_j is large), it will take a very long time for a second migrant to arrive into a newly colonized region (τ_2 is large as well). Therefore, we use the same criterion, Eq. (4), to gauge whether both assumptions underlying the lattice model are satisfied in our continuum model. In the next section, we directly verify that our simulation results include regimes which violate the assumptions of instantaneous local saturation (Section IV A) and local founder-takes-all (Section IV B), thereby departing strongly from the prior lattice models.

In summary, to violate the lattice model assumptions we require local dispersal probability values comparable to or lower than $1 - 1/K$. If we evenly sample values of p between zero and one, we find that the lattice model assumptions are violated at most parameter values. For instance, if we set the carrying capacity to $K = 10$, the criterion is violated for p values up to around 0.9; when

605 $K = 100$, the criterion is satisfied only for $p > 0.99$. In
606 our simulations, we choose values of carrying capacity K
607 between 10 and 100, and local dispersal probabilities in
608 the range $0 \leq p \leq 0.997$. We expect the lattice model
609 assumptions to be violated over most of these parameter
610 values, except at the upper range of values of p .

611 IV. RESULTS

612 A. Local dynamics are consistent with logistic 613 growth

614 We first analyze the effect of modifying the local dis-
615 persal probability p on the population dynamics within
616 interaction regions. Consider the fate of the interaction
617 region surrounding a pioneer that has landed in an empty
618 part of the range. If all local dispersal events experienced
619 by the pioneer and its offspring landed within the pion-
620 eer's interaction region, we would expect exponential
621 growth of the local population with rate p until the carry-
622 ing capacity K is reached. In practice, the interaction
623 regions of the offspring only partially overlap with that of
624 the pioneer, so the population growth levels off smoothly
625 upon approaching the maximum value. When saturation
626 curves across many interaction regions are averaged for
627 a given set of parameters, the average curve takes on the
628 form of a logistic function as shown in Fig. 4a–b. Upon
629 varying p and μ independently, we find that the satura-
630 tion proceeds faster as p is increased whereas it is not
631 strongly affected by the kernel exponent (Fig. 4b).

632 We use the logistic growth rate, extracted from a two
633 parameter fit to the average growth curves (see SI Sec-
634 tion VIC for details), to quantify the local saturation
635 dynamics. As expected, we find that the growth rate
636 is largely independent of carrying capacity and is de-
637 termined by the local probability p (SI Fig. 12). The
638 growth rate remains nonzero as $p \rightarrow 0$, due to multi-step
639 colonization: although no direct offspring of the pioneer
640 can land in its own interaction region, the descendants
641 of these offspring can land within the interaction region
642 of the pioneer which eventually gets filled. Multi-step ef-
643 fects are also responsible for generating saturation curves
644 whose final population values do not exactly equal the
645 carrying capacity K (plateaus at large t in Fig. 4a–b),
646 as outlined in SI Section VIC. The true saturation value
647 of the population within an interaction region can be ex-
648 tracted from the logistic fit and is denoted as K' .

649 Although the logistic growth rate is set by the local dis-
650 persal probability and not the carrying capacity, the typ-
651 ical time taken to fill the interaction region of a pioneer
652 depends on both quantities. Since the logistic growth
653 function is continuous and strictly reaches K' only as
654 $t \rightarrow \infty$, we define the time taken to reach a local popu-
655 lation of $K' - 1$ as the saturation time for an interaction
656 region. We find that the saturation time falls with in-
657 creasing local dispersal levels, and rises with increasing
658 local carrying capacity, as shown in Fig. 4c. The interac-

659 tion region around a pioneer that seeds a distant satellite
660 takes longer to fill up at low local dispersal rates and/or
661 at high carrying capacities. Notably, the saturation time
662 falls linearly with p , but has a slow (roughly logarithmic)
663 functional dependence on the carrying capacity.

664 B. Slow local saturation invalidates 665 founder-takes-all assumption within interaction 666 regions

667 Slow saturation of the pioneer's local region increases
668 the chance that other individuals who are not descen-
669 dants of the original pioneer will disperse into the region
670 and establish themselves before the region is full. If an
671 individual who arrives later has a different allele than the
672 original pioneer, there will be multiple alleles within the
673 region, which introduces genetic diversity within interac-
674 tion regions in stark contrast to the homogeneous demes
675 imposed by the lattice model. This creates a measurable
676 signal that local saturation times are now comparable to
677 or slower than the typical time gap between the arrivals
678 of first and second migrants by long-range dispersal, τ_2 .

To quantify the deviation of local population structure
from the local founder-takes-all assumption as the satura-
tion time is increased, we introduced neutral genetic
variation in the initial population. Every individual in
the initial population was assigned a unique allele, which
did not affect the dispersal or reproduction dynamics but
was passed on to offspring. The establishment of multi-
ple alleles in the same interaction region was detected by
computing the local heterozygosities in the interaction
region of isolated pioneers. The heterozygosity, H , is the
probability that any two randomly selected individuals
will have different alleles. Upon counting the fraction f_i
of individuals with each neutral allele i in an interaction
region, the heterozygosity of that region is computed as

$$H = 1 - \sum_i f_i^2.$$

679 A nonzero heterozygosity indicates that more than one
680 allele is present in the region; the larger the heterozygos-
681 ity, the more evenly distributed the different alleles are
682 in frequency, corresponding to a region in which no single
683 allele dominates.

684 We averaged the local heterozygosity within the in-
685 teraction regions of many independent pioneers to ob-
686 tain a characteristic measurement of the local diversity
687 for each parameter value. The averaged heterozygosities
688 are normalized against the value at which one ex-
689 pects a fully occupied interaction region to have exactly
690 one individual with a different allele than the pioneer:
691 $H_N \equiv 2(1/K)(1 - 1/K)$. With this definition, the nor-
692 malized average heterozygosity $\langle H \rangle / H_N$ has the following
693 interpretation: normalized average heterozygosities less
694 than one indicate that interaction regions typically have
695 a single allele, whereas values greater than one indicate
696 the expected presence of more than one allele signaling

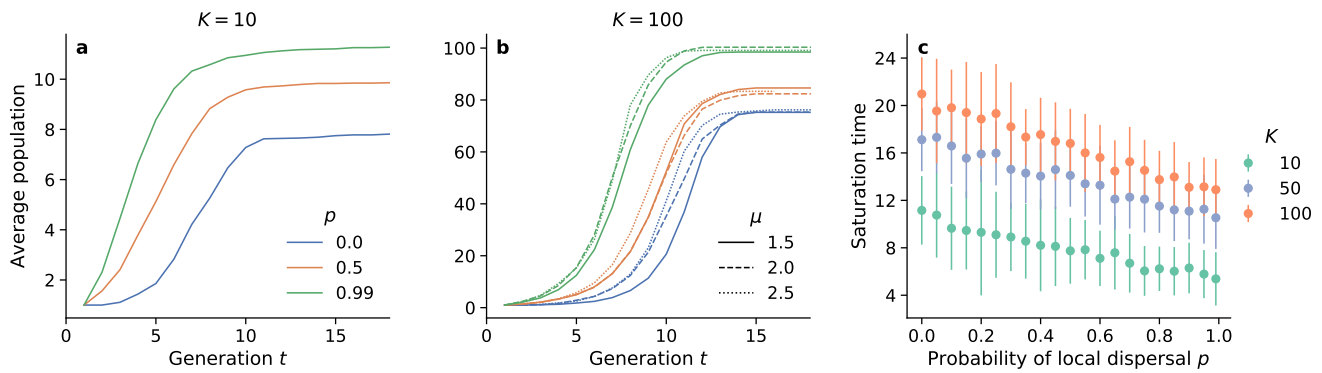


FIG. 4. Saturation dynamics of interaction regions around pioneers. **a.)** and **b.)** show the population growth within the interaction region of pioneers (individuals which land in an empty region) as a function of time from establishment of the pioneer, averaged across many pioneers for different values of p (colors). **a.**, $K = 10$ and $\mu = 1.5$; **b.**, $K = 100$ and three different kernel exponents (dashes). Each curve in panels (a.) and (b.) is the average of the local saturation around approximately 60 pioneers gathered across multiple simulations. **c.)** Saturation time of interaction regions, defined as the time taken for the fitted logistic growth function describing the population within an interaction region to reach one less than the saturating population (see SI Section VIC for details), for $\mu = 1.5$. We fit the logistic growth function to the local saturation data of approximately 60 interaction regions around pioneers and then computed the saturation time for each region based on the fitted growth rate and carrying capacity. The points in the plot are averages and the error bars are the standard deviations of the computed saturation times of individual interaction regions at each set of parameters.

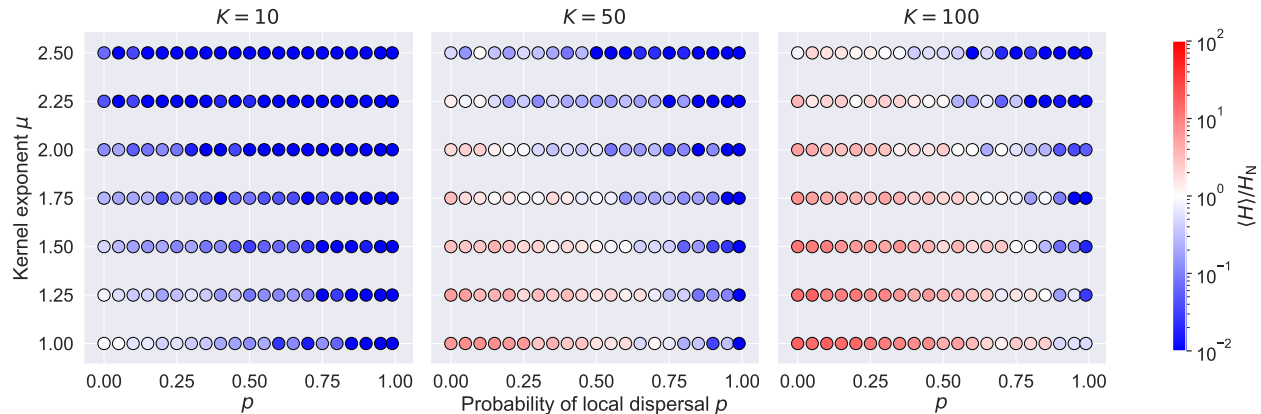


FIG. 5. Influence of slow local dynamics on local diversity. Each symbol represents a triplet of parameter values (K, p, μ) and its color shows the average heterozygosity within the interaction regions around several pioneers who seeded distant satellites, normalized against the heterozygosity at which a fully occupied interaction region is expected to have one individual with an allele different from everyone else in the region. Interaction regions are expected to be homogeneous at parameter combinations where the average normalized heterozygosity is less than one (blue points). They are expected to have more than one allele where the average normalized heterozygosity is greater than one (red points), indicating that other individuals typically disperse into and establish themselves within a pioneer’s interaction region before it fills up with descendants of the pioneer. The values reported come from the averages across about 50 interaction regions gathered from multiple simulations at each set of parameters.

697 a deviation from the founder “taking all” at the level of
698 the interaction region.

699 We find that the local heterozygosity is high at low local
700 dispersal rates and high carrying capacities (Fig. 5),
701 consistent with our expectations from the slow saturation
702 dynamics in this part of parameter space. At the
703 smallest carrying capacity ($K = 10$), heterozygosity levels
704 are low across nearly all jump kernels: local saturation
705 occurs fast enough that interaction regions are filled by

706 descendants of the pioneer individual that first arrived
707 in the vicinity. This situation most closely parallels the
708 lattice models. As the carrying capacity is increased,
709 however, we observe appreciable levels of heterozygosity
710 at low levels of local dispersal where the saturation dy-
711 namics of regulation regions is slowest (Fig. 4c). As the
712 local dispersal rate increases, a smooth crossover occurs
713 from high to low heterozygosity. The value of p at which
714 this crossover occurs is larger for broader jump kernels

715 (lower μ): longer dispersal events favor mixing of alleles.
716 We expect these trends to continue for carrying capacities
717 on either side of the range we show here. For lower carry-
718 ing capacities, local diversity would become lower ev-
719 erywhere. For higher carrying capacities, the boundary
720 between pioneer-dominated and not pioneer-dominated
721 (blue points and red points, respectively) would continue
722 to move to the right. The region of parameter space
723 where founders typically “take all” will continue to shrink
724 as carrying capacity increases.

725 In summary, measurements of local heterozygosity
726 (Fig. 5) indicate a breakdown of founder takes all over
727 wide swaths of parameter space, especially for high carry-
728 ing capacities and broad jump kernels. While local
729 interaction regions remain largely monoallelic when
730 long-range dispersal is very rare ($p \gtrsim 0.9$), we find evi-
731 dence that multiple incursions into the same region leave
732 a persistent contribution to the local genetic makeup
733 within interaction regions when long-range and local dis-
734 persal rates are of similar order. We next investigate
735 the extent to which these *local* deviations from founder
736 takes all impact *global* features of the population ex-
737 pansion, and in particular whether they lead to depart-
738 ures from the population-level behavior of jump-driven
739 range expansions predicted using lattice-based models in
740 Refs. [16, 27].

741 C. Increased long-range dispersal favors faster 742 population growth

743 The salient feature of the global population growth un-
744 der jump-driven expansions is their dramatic speedup
745 compared to expansions that only involve short-range
746 jumps: the typical radial extent of the core region $\ell(t)$
747 grows faster-than-linearly with time when $\mu < d + 1$.
748 This boost occurs because offspring attempting short-
749 range jumps will land close to their parents and siblings,
750 and are more likely to be unsuccessful due to a lack of
751 local carrying capacity. By contrast, long-range jumps
752 tend to transport offspring to empty areas where they
753 establish and proliferate successfully. Therefore, lower
754 values of the local dispersal probability p are expected to
755 favor faster population growth overall, even though the
756 local saturation is slower.

757 We measured the population growth with time, $M(t)$,
758 for many independent range expansions at each parame-
759 ter value. To connect with the results from lattice-based
760 models described in Section II A, we need an estimate of
761 the core region within which the population has reached
762 saturation. When growth is driven by long-range jumps,
763 there is no sharp boundary between occupied and empty
764 regions even in the lattice model. Rather, the local den-
765 sity is close to ρ out to some distance from the origin, be-
766 yond which it crosses over to a power-law decline in den-
767 sity determined by the value of μ [16, 39]. This smoothly
768 varying occupancy profile leaves some ambiguity in pre-
769 cisely defining the core region. We follow Ref. 39 in using

770 the mass-equivalent radius of the population as our best
771 estimate of the core radius from our simulation data:

$$\ell(t) \equiv \sqrt{\frac{M(t)}{\pi\rho}}, \quad (5)$$

772 which provides the required scaling $M(t) \sim [\ell(t)]^d$ [16].
773 This definition assumes that the bulk of the population
774 is present in regions where the population has reached its
775 maximum density locally. We averaged $\ell(t)$ trajectories
776 across different instances at each set of parameters to
777 get a *growth curve* characterizing the average growth in
778 extent of the population.

779 We found that the acceleration of range expansion due
780 to long-range dispersal is preserved in the continuum
781 model, as shown by the growth curves in Fig. 6. We
782 focus on the behavior at long times beyond the satura-
783 tion time scale of a single interaction region (which is of
784 order 10 for $K = 10$, see Fig. 4c). When all dispersal is
785 short-range ($p = 1$), the average colony size approaches
786 a linear relationship at long times (dashed curves; linear
787 fit shown with solid curves at upper right), signifying the
788 expected constant-speed outward advance of the popula-
789 tion front [30]. Small levels of long-range dispersal (solid
790 curves) are sufficient for the size to grow faster than lin-
791 early with time, as evidenced by a steeper slope on log-
792 log axes compared to the dashed curves. The growth
793 at long times appears to be faster than any power law
794 (i.e. faster than linear on log-log axes) for all values of
795 p at $\mu = 1.5$ and $\mu = 2.0$ (Fig. 6a–b), in line with ex-
796 pectations from the lattice model. Growth approaches a
797 power law in time with exponent greater than one at the
798 the two largest p values for $\mu = 2.5$, but is faster than
799 power-law for the smaller values of p over the population
800 sizes simulated. In all cases, decreasing the probability
801 of short-range dispersal speeds up the colony expansion,
802 as expected: long-range jumps are far more likely to land
803 in empty regions and succeed, compared to local jumps.
804 Many consequential features of the expansion, how-
805 ever, are determined not by the absolute growth of the
806 population size with time but by the functional form
807 of the growth. For instance, the qualitative differences
808 in global diversity among different kernel ranges (Sec-
809 tion II B) are owed to the different functional forms of
810 $\ell(t)$ observed in the lattice model (see Section II for a
811 summary). It would be useful to quantify whether and
812 how the local dispersal rate influences the functional form
813 of the population growth curves. A direct comparison
814 of the growth curves to the asymptotic forms derived
815 using the lattice model is not expected to succeed, be-
816 cause the growth curves can take a long time to reach
817 their asymptotic forms, especially for values of μ near the
818 space dimension $d = 2$ [16]. This feature of jump-driven
819 growth is apparent in Fig. 6c, in which the measured
820 growth curves for $\mu = 2.5$ are nonlinear on logarithmic
821 axes and deviate from the asymptotic power-law form
822 even at long times. Instead, we use the self-consistency
823 condition from Ref. 16, Eq. (1), which is expected to

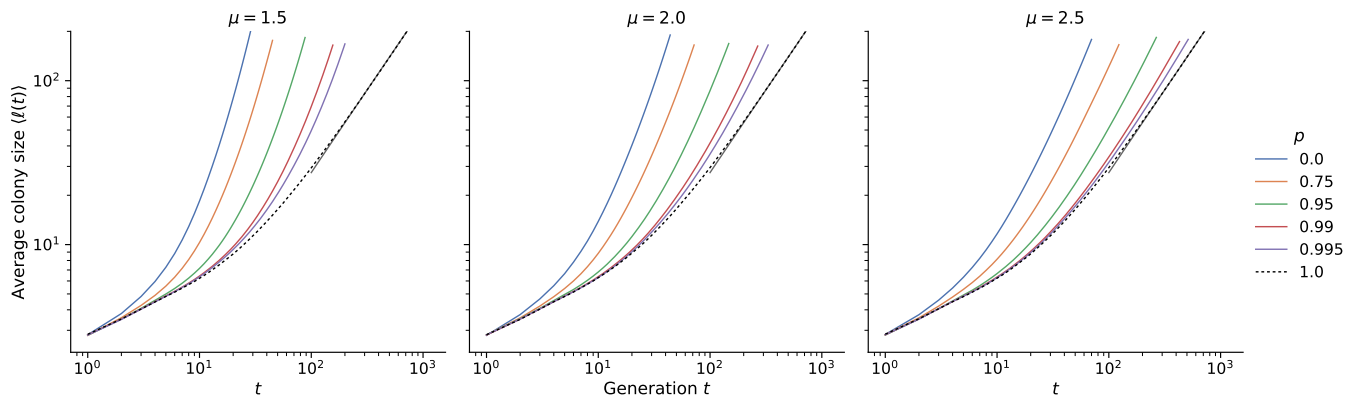


FIG. 6. Average growth curves for different μ and p at $K = 10$. These are averages of growth curves from 241 individual simulations at each set of parameters. Average curves at $K = 100$ are shown in Fig. 11. The dashed line corresponds to simulations with only local dispersal; the resulting growth at long times is consistent with a linear relationship (gray line in the upper right of each panel).

824 hold for times beyond the local saturation time but
 825 well before the time at which the asymptotic regime is
 826 reached in the lattice model. If the entire population
 827 in our continuum model were contained in regions that
 828 have reached local saturation at all times, then the hier-
 829 archy depicted in Fig. 1 would translate to the continuum
 830 model as well, and we would expect Eq. (1) to be satisfied
 831 exactly. This would enable us to predict future popula-
 832 tion growth given only the current population size and
 833 the exponent that characterizes the jump kernel. The
 834 size of deviations from the exact relation could be used
 835 to quantify differences in satellite structure between the
 836 continuum model and the lattice model.

837 To test the validity of the consistency condition and its
 838 ability to predict population growth, we measured the re-
 839 lationship between the colony size $\ell(t)$ at time t and the
 840 quantity $t\ell(t/2)^{2d}$ in our simulations. For t values larger
 841 than the local saturation time (order 20 or less for all pa-
 842 rameters, Fig. 4c), we found that the simulated growth
 843 curves are consistent with a power-law relationship be-
 844 tween the two quantities across the entire range of local
 845 dispersal probability values tested. Data for two repre-
 846 sentative values of p and two local carrying capacities are
 847 shown in Fig. 7; additional curves are shown in SI Fig. 14.
 848 For parameter values which best approximate the as-
 849 sumption of instantaneous filling of density regulation
 850 regions (local dispersal probability close to one and low
 851 carrying capacity), the power-law exponent quantifying
 852 the relationship between $\ell(t)$ and $t\ell(t/2)^{2d}$ also matches
 853 the expected exponent of $d + \mu$ (compare green discs to
 854 dashed line in Fig. 7). By contrast, the relationship no
 855 longer quantitatively matches the consistency condition
 856 when local saturation is slowed down by low values of
 857 p or high values of K . Instead, the population size at
 858 time t is larger than that predicted by the population at
 859 time $t/2$ according to Eq. (1) (square symbols and or-
 860 ange discs in Fig. 7). The functional form of the growth
 861 curve appears to be *faster* than would be expected from

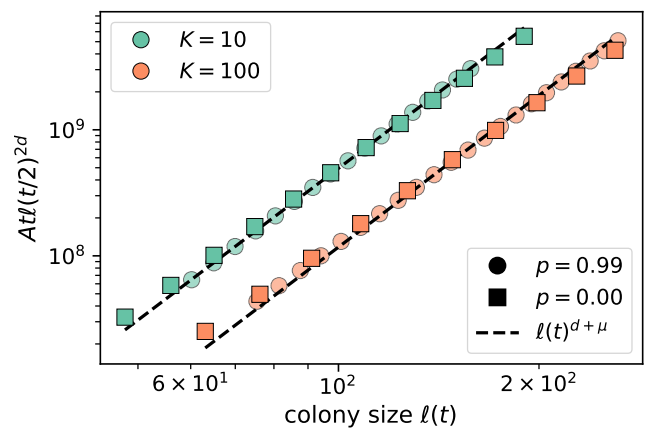


FIG. 7. Quantitative test of the hierarchical time-doubling structure. Plots show the RHS of the consistency condition (Eq. (1)) versus the colony size $\ell(t)$ for $\mu = 2$. Data are from the average of about 200 growth curves at each set of parameters, and only include the second half of the simulation to exclude expected deviations at short times (see SI Section VID for details). The scaling factor A was adjusted manually to overlay data from different p values for ease of comparison of the apparent power-law exponent (slope of curves on log-log scale). Analogous plots at $\mu = 1.5$ and $\mu = 2.5$ are shown in SI Fig. 14.

862 the time doubling hierarchy, so using Eq. (1) leads to an
 863 underestimate of the colony size at time t given its size
 864 at time $t/2$. Note that Fig. 7 is plotted on logarithmic
 865 axes, so the visibly slight difference between the slopes
 866 of sets of symbols and dashed lines corresponds to dif-
 867 ferent power law relationships between $\ell(t)$ and $t\ell(t/2)^{2d}$
 868 in our continuum expansions than what is predicted by
 869 the time doubling hierarchy derived using lattice models
 870 that assume instant saturation of local regions.

871 To quantify the extent of the deviation from the lattice-
 872 model behavior, we fit measurements of the quantity

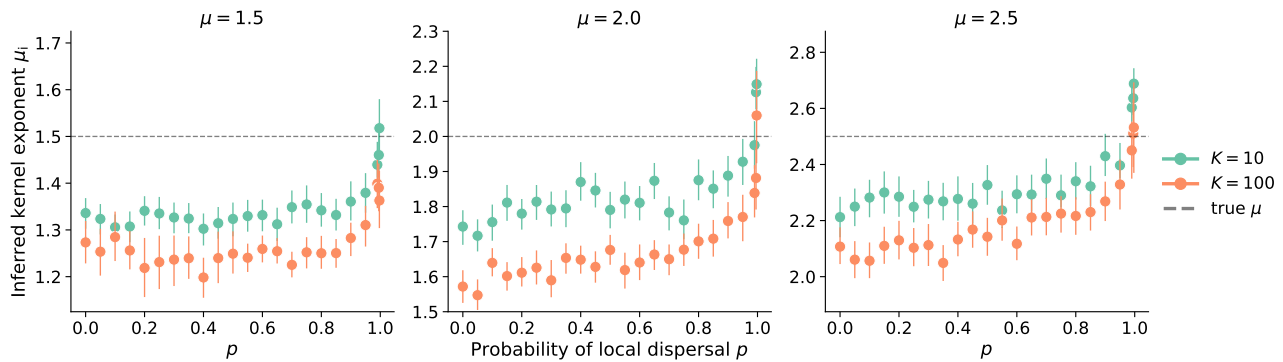


FIG. 8. Inferring kernel exponents using the consistency condition. Symbols show the kernel exponent μ_i inferred for the power law relationship between measured $\ell(t)$ and $t\ell(t/2)^{2d}$ (i.e. the slope in Fig. 7) from many individual simulations. Panels are labeled by the true kernel exponent μ used in simulations. The dashed line indicates $\mu_i = \mu$. Each point represents the mean of the individual inferences from roughly 200 independent simulations and the error bars are the 95% confidence interval of the distribution of bootstrapped mean inferred kernel exponents.

873 $t\ell(t/2)^{2d}$ to the form $B\ell(t)^\nu$ to extract the power-law ex- 912
 874 ponent ν (see SI Section VID for details). This exponent 913
 875 was used to infer a kernel exponent $\mu_i \equiv \nu - d$ from data
 876 such as those shown in Fig. 7, which can be compared
 877 to the true kernel exponent μ . To cover the two dis-
 878 tinct jump-driven growth regimes and the marginal value
 879 $\mu = d$ separating them (as referenced in Section II), we
 880 estimate the kernel exponent from growth curves of pop-
 881 ulations whose jump kernels decay with μ equal to 1.5,
 882 2.0, and 2.5. We find that the inferred kernel exponent
 883 is close to the true exponent when the local dispersal
 884 probability approaches one across all jump kernels and
 885 carrying capacities tested (Fig. 8). This observation is
 886 consistent with our expectation that the limit $p \rightarrow 1$ best
 887 approximates the lattice model assumptions. However,
 888 the inferred kernel exponent is systematically lower than
 889 the true value for much of the range $0 < p < 1$, reflecting
 890 the shallower-than-expected slopes at low local dispersal
 891 in Fig. 7. The inferred exponent grows slowly with the
 892 local dispersal probability up to $p \approx 0.9$, and then rises
 893 sharply toward the true value as $p \rightarrow 1$. This suggests
 894 that there could be some functional change to the struc-
 895 ture of colony expansion as the parameter changes to
 896 nearly all short-range dispersal, while anything less than
 897 nearly all short-range dispersal seems to behave similarly
 898 regardless of p . The deviations also systematically differ
 899 depending on the local carrying capacity, with inferred
 900 exponents at $K = 100$ consistently lower than those
 901 at $K = 10$.

902 We have not isolated the mechanism leading to an in-
 903 ferred kernel exponent μ_i that deviates from the true ker-
 904 nel exponent μ . The fact that $\mu_i < \mu$ implies that the
 905 time-doubling hierarchy from the lattice model, quanti-
 906 fied in Eq. (1), does not hold exactly over much of the
 907 range of p values. Furthermore, it shows again that the
 908 functional form of the population growth with time is
 909 faster in the continuum model than the lattice model.
 910 However, this observation by itself does not provide infor-
 911 mation about how the hierarchy breaks down in the con-

tinuum model, or whether a modified version of Eq. (1)
 might be found for continuum space models.

914 We can nevertheless identify the likely sources of the
 915 discrepancy between the continuum and lattice models
 916 based on our knowledge of the local and global dynam-
 917 ics. The hierarchy in the lattice model was derived under
 918 the assumption that satellites which drive the expansion
 919 originate in a core region that has reached its satura-
 920 tion density nearly everywhere, and whose size scales as
 921 $[M(t)]^{1/d}$. In our simulations, local regions take some
 922 finite amount of time to fill up, but they can begin send-
 923 ing out long range migrants as soon as they are seeded.
 924 An appreciable fraction of satellites may be seeded by
 925 individuals dispersing from regions with local densities
 926 between zero and ρ ; furthermore, the local density could
 927 itself vary significantly through the population. These
 928 deviations become more prevalent for larger carrying ca-
 929 pacities (Fig. 4c), which would suggest larger deviations
 930 at higher values of K consistent with the behavior of the
 931 inferred kernel exponents in Fig. 8.

932 Altogether, measurements in the continuous-space
 933 model reveal small but consistent deviations in the pop-
 934 ulation growth curves from the time-doubling hierarchy
 935 predicted in the lattice model. Our simulations indi-
 936 cate that slow local dynamics introduce corrections to
 937 the time-doubling hierarchy over a large range of values
 938 of the local dispersal probability, consistent with our es-
 939 timates of the parameter regimes for which the lattice
 940 model assumptions break down (Section III). Next, we
 941 numerically investigate the impact of these corrections
 942 on the dynamics of global diversity, for which the hierar-
 943 chy of satellite sizes determined the long-time behavior
 944 in the lattice model as summarized in Section IIB.

D. Increased local diversity boosts global heterozygosity but does not overcome long-term trends

Finally, we investigated the consequences of the enhanced local diversity generated by slow local dynamics (Section IV B and Fig. 5) on the fate of the initial neutral diversity. Recall the predicted evolution of heterozygosity in prior models assuming fast local saturation and local founder-takes-all effects (summarized in Section II B): initial variation decayed steadily towards zero for jump kernels with $2 < \mu < 3$ in two dimensions, but some proportion of the initial diversity was preserved for broader ($\mu < 2$) or narrower ($\mu > 3$) kernels. We simulated range expansions where the initial population had equal proportions of two fitness-equivalent alleles (initial global heterozygosity $H_G = 0.5$) and measured the evolution of global heterozygosity. While the outcome of a single simulation is stochastic, we estimated the expected value of the heterozygosity as a function of population size by averaging the outcomes of many independent runs at each set of parameters. Recall that no new mutations appear during the expansions; here we study the long term fate of any pre-existing diversity present in the initial population rather than the emergence of some balance between the loss of diversity (e.g. due to drift) and the promotion of diversity due to new mutations. Although we used a specific initial heterozygosity in our simulations, we expect the observed trends in the *proportion* of initial diversity over time to hold for other values of initial global heterozygosity as well. This proportion is obtained from our simulation data (Fig. 9) by dividing the reported heterozygosity values by 0.5.

We first considered a set of parameters ($K = 10$, $p = 0.5$) for which each interaction region is dominated by the offspring of the seed individual (Fig. 9a). This situation approximates the local founder-takes-all mechanism of the lattice models, but does not replicate it exactly as multiple incursions into interaction regions are not strictly excluded. Despite the deviations, we find that the evolution of global diversity in the continuum simulations is consistent with expectations from the lattice model when different kernel exponents are compared. (See SI Section VI F for a quantitative comparison.) Average population heterozygosity has settled to a constant proportion of its initial value for $\mu = 1$, and appears to be approaching a constant value as well for $\mu = 1.5$. The slow decay of heterozygosity for $\mu = 2$ is expected; the population may have to grow by several more orders of magnitude before converging to a constant heterozygosity [27]. At $\mu = 2.5$, the heterozygosity decays steadily with no sign of convergence to a finite value, as predicted for lattice models in the range $d < \mu < d + 1$. At $\mu = 4$, a constant heterozygosity is attained at large population sizes due to the formation of persistent sectors with distinct allelic identities (Fig. 2a–c). In each of the growth regimes separated by the critical kernel exponent values of d and $d+1$ (2 and 3 respectively in our two-dimensional

expansions), the behavior of the global heterozygosity follows the qualitative patterns derived in the lattice model. In spite of the small quantitative differences in the hierarchical structure of satellites merging with the core (Fig. 8), the overall differences in structure which determine the balance between diversification and coarsening in jump-driven expansions are maintained deep within the different growth regimes.

Next, we considered parameters $K = 100$, $p = 0$ for which the local founder-takes-all assumption is violated across all kernels tested according to local heterozygosity measurements. We found that the increased local diversity at these values (as indicated by colors in Fig. 5c) contributes to higher global heterozygosities compared to the fast saturation region, as seen in Fig. 9b when compared to Fig. 9a and SI Fig. 16. For instance, at $\mu = 2.5$ the heterozygosity has decayed by around 8% of its initial value when $M/M_0 = 10^4$ in Fig. 9b, in contrast to a reduction by over 20% in Fig. 9a. The same trend is observed at all kernel exponents: The mix of allelic identities within each interaction region under slower local dynamics provides a reservoir of genetic diversity that allows populations to retain much more diversity than possible under the monoallelic regions imposed by fast local saturation. Nevertheless, the qualitative trends in diversity as the kernel exponent is varied continue to track the expectation for lattice models. In particular, the global heterozygosity steadily decays towards zero for $\mu = 2.5$, albeit at a slower rate compared to the $K = 10$ simulations.

A steady decay in heterozygosity is also observed for other values of the local dispersal probability for the same kernel exponent $\mu = 2.5$, see Fig. 9c. Slowing down local dynamics by increasing K and reducing p raises the value of heterozygosity at each population size, but does not prevent the steady decay as a function of M/M_0 . These results show that at long times, the diversity-reducing effect of bottlenecks outweighs the local mixing due to slow saturation dynamics for $\mu = 2.5$. We expect that continual heterozygosity loss will be experienced for other kernels in the range $d < \mu < d + 1$ as well, although the rate of decay will be very slow for kernels close to the critical value of $\mu = d$, and for kernels with slower local dynamics (i.e. large carrying capacity and low local dispersal probability). In this regard, the high local heterozygosities observed for kernels with $\mu > 2$ and low p values in Fig. 5 are transients which we expect to decay to lower values if the expansions are allowed to run longer.

V. DISCUSSION

Range expansions in populations experiencing long-range dispersal can be dominated by the pioneers who travel long distances and seed satellite colonies. Lattice models that assume that these pioneers quickly saturate the carrying capacity within their local interaction re-

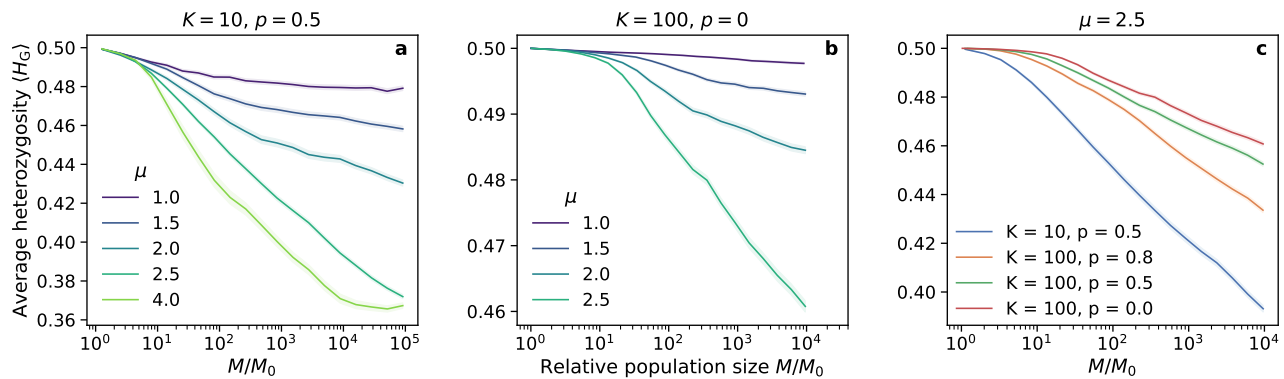


FIG. 9. Evolution of global heterozygosity for different kernels and local dispersal rates. **a.**) Average global heterozygosity as a function of the growing population size for different jump kernels, with $K = 10$ and $p = 0.5$. At these parameters, each interaction region is dominated by a single allele (Fig. 5). **b.**) Same as **a** for $K = 100$ and $p = 0$; at these parameters interaction regions tend to harbor multiple alleles. **c.**) Global heterozygosity curves for $\mu = 2.5$ and different local dynamics traversing the spectrum from monoallelic to multiallelic local interaction regions (blue points to red points in Fig. 5). The $K = 10$ data is the same as in panel (a.) but has been truncated for this plot. Data as a function of relative population size were generated by binning the population sizes from all available simulations and then computing the within-bin $\langle H_G \rangle$; see SI Section VI E for details. Shading reports the standard error of the mean within each bin in all panels, as an estimate of the uncertainty in our estimate of the ensemble average. Data come from about 200 independent simulations for $\mu \leq 2$ in panel (a.) and about 400 simulations for $\mu = 2.5$ in panel (a.) and all of panels (b.) and (c.). The curve for $\mu = 4$ in panel (a.) comes from just 24 runs since simulations with $\mu > d + 1$ take much longer and the sectoring mechanism for preserving diversity is well understood (see Fig. 2a–c).

1057 gion have provided many insights into the dynamics and
 1058 population structure of such range expansions [16, 27].
 1059 However, real populations operate in continuous space
 1060 and with local population dynamics which play out con-
 1061 currently with the global dynamics driven by long jumps.
 1062 In particular, the limits on the rates of long-range disper-
 1063 sal for lattice models to be accurate become increasingly
 1064 strict as the local carrying capacity increases (Eq. (4)).
 1065 We have introduced a continuous-space simulation of
 1066 range expansions which departs from the gridlike spa-
 1067 tial structure and instantaneous local dynamics implied
 1068 in lattice models, enabling us to quantitatively investi-
 1069 gate population growth and neutral diversity in parame-
 1070 ter regimes where the lattice models are not expected to
 1071 be valid.

1072 We found that introducing explicit local dynamics is
 1073 associated with slow local saturation at low local disper-
 1074 sal rates and especially at high local carrying capacities
 1075 (Fig. 4). By contrast, the global population growth oc-
 1076 curs faster when local dispersal rates are low, because of
 1077 the increase in long-range jumps that seed satellite pop-
 1078 ulations in unoccupied regions (Fig. 6). The functional
 1079 forms of the population growth curves show similarities
 1080 with those from lattice-based models (Fig. 7), but with
 1081 small yet quantifiable differences (Fig. 8). We suspect
 1082 that these differences arise due to a violation of a cen-
 1083 tral assumption of the lattice model: that satellites are
 1084 seeded by long-range migrants who disperse from *fully*
 1085 *occupied* source regions. In our continuum model, satel-
 1086 lites can begin sending out long-range migrants as soon
 1087 as they are seeded, which can occur several generations
 1088 before they saturate at high carrying capacities and low

1089 local dispersal rates. In future work, we aim to incorpo-
 1090 rate this feature into the model of hierarchical population
 1091 growth sketched in Fig. 1, which would improve the ac-
 1092 curacy of theoretical predictions for jump-driven range
 1093 expansions in situations where local interaction regions
 1094 are not immediately saturated upon the arrival of a new
 1095 migrant.

1096 We investigated the effects of departing from instan-
 1097 taneous local saturation on both local and global mea-
 1098 surements of neutral diversity. Interrogating the popu-
 1099 lations within individual interaction regions originally
 1100 seeded by a long-range dispersal event reveals that mul-
 1101 tiple lineages, rather than just descendants of the pioneer,
 1102 become likely as local saturation becomes slower (Fig. 5):
 1103 our continuum model violates the assumption of a strictly
 1104 enforced local founder-takes-all effect. Having multiple
 1105 lineages within interaction regions provides a reservoir
 1106 of genetic diversity that also enables greater global het-
 1107 erozygosity outside the regime where local founder-takes-
 1108 all applies: generically, expansions with slower local dy-
 1109 namics exhibit higher global diversity at every stage in
 1110 the expansion (Fig. 9). Nevertheless, the enhancement
 1111 in local diversity is not sufficient to overcome long-time
 1112 trends in global diversity, which continue to be deter-
 1113 mined by the kernel exponent as was shown in the lat-
 1114 tice model [27]. In particular, when $\mu < 2$ the global
 1115 heterozygosity settles to a stable value after an initial
 1116 period of decay, whereas for $2 < \mu < 3$ the heterozy-
 1117 gosity decays steadily as the range expansion progresses
 1118 albeit at a slow rate. The decay is a consequence of
 1119 the repeated coarsening of diversity due to bottlenecks
 1120 as pioneers expand into their newly occupied surround-

1121 ings (Fig. 2d–f). Our results show that this coarsening
1122 is slowed down by the increased local diversity when the
1123 local founder-takes-all assumption is violated, but it is
1124 not completely mitigated and the qualitative long-term
1125 trends in global diversity are similar to those predicted
1126 using the lattice model. This qualitative agreement with
1127 lattice-based predictions is a non-trivial result in light
1128 of recent research [35] showing that models based on a
1129 discretization of space can leave surprising artifacts in
1130 measures of population genetic variation.

1131 Our method of discovering local diversity outside the
1132 local founder-takes-all regime was unable to detect if de-
1133 scendants of an individual other than the pioneer were
1134 within a local region if they happened to have the same
1135 allele as the pioneer by chance. Such information would
1136 be useful to investigate genealogical structure beyond the
1137 fate of the initial neutral diversity in the population, for
1138 example to determine if the pioneer is the most recent
1139 common ancestor of everyone else in the interaction re-
1140 gion or to study the accumulation of additional neutral
1141 mutations during the expansion. A tool like tree se-
1142 quences [41] could readily be incorporated into our com-
1143 putational model to study such questions, which are a
1144 promising target of future work. Understanding the com-
1145 peting effects of local and long-range dynamics on ge-
1146 nealogies in our forward-in-time simulations could also
1147 aid the construction of backward-in-time models that in-
1148 corporate long-range dispersal [42, 43].

1149 Another promising future direction would be to incor-
1150 porate ongoing local competition among all individuals
1151 in the population. In this work, we assumed that estab-
1152 lished individuals never move or die, modeling popula-
1153 tions such as trees which release large numbers of seeds
1154 annually and where young saplings stand little chance
1155 of outcompeting mature trees around them. However,
1156 there are many species of perennial plants, for exam-
1157 ple, where younger individuals can successfully compete
1158 against older individuals in their surroundings. Incorpor-
1159 ating population renewal and density-dependent com-
1160 petition in simulations could provide new insights into
1161 how these species evolve during range expansions. We
1162 suspect that such competition should accelerate the de-
1163 cay of diversity relative to our results for $2 < \mu < 3$
1164 (Fig. 9). Local competition can completely remove alleles
1165 from the population, whereas in our model the “losing”
1166 allele is surrounded but not lost, and retains a nonzero
1167 probability of dispersing an offspring to a faraway vacant
1168 habitat.

1169 This work provides a better understanding of the range
1170 of validity and the limitations of models of long-range
1171 dispersal which rely on instantaneous saturation of local
1172 interaction regions and divide continuous space into a lat-
1173 tice. We have confirmed that the conclusions of the lat-
1174 tice model are upheld in populations where pioneers who
1175 disperse long distances quickly saturate their immediate
1176 surroundings with their descendants; namely in popula-
1177 tions with low local carrying capacities and high local dis-
1178 persal probabilities. Even when the local founder-takes-

1179 all condition is violated, we have shown that qualitative
1180 trends in population growth and in the evolution of neu-
1181 tral diversity mirror those in the lattice model, albeit
1182 with measurable quantitative differences. Heuristics such
1183 as the time-doubling hierarchy of Ref. 16 (Fig. 1) and the
1184 effective population of satellites identified in Ref. 27 re-
1185 main useful to understand the qualitative behavior of ex-
1186 pansion under long-range dispersal in non-lattice mod-
1187 els. Researchers could employ hybrid discrete/continuous
1188 research strategies: identify regimes of interest using the
1189 heuristics of the lattice model, and then test and refine
1190 these predictions in more realistic continuum simulations.

1191 Our results are relevant to understanding and model-
1192 ing the dynamics of range expansions in true biological
1193 populations, including invasive species, populations flee-
1194 ing climate catastrophes, and spreading viruses. We now
1195 have a better understanding of when the first individual
1196 to arrive in a region of space effectively determines the
1197 genetic outcome of all others who will later inhabit the
1198 same immediate area. Experimenters could estimate the
1199 size of the interaction region, the local carrying capac-
1200 ity, and the local dispersal probability in populations of
1201 organisms in the lab or in nature. Estimates of those
1202 quantities could allow researchers to predict whether or
1203 not the founders will “take all” when the population ex-
1204 pands its range outwards into new territory, leading to
1205 insights about how the population will evolve.

1206 DATA AVAILABILITY

1207 Simulation code and the code and data necessary to
1208 generate figures are available in the following GitHub
1209 repository: [https://github.com/paulose-group/explicit-](https://github.com/paulose-group/explicit-local-dynamics)
1210 [local-dynamics](https://github.com/paulose-group/explicit-local-dynamics)

1211 ACKNOWLEDGMENTS

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1213 of this paper. This work benefited from access to the
1214 University of Oregon high performance computing clus-
1215 ter, Talapas.

VI. SUPPLEMENTARY INFORMATION

A. Simulation details

Simulations begin with $10K$ individuals who are given random positions near the origin. Their x and y positions are random draws from a normal distribution with a standard deviation of $2r_b$. Typically about 80% of those individuals survive the density regulation in the first time step. The spatial landscape is large, so the periodic boundary conditions have no effect.

Offspring are produced by cloning without the possibility of mutations, so offspring have the same allele as their parent. Dispersal distances are drawn using inverse transform sampling. Recall, the jump kernel is

$$J(r) = \begin{cases} p/r_b & r \leq r_b \\ \frac{(1-p)}{r_b^{-\mu}} \mu r^{-(\mu+1)} & r > r_b \end{cases} \quad (6)$$

where r_b is the boundary between local and long-range and p is the probability of dispersing within the local region.

We begin the sampling procedure by drawing a random number X from the uniform distribution between 0 and 1. That number X is taken to be the the probability of drawing a dispersal distance less than or equal to some distance x (i.e. the integral of the jump kernel from 0 to x). Solving for x gives us our dispersal distance.

If $X \leq p$, the offspring disperses locally, so we only need to consider the first term of the jump kernel.

$$X = \int_0^x p/r_b dr = \frac{px}{r_b} \rightarrow x = \frac{Xr_b}{p}$$

If $X > p$, the offspring disperses a long distance, so we have

$$X = p + \frac{(1-p)\mu}{r_b^{-\mu}} \int_{r_b}^x r^{-(\mu+1)} dr$$

which leads to

$$x = \left(\frac{(1-p)r_b^\mu}{1-X} \right)^{1/\mu}$$

The dispersal direction is chosen at random from the uniform distribution between 0 and 2π .

All individuals in the population get a chance to produce offspring each time step. Offspring generation is the first thing that happens each time step; the number of offspring for each individual is a random draw from the Poisson distribution with mean 1. Then all newborns *simultaneously* count how many other individuals are within their density regulation regions. This means newborns will count other newborns if they happen to land near each other by chance. It also means that space often doesn't quite fill up to the population density $\rho = K/(\pi r_b^2)$ (as defined in section III). SI Fig. 10

shows how regions of space may appear habitable, and indeed would be if one single offspring were generated and counted its neighbors at a time, but do not saturate since everyone in the population typically produces an offspring every generation and all newborns count their neighbors simultaneously. All individuals produce one offspring per generation on average, so a region saturated to K individuals is expected to have roughly K newborn individuals attempting to establish within that same region every generation. Our density regulation mechanism mimics the biological scenario where none of those newborn individuals are able to get enough resources to survive since there are so many competing for what little is left, a situation termed "scramble competition" in ecology [44]. The typical population that is actually attained in a local density region, which we term K' , is estimated using a fit to a logistic growth curve (see SI Section VI C below), and deviates by at most 20% from K (SI Fig. 12). Alternative choices for the density regulation step, such as randomly choosing a subset of newborns to survive so that local density regions can saturate up to the target value K (the "contest competition" scenario), could also be implemented, but at the cost of additional computational resources which would affect the maximum population sizes and growth times that could be simulated.

We typically let the populations grow by about four orders of magnitude, so simulations were ended once the populations exceeded 10^6 or 10^7 individuals for K equal to 10 or 100, respectively. This allowed core radii to grow by about two orders of magnitude, as shown in the average growth curves at $K = 10$ in Fig. 6 and at $K = 100$ in SI Fig. 11. The solid line indicating the linear relationship between $\langle \ell(t) \rangle$ and t at $p = 1$ in Fig. 6 was generated by fitting a line to the average growth curve from generations 100 to 1000 using NumPy's `polyfit()` function.

B. Time scales

The assumption of instant local saturation in the lattice models relied on a separation of time scales between local and global dynamics: it is valid provided the time scale for saturation of local regions $\tau_s = 1/\alpha$ is small compared to the typical time between long-range dispersal attempts from each "deme" or interaction region, which we call τ_j . In our tunable model, our time units are set such that the characteristic time between reproduction attempts is one. The rate of divisions that land within the interaction region is p , which sets the time scale of the logistic growth. Therefore, the characteristic saturation time of local regions is $\alpha = p$, and as a zeroth-order estimate we have $\tau_s \approx 1/p$. This form is only useful for p close to one, because it ignores the effect of secondary events which land in the interaction region. As a result, the true dependence of α on p is weaker: α grows from 0.4 to 1 as p varies from zero to one (Fig. 12a). Therefore τ_s varies weakly from roughly 2.5 to one over the range

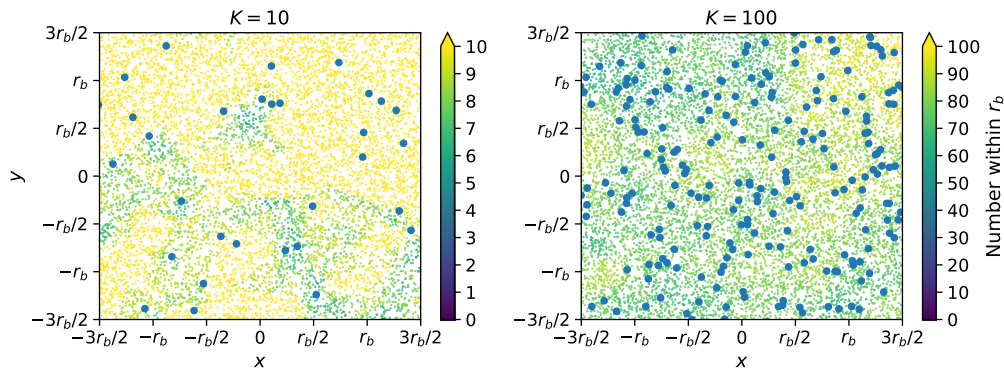


FIG. 10. Space doesn't quite fill up to the local maximum population density ρ . The two panels are snapshots from simulations that grew to roughly fifty thousand individuals. The blue points are individuals, and the color of the small yellow and green dots represents how many individuals are within a distance of r_b of that point. Yellow points represent saturated regions; an individual born there would count at least K within its density regulation region. Non-yellow points look hospitable, and one individual born there would count less than K within its density regulation region, but individuals can't fill those spaces since typically everyone produces an offspring every generation and the newborns "destructively interfere".

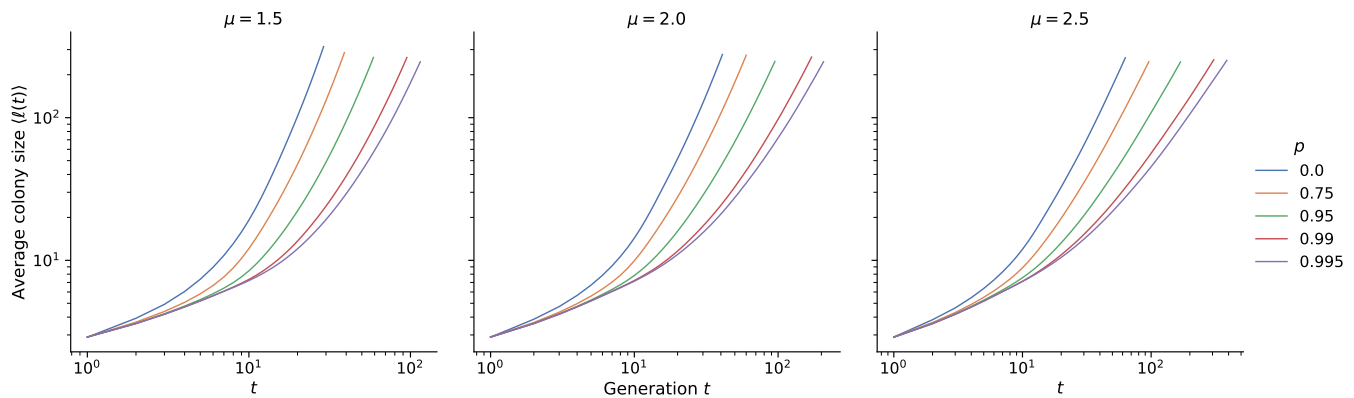


FIG. 11. Average growth curves for different μ and p at $K = 100$. Average curves for $K = 10$ are shown in Fig. 6. These are averages of about 140 growth curves at each set of parameters.

1306 of p values. For a more accurate estimate, we can use the 1312
 1307 phenomenological form $\alpha \approx (1 + p)/2 \Rightarrow \tau_s \approx 2/(1 + p)$ 1313
 1308 which does not diverge as $p \rightarrow 0$.

When regions have reached local saturation, the rate at which each interaction region sends out long-range jumps is $K(1 - p)$. If we assume that the expansion is driven by jumps out of regions that have reached saturation, we have $\tau_j = 1/(K(1 - p))$. Therefore, the condition $\tau_j \gg \tau_s$ reduces to

$$\frac{1}{K(1 - p)} \gg \frac{1}{p},$$

or

$$K \ll \frac{p}{1 - p}.$$

1309 According to this criterion, most of our simulations 1327
 1310 explicitly do not satisfy the separation of time scales as- 1328
 1311 sumed in the lattice model. 1329

C. Logistic growth description of population dynamics within interaction regions

1314 We started the logistic growth measurements by 1315
 1315 searching for sufficiently isolated individuals. To find 1316
 1316 individuals worthy of tracking, we searched at the end 1317
 1317 of every generation for individuals who had no one else 1318
 1318 within a distance of $10r_b$. Those individuals must have 1319
 1319 dispersed a long distance. We searched at the end of ev- 1320
 1320 ery generation until we found at least a predetermined 1321
 1321 minimum number of isolated individuals at the same 1322
 1322 time. We required several at the same time purely for 1323
 1323 convenience on the data processing side; these measure- 1324
 1324 ments could just as well have been gathered one at a 1325
 1325 time as we found the isolated individuals. Nevertheless, 1326
 1326 once we found the isolated individuals, we recorded the 1327
 1327 number within their interaction regions every generation 1328
 1328 until the end of the simulation. The local saturation data 1329
 1329 was then used to fit for logistic growth parameters. We

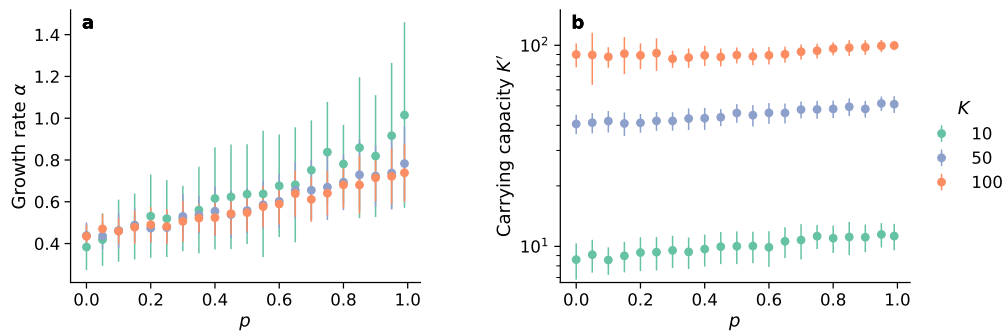


FIG. 12. Fitted logistic growth parameters. **a.)** The growth rate increases with increasing short-range dispersal as expected. It does not depend on the carrying capacity because the growth rate is determined by the early growth of the population before the density regulation restricts population growth. **b.)** The fitted local carrying capacity increases slightly with increasing short-range dispersal. Regions often don't saturate all the way to K as discussed above and shown in Fig. 10. We fit the logistic growth function to the saturation data of about 60 interaction regions across multiple simulations at each set of parameters. The points are averages and the error bars are standard deviations of the individual fits. This data comes from expansions with $\mu = 1.5$ and is what formed the saturation times reported in Fig. 4c.

1330 fit to the logistic function of the form

$$N(t) = \frac{K'}{1 + \left(\frac{K' - N_0}{N_0}\right) e^{-\alpha t}} \quad (7)$$

1331 where $N(t)$ is the population at time t , K' is the local
1332 carrying capacity, α is the growth rate, and the initial
1333 population is $N_0 = 1$. We used SciPy's `curve_fit()` func-
1334 tion to make the fits and obtain K' and α . We performed
1335 the fits on all individual interaction regions around the
1336 initially isolated individuals that we found that filled up
1337 to at least 60% of the local carrying capacity K . Average
1338 values and standard deviations are shown in SI Fig. 12.

1339 We computed the saturation time for an interaction
1340 region by setting the population size in Eq. (7) equal to
1341 $K' - 1$ and then solving for t , which leads to

$$t_{\text{sat}} = \frac{1}{\alpha} \log((K' - 1)^2) \quad (8)$$

1342 In addition to the dominant dependence $\sim 1/\alpha$, where
1343 α is itself proportional to p (see SI Section VIB), we
1344 find a logarithmic dependence of the saturation time on
1345 the local carrying capacity, which arises from the discrete
1346 nature of the local population within a deme. We com-
1347 puted the saturation time for every individual interaction
1348 region for which we fit the logistic growth function, using
1349 values of α and K' from the fits to the logistic function.
1350 We report averages and standard deviations at $\mu = 1.5$
1351 in Fig. 4c.

1352 For the local heterozygosity measurements, every in-
1353 dividual in the initial population had a unique allele.
1354 We tracked the heterozygosity in the interaction regions
1355 of the same individuals for whom we measured logistic
1356 growth as described above (i.e. initially isolated individ-
1357 uals). The heterozygosities reported in Fig. 5 are aver-
1358 ages of heterozygosities measured across typically about
1359 50 separate interaction regions in the final generation of

1360 simulations and gathered from initially isolated individ-
1361 uals in multiple different simulations.

1362 D. Quantitative assessment of time-doubling 1363 hierarchy

1364 We assessed the validity of simulation run times using
1365 the consistency condition $\ell(t)^{d+\mu} \sim t\ell(t/2)^{2d}$ (eq. 1).
1366 The consistency condition is only valid after enough time
1367 has elapsed for long dispersal distances to be the driving
1368 factor behind a colony's growth [16]. It is necessary to
1369 avoid the early times when applying the consistency con-
1370 dition, such as when estimating the kernel exponent as
1371 in Fig. 8. Colony growth remains self-consistent once
1372 the consistency condition becomes valid. For simulations
1373 that ran for T time steps, the values of t we used when
1374 applying the consistency condition ran from $T/2$ to T ,
1375 so the values of $t/2$ ran from $T/4$ to $T/2$. The first data
1376 point we used with the consistency condition is marked
1377 with a red \times in SI Fig. 13. We need at least a handful
1378 of data points after the first one to check for agreement
1379 with the consistency condition and to estimate the kernel
1380 exponent. Our run times were just enough at the lowest
1381 probabilities of local dispersal and gave us many useful
1382 data points at high local dispersal. We compared our
1383 data at $\mu = 2$ against Eq. (1) in Fig. 7; analogous plots
1384 at $\mu = 1.5$ and 2.5 are shown in SI Fig. 14.

1385 The expansions at high local dispersal require many
1386 more time steps to reach the predetermined population
1387 threshold necessary to end simulations than those at low
1388 local dispersal. Expansions at high local dispersal take
1389 longer and grow slower than those at low local dispersal
1390 since offspring are much more likely to land near their
1391 parent in regions that may already be saturated, which
1392 means the times t and sizes $\ell(t/2)$ used here are higher
1393 at high local dispersal. A scaling factor of $A \approx 20$ was
1394 needed to raise the points at low local dispersal to the

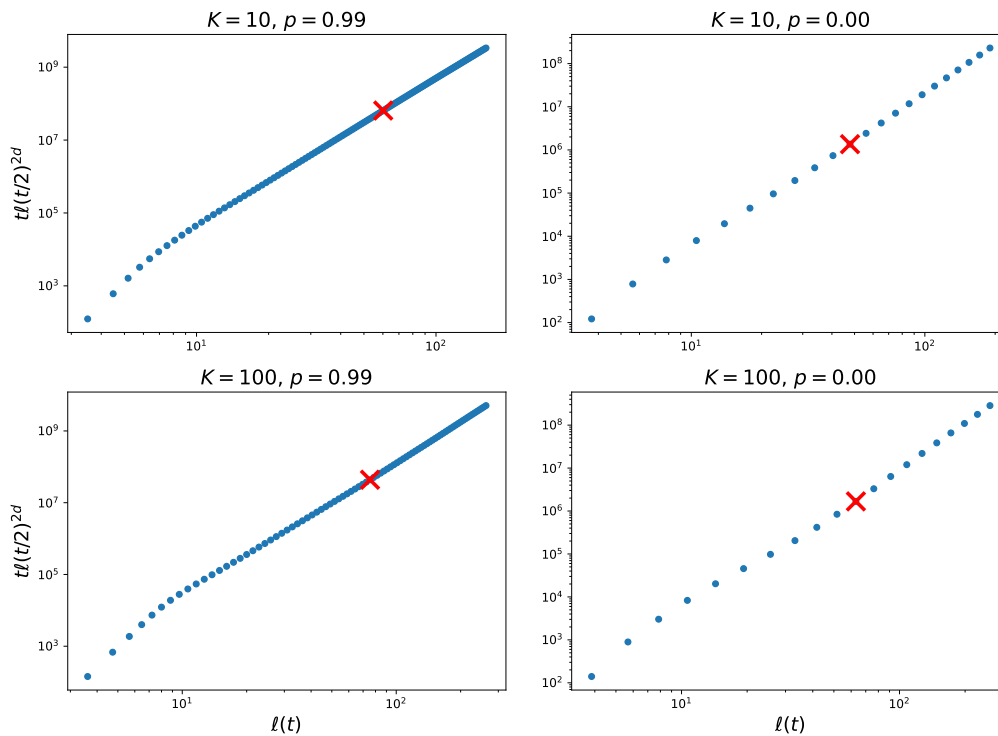


FIG. 13. We show $t\ell(t/2)^{2d}$ plotted against $\ell(t)$ from average growth curves at all sets of parameters that went into figure 7. The dots are points from all even-numbered time steps. Simulations with high values of p require many more time steps to reach a given population size than those with low values of p . We use only the points after the red \times in figure 7 and for inferring the kernel exponent as in figure 8. For simulations to be “long enough,” we needed at least a handful of points once the growth became self-consistent (i.e. linear on these plots). Using average growth curves from expansions at intermediate probabilities of local dispersal result in plots somewhere between these two extremes: more data points in the linear sections than the $p = 0$ case but not as many as in the $p = 0.99$ case.

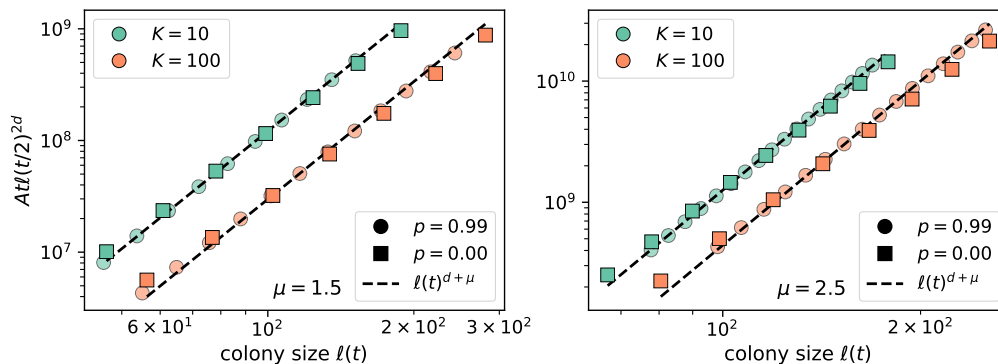


FIG. 14. Analogous to Fig. 7.

1395 level of those at high local dispersal. Bringing them to- 1404
 1396 gether highlights the difference in power laws (slopes) 1405
 1397 between the sets of points at each value of K .

1398 We found the inferred kernel exponent μ_i from the 1404
 1399 growth curves by fitting $B\ell(t)^\nu$ to the quantity $t\ell(t/2)^{2d}$ 1405
 1400 using SciPy’s `curve_fit()` function. We obtained values 1406
 1401 for both the prefactor B and the exponent ν , but only 1407
 1402 the exponent was of any interest for estimating the ker- 1408
 1403 nel exponent from the growth curves. We estimated the 1409
 1410

kernel exponent by performing this fit using data from 1404
 only a later subset of the time steps as discussed in the 1405
 previous paragraph. We then compute the inferred ex- 1406
 ponent as $\mu_i \equiv \nu - d$. We computed μ_i using all available 1407
 growth curves (typically about 200 at any given set of 1408
 parameters) to get the averages and confidence intervals 1409
 reported in Fig. 8. 1410

The exact value of μ_i somewhat depends on the fit 1411
 method. For comparison, we repeated the process of ex- 1412

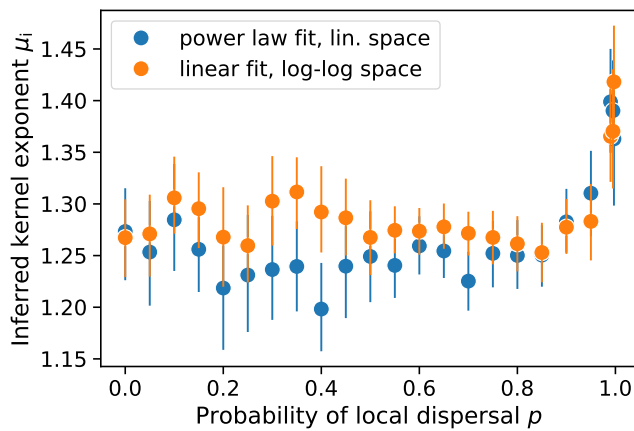


FIG. 15. Example comparison between inferring kernel exponents by directly fitting power laws in linear space and fitting for the slope in log-log space. This example data comes from growth curves with $K = 100$ and $\mu = 1.5$ (same data as the orange points in the left panel of Fig. 8); analogous plots look similar at other pairs of parameters. Each point represents the mean of the individual inferences from roughly 50 independent simulations below $p = 0.5$ and roughly 150 simulations above $p = 0.5$. The error bars are the 95% confidence interval of the distribution of bootstrapped mean inferred kernel exponents.

1413 tracting μ_i by finding the best fit line to the relevant
 1414 data in log-log space, where the exponent could be found
 1415 from the inferred slope. These two values would exactly
 1416 match if we had infinitely long simulations that had perfectly
 1417 converged to constant power laws, but in practice
 1418 that is not the case. There is often a slight difference
 1419 between the average values of μ_i from the two procedures,
 1420 as shown at the example parameters in SI Fig. 15.
 1421 However, we take the generally overlapping error bars as
 1422 a signal that it's safe to proceed with our inferred values.
 1423 This sort of comparison could be used as a test of
 1424 whether or not population growth has converged to the
 1425 expected time-doubling hierarchy: consistent gaps between
 1426 error bars are a warning that simulations may not be long
 1427 enough. This test led us to run longer simulations to
 1428 generate the data shown at $p \leq 0.5$ in SI Fig. 15
 1429 and the corresponding data points in Fig. 8. The longer
 1430 simulations ran until they reached population sizes of 30
 1431 million individuals, triple the size of our usual cutoff for
 1432 simulations with $K = 100$.

1433 E. Reporting the evolution of global heterozygosity

1434 There are multiple reasonable ways to compute and
 1435 display the global heterozygosity as a function of the
 1436 growing population size as in Fig. 9 and SI Fig. 16; here
 1437 we discuss some options and justify our choice. The true
 1438 independent variable in our simulations is time. Every
 1439 time step consists of offspring generation and dispersal
 1440 followed by density regulation as discussed in Section III

1441 and SI Section VI A. Population size and heterozygosity
 1442 are recorded at the end of each time step, after individuals
 1443 have been removed from the population if their birthplaces
 1444 are too densely occupied. This suggests that the “ground truth”
 1445 for reporting the evolution of global heterozygosity might
 1446 be plots of $\langle H_G \rangle$ versus time, where averages and standard
 1447 errors are computed with all available data at a given time
 1448 step.

1449 However, for generalizing results or comparing with the
 1450 results of Ref. 27, it would be useful to compute $\langle H_G \rangle$ as
 1451 a function of the population size. One method of doing this
 1452 would be to compute the averages $\langle H_G \rangle$ and $\langle M/M_0 \rangle$
 1453 each time step. This method ignores what can be significant
 1454 variation in population growth rates between individual
 1455 simulations and generates points whose horizontal and vertical
 1456 coordinates in the plots of Fig. 9 are both functions of time.

1457 We sought to compute $\langle H_G \rangle$ directly as a function of
 1458 population size by generating binned population sizes and
 1459 computing the average heterozygosity from all available
 1460 simulation time steps where the population size was within
 1461 a given bin. This means that a single simulation can contribute
 1462 to a given data point on the $\langle H_G \rangle$ versus M/M_0 curve
 1463 multiple times or not at all depending on how many time steps
 1464 the population size was within that bin in that simulation.
 1465 We used the R function `cut()` to place population sizes
 1466 within 20 bins of equivalent width in logarithmic space,
 1467 thus generating equally spaced data points for Fig. 9 and
 1468 SI Fig. 16.

1469 We use the standard error of the mean to estimate our
 1470 uncertainty in $\langle H_G \rangle$. A consequence of the binning procedure
 1471 is that standard errors of the mean heterozygosity get
 1472 vanishingly small in Fig. 9 and SI Fig. 16, despite the fact
 1473 that the heterozygosity trajectory can vary quite a bit
 1474 between individual simulations. The bins in those figures
 1475 often consist of multiple data points from each simulation,
 1476 especially for the bins at larger population sizes. Even
 1477 though we generally have 200-400 independent simulations
 1478 at each parameter combination shown in those figures, the
 1479 points in the figures are often averages of thousands of
 1480 data points that fall within each bin, resulting in nearly
 1481 invisible uncertainty bands since the standard error of the
 1482 mean is s/\sqrt{N} where s is the sample standard deviation
 1483 and N is the number of samples. Such a large number of
 1484 samples within each bin gives us a small uncertainty in our
 1485 estimate of the average $\langle H_G \rangle$.

1487 F. Direct comparison to lattice model

1488 We used data for lattice-based simulations from Ref. 27
 1489 to compare results between continuum simulations at parameter
 1490 values $K = 10$, $p = 0.5$ where the averaged normal heterozygosity
 1491 is less than one (see Fig. 5), approximating local founder-
 1492 takes-all, and lattice-based simulations where founder-
 1493 takes-all is imposed at the deme level. The initial conditions
 1494 in the two types of simulations were not exactly matched:
 1495 both began with a 50/50

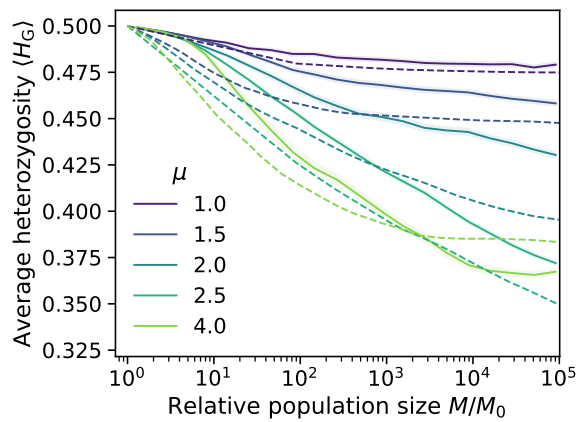


FIG. 16. Direct comparison of heterozygosity evolution in the continuum simulations with fast local dynamics ($K = 10$, $p = 0.5$; solid lines and shading are same as in Fig. 9a) to that of the lattice-based simulations reported in Ref. 27 (dashed lines). In both cases, the initial population had a 50/50 mix of two alleles (initial heterozygosity of 0.5). Kernel exponents match at all values except $\mu = 2.5$ (continuum), for which the same color refers to $\mu = 2.4$ (lattice).

1496 mix of two alleles, but the continuum simulations began
1497 with typically about 80 individuals near the origin (SI
1498 Section VIA) while the lattice-based simulations began
1499 with 111 occupied demes packed in a disc around the
1500 origin. Note that a deme is roughly a discrete analogue
1501 of an interaction region, so the continuum simulations'
1502 80 individuals correspond to roughly $80/K = 8$ occu-
1503 pied demes. Another discrepancy is that Ref. 27 did not
1504 generate data at $\mu = 2.5$, so we include their data from

1505 $\mu = 2.4$ as a comparison with our $\mu = 2.5$ data.

1506 We observe that the difference in initial conditions
1507 leads to different dynamics at early times/small popu-
1508 lation sizes. In the continuum simulations, most of the
1509 early dynamics involves local events which mix and even
1510 out the starting population near the origin, and signifi-
1511 cant changes in heterozygosity only kick in when the pop-
1512 ulation has reached ten times its initial size. By contrast,
1513 the lattice simulations only included long-range jumps,
1514 and the heterozygosity begins to fall earlier. This dis-
1515 crepancy leads to early differences in the observed het-
1516 erozygosities between the two sets of models. However,
1517 the later trends, especially the contrast between a quick
1518 saturation of heterozygosity to a constant value at $\mu = 1$
1519 as opposed to a persistent decay for $\mu = 2.5$ and a decay
1520 followed by a delayed saturation for $\mu = 4.0$, are success-
1521 fully captured by the lattice model. The quantitative
1522 discrepancy between the lattice and continuum values of
1523 $\langle H_G \rangle$ is largest at $\mu = d = 2$, which is a special point
1524 for the underlying dynamics that leads to extremely slow
1525 changes in the heterozygosity [16, 27]; we hypothesize
1526 that the small discrepancy in the initial conditions per-
1527 sists the longest at this special kernel exponent.

1528 We also observe that the continuum $\langle H_G \rangle$ at large
1529 population sizes is higher than that from lattice-based
1530 simulations for all jump-driven kernels ($\mu < 3$). This
1531 is consistent with the observation that while local het-
1532 erozygosity is small in the continuum simulations, it is
1533 not zero for the chosen parameter values of $K = 10$,
1534 $p = 0.5$ (left panel in Fig. 5) and the slight deviations
1535 from local founder takes all promote higher heterozygos-
1536 ity compared to the strict founder-takes-all assumption
1537 of the lattice model.

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