Neutral processes forming large clones during colonization of new areas

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Abstract

In species reproducing both sexually and asexually clones are often more common in recently established populations. Earlier studies have suggested that this pattern arises due to natural selection favouring generally or locally successful genotypes in new environments. Alternatively, as we show here, this pattern may result from neutral processes during species’ range expansions. We model a dioecious species expanding into a new area in which all individuals are capable of both sexual and asexual reproduction, and all individuals have equal survival rates and dispersal distances. Even under conditions that favour sexual recruitment in the long run, colonization starts with an asexual wave. After colonization is completed, a sexual wave erodes clonal dominance. If individuals reproduce more than one season, and with only local dispersal, a few large clones typically dominate for thousands of reproductive seasons. Adding occasional long-distance dispersal, more dominant clones emerge, but they persist for a shorter period of time. The general mechanism involved is simple: edge effects at the expansion front favour asexual (uniparental) recruitment where potential mates are rare. Specifically, our model shows that neutral processes (with respect to genotype fitness) during the population expansion, such as random dispersal and demographic stochasticity, produce genotype patterns that differ from the patterns arising in a selection model. The comparison with empirical data from a post-glacially established seaweed species (Fucus radicans) shows that in this case, a neutral mechanism is strongly supported.

Introduction

Most species in northern Europe, Asia and America established their present distributions following the last glacial maximum about 17 000 years ago. Currently, various human activities bring species into new territories, and this trend is expected to increase rapidly (Bax et al., 2003; Liu et al., 2006; Molnar et al., 2008; Franks et al., 2014). Thus, for a large number of species, it is relevant to ask: what happens to species during and after an expansion into a new territory? Many studies focus on the effects of altered selection pressures (e.g. Keane & Crawley, 2002; Buckley & Bridle, 2014; Svenning et al., 2014), whereas there is surprisingly little work examining the role of neutral mechanisms, that is, mechanisms that do not invoke any selection for or against particular genotypes. During the expansion, neutral processes, such as random dispersal and demographic stochasticity, may be much more
prominent than otherwise and affect the genetic structure of species over extended periods of time (Ibrahim et al., 1996; Excoffier et al., 2009). For example, experimental studies using unicellular and completely asexual organisms that expand into new areas show that populations that are originally composed of a homogeneous mix of genotypes turn into highly structured populations with dominance of single genotypes over large areas solely due to sampling effects (Hallatschek et al., 2007; Excoffier & Ray, 2008).

Many species have the potential to alternate or simultaneously reproduce both sexually and asexually (e.g. Schön et al., 2009; Vallejo-Marín et al., 2010; Dahl et al., 2012; Reichel et al., 2016). Among these, the incidence of asexual recruitment is commonly higher in new territories and in young habitats (Ting & Geller, 2000; Eckert, 2002; Kearney, 2003; Kliber & Eckert, 2005; Tatarov et al., 2005; Liu et al., 2006; Kawecki, 2008; Silvertown, 2008; Vrijenhoek & Parker, 2009). Earlier studies suggest this bias is due to selection favouring specific genotypes that are generally, or locally, successful in the new environment (Parker et al., 1977; Vrijenhoek, 1984; Peck et al., 1998; Stenberg et al., 2003; Kearney, 2005; Hörandl, 2009). Other studies suggest that selection removes the sexual function to prevent inbreeding in small marginal populations (Haag & Ebert, 2004; Pujol et al., 2009). Both groups of models have, however, difficulties in explaining why a majority of species with asexual reproduction has preserved sexual function in the absence of stabilizing selection maintaining sexual traits (Green & Noakes, 1995; Johnson et al., 2010).

Alternatively, and as we suggest here, increased asexual recruitment in colonized territories may be explained by neutral processes, with prominent effects on the sex ratio and the genetic structure of populations. Asexual reproduction is uniparental, and uniparental reproduction generally provides a higher reproductive assurance than bi-parental reproduction when individuals have low mobility, low dispersal capacity of gametes and live thinly scattered (Tomlinson, 1966; Pannell & Barrett, 1998). During establishment of species in new territories, populations at the front of the expansion have low densities, and asexual reproduction is in this case likely to be more efficient than sexual reproduction, unless selfing is possible. For similar reasons, uniparental reproduction is favourable if new habitats are reached by long-distance dispersal (Baker, 1955; Pannell & Barrett, 1998; Bialozym et al., 2006).

The importance of increased asexual (uniparental) reproduction during colonization of new territory in species that may not self-fertilize is poorly understood. Indeed, it is unclear how the spatial and temporal population genetic structure evolves over time if colonization of new areas is by a combination of asexual and sexual recruitment. In large populations, very small proportions of sexual recruitment lead to similar equilibrium genotype diversity as for fully sexually recruiting populations (Bengtsson, 2003). However, during the transient phase of expansion into new areas, when populations have low densities and are fragmented, genotype distribution is likely to be away from equilibrium. This raises an important question: can neutral processes (deterministic and/or stochastic processes that do not involve any selection for or against particular genotypes), and to which extent, contribute to establishing single-clone colonies in newly colonized areas?

To answer this question, we use a spatially explicit model and analyse colonization of a new territory by a species with separate sexes (dioecious), and both sexual and asexual reproduction. Most importantly, our model is fully neutral with respect to genotype survival, dispersal capability and reproduction capacity (in terms of the number of gametes and asexual propagules produced by an individual). As such, our model contrasts with earlier models in which selection is assumed to act on genotype variation (e.g. Parker et al., 1977; Vrijenhoek, 1984; Peck et al., 1998). We have primarily designed the model to investigate an alternative explanation to the strong spatial genetic structure of a young dioecious marine macroalga, Fucus radicans, that recently (less than 8000 years ago) evolved and expanded its distribution in the Baltic Sea (Pereyra et al., 2009), because we failed to generate evidence for genotype selection (see Discussion). The main characteristics of the geographic pattern of sex and clonal bias observed in this species is, however, similar to what is found in several other species of plants, macroalgae and invertebrates with recent range-expansion histories (Ting & Geller, 2000; Eckert, 2002; Saltonstall, 2002; Kliber & Eckert, 2005; Liu et al., 2006; Kawecki, 2008; Silvertown, 2008; Miggletta & Lessios, 2009; Vrijenhoek & Parker, 2009; Halling et al., 2013).

We conclude the study by comparing a number of qualitative predictions arising from our neutral model with the corresponding predictions of a selection-based model, to infer the relative importance of the neutral and selection-based mechanisms for establishing a clonal-biased pattern, as, for example, observed in the seaweed Fucus radicans.

Model and methods

The biology and spatial genetic structure of Fucus radicans

The seaweed Fucus radicans formed less than 8000 years ago from Fucus vesiculosus inside the Baltic Sea (Pereyra et al., 2009). It has since spread and established along the coasts of the northern Baltic Sea (Bothnian Sea), and along the coast of Estonia in the Baltic Proper (Pereyra et al., 2013). Fucus radicans is a perennial, dioecious, facultative asexual species with seasonal
reproduction during the summer. The lifetime of an individual (the diploid thallus) is perceived as relatively long (~10 years, on average, see Discussion). After having reached maturity, both males and females produce gametes as well as asexual fragments (Tatarenkov et al., 2005). Gametes are shed into the water and fertilized externally. The fertilized eggs settle close to the female because of their negative buoyancy (Serra & et al., 1997). Fragments detach from the thallus and reattach to rocks and stones by formation of rhizoids (Tatarenkov et al., 2005). There is no experimental data on how far from the parental plant a fragment usually lands, but it has negative buoyancy and is likely to land close to the parental individual in most cases. However, in very turbulent water (e.g. during storms), fragments as well as larger pieces of thalli are occasionally transported long distances (as has been observed, see Fig. 1). Notably, a new individual grown from a fragment is functionally indistinguishable to one grown from a fertilized egg, that is, both produce gametes and asexual fragments.

Fucus radicans shows a remarkably complex genetic structure. In some areas of its distribution, populations are almost completely sexually recruited whereas in other areas populations are dominated by single clones (Johannesson et al., 2011; Ardehed et al., 2015). Variations among populations within the same region may be large, but the overall trend is a strong dominance of sexual recruitment in south-east and dominance of a few large clones in north-west of the species’ distribution (Fig. 1). One notable observation is the presence of a large female clone that is dominant over more than 550 km of the Swedish coast (Fig. 1, blue sector). This may be due to this clone having superior fitness to other genotypes. Alternatively, neutral processes during the range expansion of F. radicans, that exhibits predominantly short-range dispersal with occasional long-range dispersal, may have contributed significantly to the heavily biased spatial distribution of clonal genotypes and made this clone dominant. To test this hypothesis, we formulate and analyse a mathematical model.

Model

We assume a dioecious species colonizing a new habitat in which each individual may reproduce both sexually and asexually. We do not take into account any adaptation to the conditions of the environment, that is, in our model, all genotypes have exactly the same capacity for both sexual and asexual reproduction, the same dispersal capabilities and the same death rates. In this respect, our approach offers an alternative to existing models analysing establishment in new habitats (e.g. post-glacial, temporal or ecologically marginal environments) as these models assume selection among genotypes (see e.g. Peck et al., 1998; Hörandl, 2009).

Our model is constructed as follows (see also Supporting Information). A habitat consists of $N$ patches of equal quality. Each patch can either be empty or occupied by one individual of known sex. In the model, the patches are arranged linearly in a circle with periodic boundary conditions. This spatial configuration of patches bears a resemblance to the colonization of a coastal region, but it is also relevant for populations distributed in a watershed of interconnected rivers and lakes, a high-altitude area surrounding an alpine landscape or the peripheral parts of a desert.

In the model, individuals have either one (annuals/semelparous) or multiple (perennials/iteroparous) reproductive seasons during their lifetime. In the beginning of each reproductive season, all adults disperse gametes and asexual propagules locally to their near-by sites (short-range dispersal). For simplicity, the short-range dispersal capability of gametes is assumed to be sex-independent and equal to that of asexual propagules. The short-range dispersal displacement $\Delta$ takes integer values from $[-\frac{1}{2}, \frac{1}{2}]$, where $\lfloor x \rfloor$ denotes...
the maximum integer not larger than \( x \), and \( [x] \) denotes the minimum integer not smaller than \( x \). The displacement is sampled from a Gaussian distribution that is symmetric around zero. The distribution is described by a parameter \( \sigma \) such that the mean short-range dispersal distance in units of habitat patches is roughly proportional to \( \sigma \). In particular, the probability \( K_s(\Delta) \) that an individual disperses a gamete or an asexual propagule by a displacement \( \Delta \) via the short-range dispersal is given by

\[
K_s(\Delta) = \frac{1}{N_s} \sum_{k=\infty}^{\infty} \exp \left[ -\frac{(\Delta + kN)^2}{\sigma^2} \right], \quad \text{where} \quad \Delta = -\left\lfloor \frac{N-1}{2} \right\rfloor, \ldots, \left\lceil \frac{N-1}{2} \right\rceil.
\]

(1)

Here, the coefficient \( k \) takes integer values from \(-\infty\) to \( \infty \). Note that this coefficient is introduced for mathematical reasons, due to periodic boundary conditions in the circular habitat with finitely many patches (because, mathematically speaking, such a circular habitat is infinitely long). However, for the values of the parameter \( \sigma \) used in this study, the terms with \( k \neq 0 \) in eqn (1) are negligible compared to the terms with \( k = 0 \). Furthermore,

\[
N_s = \sum_{\Delta=\left\lfloor \frac{N-1}{2} \right\rfloor}^{\left\lceil \frac{N-1}{2} \right\rceil} \sum_{k=\infty}^{\infty} \exp \left[ -\frac{(\Delta + kN)^2}{\sigma^2} \right]
\]

(2)

is a normalization factor. We set the per-season per-individual number of produced fertile eggs (for females), and sperms (for males) that survive dispersal to two. Note that this is not the total per-season number of gametes produced by an individual but rather it corresponds to having one sexual recruit per-individual per-season in a well-mixed population with equal numbers of males and females. Similarly, the per-season per-individual number of produced viable asexual propagules that survive dispersal is set to a constant denoted by \( c \). To allow for comparison of our model to other relevant models with mixed sexual and asexual reproduction, though without a spatial structure (e.g., Bengtsson, 2003), we note that in a well-mixed population with equal number of males and females, \( c = 1 \) means that asexual reproduction has the exact same potential for recruiting a new individual as sexual reproduction (because two gametes of the opposite type are needed for each successful sexual recruitment). Furthermore, when \( c < 1 \), asexual reproduction is expected to be less frequent than sexual reproduction, and the opposite is true for \( c > 1 \). Finally, the frequency of asexual recruits in such a well-mixed population with equal number of males and females is expected to be equal to \( c/(c+1) \). However, a spatial structure may alter the frequencies of asexual and sexual recruits by, for example, introducing an implicit cost of sexual reproduction (because local sexual reproduction is possible only if both sperms and eggs are present locally). Below we evaluate the importance of this effect, and whether it differs during the population-expansion phase and in the equilibrium. We mainly focus on situations where \( c < 1 \) (in which case the cost of sex could potentially lead to having more clonal than sexual recruits, unlike the expectation under the well-mixed model explained above), but we also analyse cases with \( c \geq 1 \). For simplicity, in what follows we refer to \( c \) as the ‘clonal-reproduction parameter’.

Given the dispersal capabilities of propagules, and their rates of production, we compute the birth rates of sexual and asexual recruits in patch \( i = 1, \ldots, N \) in a given reproductive season as follows. First, as sexual reproduction requires the presence of both male and female gametes in the same patch, we estimate the total contributions \( p_f(i) \) and \( p_m(i) \) to patch \( i \) from dispersals by females and males, respectively. In our model, \( p_f(i) \) is given by

\[
P_f(i) = \sum_{j=1}^{N} \left( K_s(\Delta(i,j)) \right), \quad \text{if individual in patch } j \text{ is female,}
\]

\[
P_m(i) = \sum_{j=1}^{N} \left( K_s(\Delta(i,j)) \right), \quad \text{if individual in patch } j \text{ is male,}
\]

\[
P(i) = \begin{cases} 0, & \text{if patch } j \text{ is empty,} \\ 0, & \text{if patch } j \text{ is female,} \\ 1, & \text{if patch } j \text{ is male.} \end{cases}
\]

(3)

Here, \( \Delta(i,j) \) is the displacement between patches \( i \) and \( j \). The corresponding contribution \( p_m(i) \) from dispersals by males to this patch is obtained by replacing ‘male’ by ‘female’, and vice versa on the right-hand side in eqn (3). Thus, females and males contribute \( p_f(i) \) and \( p_m(i) \) asexual propagules, and \( 2p_f(i) \) and \( 2p_m(i) \) gametes to patch \( i \). Second, we assume that the birth rate \( b_j(i) \) of asexual recruits in patch \( i \) is

\[
b_j(i) = c[p_f(i) + p_m(i)].
\]

(4)

Third, the birth rate \( b_j(i) \) of sexual recruits in patch \( i \) is assumed to be limited by the minimum of the total number of potentially successful gametes (as described above) contributed by females, and those contributed by males to this patch, namely

\[
b_j(i) = \min[2p_f(i), 2p_m(i)].
\]

(5)

As already noted, when \( c = 1 \) and \( p_f(i) = p_m(i) = 1/2 \), the potential for sexual reproduction is equal to the potential for asexual reproduction in patch \( i \).

After reproduction adults die at a per-season per-individual death rate \( d \), that is, individuals have on average \( d^{-1} \) reproductive seasons in their lifetime. When \( d = 1 \), all adult individuals die after the first reproductive season (an annual life cycle). Otherwise, when \( d < 1 \), an individual on average experiences multiple reproductive seasons, and the model describes a
perennial life cycle. An adult that dies empties its patch. Each empty patch can be occupied by a single recruit sampled randomly from the sexual and asexual recruits produced in this patch. We assign to a clonal offspring the sex of its parent, whereas sexual recruits are males or females with equal probability. At the end of the reproductive season, the new recruits that establish in the habitat are treated as reproductively mature adults.

Finally, prior to the next dispersal of propagules, the adults or vegetative fragments may relocate through the process of long-range dispersal at a per-individual per-season rate $r$. When $r = 0$, long-range dispersal does not occur. Otherwise, when $r > 0$, long-range dispersal occurs, and we assume that it occurs rarely ($r \ll 1$). The destination patch is drawn from a symmetric power-law distribution with a parameter $\beta$ (Supporting Information). When $\beta$ is larger than, but sufficiently close to unity, typical long-range dispersal distances are of the order of the size of the available habitat. If the destination patch is already occupied, the dispersing individual dies. Otherwise, the dispersing individual occupies the destination patch. Note that rare long-range dispersal of clonal fragments, asexual offspring or apomorphic seeds (hereafter collectively referred to as ‘asexual propagules’) are valid alternatives to rare long-range dispersal of adult individuals in the model (see Supporting Information).

In addition to the model described, we also analyse two modified versions. In one (see Supporting Information), we assume that only females have the capacity for both sexual and asexual reproduction, whereas males are not able to reproduce asexually (all else being the same as in the model explained above). In this model, the birth rate of clonal recruits in patch $i$ is computed as

$$b_c(i) = c \lambda n(i),$$

whereas the birth rate of sexual recruits is computed according to eqn (5). In another modified version, we assume long-range dispersal of sexually produced seeds instead of adults or asexual propagules. For further details, see Supporting Information.

**Parameter choices**

We investigate the models for different combinations of parameter values (Table 1). The values of the death rate $d$ are chosen from a wide range to include annual species ($d = 1$) up to very long-lived perennial species ($d = 0.005$, 200 reproductive seasons). For the clonal-reproduction parameter $c$, we mostly use $c \leq 1$, but we also consider cases where $c > 1$. In most of the simulations, we set the habitat size (total number of patches) to $N = 4000$, but we also analyse the model for $N = 2000$, 8000, and 16 000. To obtain a mean short-range dispersal distance that is much smaller than the habitat size, we set $\alpha = 3$, or 6. Conversely, to accomplish long dispersal distances in the process of long-range dispersal, we set the parameter $\beta$ to a value close to unity ($\beta = 1.25$). For long-range dispersal to be rare, we choose small values of the long-range dispersal rate ($r \ll 1$). Most of the simulations are run for up to 20 000 reproductive seasons.

To be able to characterize the genetic structure of the population, we label each individual at the start of each simulation with a unique number (‘ID’) that is copied upon long-range dispersal and asexual reproduction. Individuals originating from sexual reproduction receive a new unique ID. Simulations are initialized with 100 populated patches arranged side by side along a single origin, neighbouring individuals having opposite sexes (50 females and 50 males). We specifically choose this initial condition because it assures maximum mixing of males and females at the start of the expansion (alternating sexes), has no sex bias at small local scales and hence minimizes the risk that asexual reproduction is initially promoted over sexual. This starting arrangement mimics a population that has survived through a perturbation (e.g. a glacial period) in a small area and from there expands into an empty habitat when conditions improve. Alternatively, it mimics a population that expands into a new territory after a human introduction to one part of the new area.

Finally, because the model is stochastic, for each set of parameters, we perform 100 independent simulations (unless stated otherwise).

**Results**

Due to the effect of random fluctuations, all populations bounded by a finite maximum size and with finite per-individual birth rates must eventually experience extinction (Eriksson et al., 2013). For the model parameters tested (Table 1), we observe that the population initialized with 100 individuals experiences rapid extinction when the death rate is high ($d = 1$, corresponding to annuals), the mean short-range dispersal distance is small ($\alpha = 3$, or 6), and the clonal-

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**Table 1** Parameters of the model, their explanations and the values used in the computer simulations.

| Parameter | Explanation | Values |
|-----------|-------------|--------|
| $N$       | Number of patches in the habitat | 2000, 4000, 8000, 16 000 |
| $c$       | Per-season per-individual number of produced viable asexual propagules surviving dispersal (‘clonal-reproduction parameter’) | $0 \leq c \leq 2$ |
| $d$       | Per-season per-individual death rate | 0.005, 0.01, 0.1, 1 |
| $\alpha$  | Short-range dispersal parameter | 3, 6 |
| $\beta$   | Long-range dispersal parameter | 1.25 |
| $r$       | Per-season per-individual long-range dispersal rate | $0, 10^{-4}, 10^{-3}$ |
reproduction parameter is low ($c \leq 0.2$). These cases are, therefore, omitted from further analysis. Furthermore, due to random sequences of births and deaths in a population of finite size, the population must eventually reach the state where one sex is globally lost and the other is fixed (unless the population experiences extinction prior to global fixation). The time to reach global fixation is, however, typically very long (much longer than the timescales analysed here), and it is expected to scale exponentially with the population size. Within the tested values of the model parameters (excluding the parameters for which the population experiences rapid extinction) and during the time span examined in the simulations, we do not find any cases of global fixation, except under the modified version of the model in which males are incapable of asexual reproduction (see Discussion and Supporting Information). Therefore, global fixation is not further considered here.

**Short-range dispersal dynamics**

When long-range dispersal is not possible ($r = 0$), the sexual structure and the underlying genetic structure of the population depend sensitively on the clonal-reproduction parameter (i.e. $c$; recall that the per-season per-individual number of produced fertile gametes surviving dispersal is set to two), as well as on the death rate ($d$). When the clonal-reproduction parameter is low ($c \ll 1$), the sexes are essentially homogeneously distributed both in space and time, with only small patches of single-sex dominance (Fig. 2a,d). By contrast, for higher values of the clonal-reproduction parameter ($c > 0.3$ for $d = 0.1$), large single-sex (and single-genotype) colonies are established, one at each edge of the expansion (Fig. 2b–c,e–f). Note, however, that $c$ need not be larger than 1 for this to happen, that is, sexual recruitment would still be more successful than asexual recruitment in a well-mixed random population.

![Fig. 2 Sexual patterns in populations with different clonal-reproduction parameter ($c$). Panels a-c: space-time patterns of local sex ratios (pools of eight neighbouring patches) obtained from single stochastic realizations of the model with $c = 0.2$ in a, $c = 0.5$ in b and $c = 1$ in c. Empty patches are coloured white. Panels d-f: time dependence of the average frequency of occupied patches (black line), and of the average frequency of asexually recruited individuals (blue line) for the parameter values in a-c, respectively. Grey lines depict the results of independent simulations (100 runs). Note that, due to periodic boundary conditions, the decrease of asexual recruitment after colonization is faster when the clonal colonies established at the different sides of the origin of colonization are of the opposite sexes (grey lines below the solid blue line in e, f) than when they are of the same sex (grey lines above the solid blue line in c, f). Initial configuration: 100 neighbouring patches occupied, alternating sexes. Remaining parameters: $N = 4000$, $a = 3$, $d = 0.1$, $r = 0$. © 2017 THE AUTHORS. J. EVOL. BIEL. 30 (2017) 1544–1560 JOURNAL OF EVOLUTIONARY BIOLOGY PUBLISHED BY JOHN WILEY & SONS LTD ON BEHALF OF EUROPEAN SOCIETY FOR EVOLUTIONARY BIOLOGY.
mating population. Similarly, with a high death rate (short life span), an essentially homogeneous distribution of sexes appears in space and time when the clonal-reproduction parameter is low (Figs 3a,d, S1A), but large single-sex colonies are formed for perennial species with longer lifetimes (Fig. 3b–c,e–f).

In cases of clone formation, we observe three phases of spatial distribution of sexes. The first phase occurs during the spread into the new territory and is characterized by an expansion of single-sex colonies consisting of single clones. The ‘asexual wave’ moves faster for higher clonal-reproduction parameters (Fig. 2b–c). Whereas sexual recruitment of new individuals is prevented in the single-sex areas, sexual reproduction progressively spreads from the centre of the expansion (‘a sexual wave’, see spread of regions with a homogeneous sex ratio in Figs 2–3). The speed of the sexual wave is slower for higher clonal-reproduction parameter (Fig. 2a–c) and for longer life spans (Fig. 3a–c).

Notably, for the parameters set in Fig. 2b (e.g. average lifetime of 10 reproductive seasons), the population is dominated by a pair of large clones during colonization and long thereafter (12 000–18 000 reproductive seasons) despite, in this case, the clonal-reproduction parameter being $c = 0.5$.

The second phase starts roughly when the habitat becomes fully occupied. In this phase, large single-sex colonies formed during colonization shrink in size as the region, where sexual reproduction is possible, expands. The sexual wave expands slowly and clonal colonies persist for longer times under higher clonal reproduction and/or longer life span of individuals (Figs 2e–f, 3e–f).

The third phase starts when the dominant clonal colonies finally disappear. In this phase, the overall frequency of asexually recruited individuals fluctuates around a constant value suggesting that the population has reached a quasi-steady state. (‘Quasi’ because, as
pointed out above, the population must eventually experience global fixation, unless it experiences extinction first.) The frequency of asexually recruited individuals in this phase is larger when the clonal-reproduction parameter $c$ is higher (compare Fig. 2d to e at the end of the time span shown, and see Fig. S2), but it is approximately the same for different values of death rate $d$ (results not shown). Note also that the sexes in this phase are essentially homogeneously distributed and single-sex colonies with up to roughly a hundred individuals appear temporarily (e.g. Fig. 2c). In contrast to the single-clone colonies that dominate during colonization, each single-sex colony in the quasi-steady state typically consists of multiple clones of the same sex. Note that due to the emergence of these temporal single-sex colonies, the frequency of asexual recruits in the quasi-steady state (Fig. S2) is slightly larger than $c/(c+1)$, which is the expected frequency in a well-mixed population with equal number of males and females (see Model). Finally, single-sex colonies and the overall frequency of asexually recruited individuals in the three phases discussed are larger for smaller values of the short-range dispersal parameter ($\alpha$) (compare Fig. 2b,e to Fig. S3A and D).

Dynamics with occasional long-range dispersal

The three phases of spatial distribution of sexes discussed above are also present in populations with occasional long-range dispersal, although with several noticeable differences to dynamics with only short-range dispersal. Firstly, long-range dispersal increases the speed of colonization of the empty habitat (Figs 4, 5). Secondly, with long-range dispersal, a clone can spread and dominate in multiple (distant) areas (Fig. 5b–c). Thirdly, more than two dominant clones typically form during the colonization phase with long-range dispersal (compare Fig. 5b–c to a). The reason is that additional clones could be established following a long-range dispersal event of a fragment (or similar) of a genotype that is a sexual descendant of dominant clones. Fourthly, the persistence time is on average shorter, and the size of individual clonal colonies formed during colonization are on average smaller with long-range dispersal. This effect is stronger for higher rates of dispersal (Fig. 5). Note, however, that the persistence time and size of the dominant clones are very different between individual runs with otherwise the same parameter values (grey lines in Fig. 5e–f).

In larger habitats, the spatial patterns emerging in the model are similar to those described above (Figs S4–S5), although large single-sex colonies, and widely spread dominant clones are more likely to be obtained in larger habitats (grey lines in Figs S4D–F and S5D–F). As expected, the number of local colonies established by a dominant clone increases with increasing the habitat size (Fig. S5A–C). These effects arise because typical long-range dispersal distances are larger in larger habitats, and so are chances for a single clonal lineage to establish in multiple, distant locations.

Dynamics in two alternative versions of the model

In the model with males reproducing solely sexually, and females reproducing both sexually and clonally, we find that the main model predictions are retained, except that clonal colonies in this case consist exclusively of females (Fig. S6), and that for very high clonal reproduction ($c \geq 1$), males are likely to go extinct during the early colonization phase (Fig. S6C).

Finally, in the model with long-range dispersal of sexually produced seeds instead of clonal fragments, we find that local clonal structures are likely to be formed (Fig. S7), but the geographic spread of a dominant clone is smaller than when clonal fragments have the potential to disperse long distances (Fig. S8). Consequently, with dispersal of sexual seeds, it is very unlikely that a single clone dominates multiple distinct and widespread geographic areas.

Discussion

Our model applies to dioecious species with predominantly local dispersal of recruits and a capacity for both sexual and asexual reproduction. Examples of such species are found frequently among seaweeds and invertebrates, and to a minor degree among aquatic and terrestrial plants. In what follows, we discuss our model results under the assumptions of sexual systems and life histories presented earlier.

General results and model mechanisms

We know from earlier studies (Baker, 1955) that local clonal colonies are expected to form when a population with long-range dispersal capacity colonizes a new area. Now our model results suggest that in perennial dioecious organisms, clonal dominance arises and persists over an extended period of time even without long-range dispersal. The clonal dominance during expansion results from single-clone colonies that compose the front of the colonization (‘an asexual wave’). Notably, an asexual wave develops even if asexual recruits will be less common than sexual recruits in the equilibrium phase (‘quasi-steady state’). Consequently, an asexual wave formed during colonization of a new habitat under these conditions is a transient phenomenon and occurs due to two effects. Firstly, sexual reproduction requires mates of opposite sexes to be present locally, and this requirement is critical at the expansion edge where the density of mates is reduced in comparison with the density in central parts of the population. This phenomenon introduces an implicit cost to sexual
reproduction that is not expected in a well-mixed random mating population. This implicit cost of sexual reproduction alone could provide reproductive advantage to asexual reproduction during the expansion, even if the opposite is true in the quasi-steady state (long after the expansion process is completed). To investigate this, we have compared the speed at which a fully sexually reproducing population expands, to the speed at which a fully asexually reproducing population expands, accounting for different values of the clonal-reproduction parameter \( c \), and the death rate \( d \) (see Figs 6, 7). This analysis allowed us to estimate the critical value of the clonal-reproduction parameter \( c_{\text{crit}} \) above which clonal reproduction is expected to have a reproductive advantage over sexual reproduction during the expansion \( c_{\text{crit}} \approx 0.34 \) for \( d = 0.1 \), and \( c_{\text{crit}} \approx 0.17 \) for \( d = 0.01 \). Note that the reduced speed of the expansion of sexually as opposed to clonally reproducing populations when the number of asexual propagules produced by an individual is less than 1 (cost of sexual reproduction, as explained above) occurs primarily because the population expands over an empty habitat where potential mates are missing (but the expansion is still possible thanks to the dispersal of gametes). This predominantly deterministic component of the cost is additionally strengthened by demographic stochastic fluctuations at the expansion edge, where a few nearby individuals may, by chance, be of the same sex.

We have additionally investigated spatial sexual and genotype patterns emerging in our model for populations reproducing by a combination of clonal and sexual reproduction with values of \( c \) that are close to, but

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**Fig. 4** Sexual patterns in populations without and with long-range dispersal of adults, fragments or asexual propagules. The values of the long-range dispersal rate are \( r = 0 \) in a and d, \( r = 10^{-4} \) in b and e, and \( r = 10^{-3} \) in c and f. For the explanation of the results shown in different panels, refer to the caption of Fig. 2. Please note that the panels differ by the time spans shown. The parameters in panel a correspond to those in Fig. 2b, but here we show the pattern obtained from a different stochastic realization of the model. The results in panel d are the same as those shown in Fig. 2e. Remaining parameters used: \( \beta = 1.25, N = 4000, x = 3, d = 0.1, c = 0.5, 100 \) stochastic realizations in d-f.
Interestingly, for \( c = 0.32 \) and \( d = 0.1 \), as well as for \( c = 0.15 \) and \( d = 0.01 \), we find that the expansion occurs also in the form of a clonal wave (Figs 6c, 7c). This occurs because stochastic demographic fluctuations at the expansion front leading to establishing, by chance, a few nearby individuals of the same sex, additionally enhance the clonal component of the reproduction in the population (in comparison to the sexual component). Indeed, once the sex ratio at the expansion edge is perturbed away from the equal sex ratio, sexual reproduction is hindered locally but individuals at the expansion front may still reproduce by means of clonal reproduction. Notably, in situations where individuals have fewer reproductive seasons during their lifetime (larger \( d \)), the perturbed sex ratio at the expansion front is expected to be retrieved more rapidly than when individuals are more long-lived (smaller \( d \)) thanks to the expansion of sexual recruits from more central areas. The retrieval is quicker when \( d \) is larger for two reasons. First, the waiting time for sexual recruits to invade on already occupied areas scales linearly with \( d^{-1} \). Secondly, the size of clonal areas at the expansion edge, that sexual recruits need to invade in order to retrieve the sex ratio, is smaller when \( d \) is larger. This implies that when the death rate \( (d) \) is smaller (longer lifetimes), the conditions for the population to maintain and expand clonal colonies at the expansion edge are weaker than when \( d \) is larger. This is consistent with results shown in Figs 3, 6 and 7.

As sexual recruits are simultaneously produced and spread from the central part of the population, unbiased sex ratios will at a later stage, by means of a ‘sexual

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**Fig. 5** Dominant clones underlying the sexual patterns depicted in Fig. 4 (note that colours in this figure have a different meaning than in Fig. 4). Panels a–c: space-time patterns of the five largest clonal colonies (coloured red, green, blue, yellow and magenta) with only short-range dispersal in a \( (r = 0) \), and with both short-range dispersal and occasional long-range dispersal of adults, fragments or asexual propagules in b, \( c (r = 10^{-4} \text{ and } r = 10^{-6}) \), respectively. Genotypes differing from the five largest clones are coloured grey. Empty patches are coloured white. Panels d–f: grey lines show the frequency of the largest dominant clone as a function of time from 100 independent realizations of the model for the parameters used in panels a–c, respectively. Red lines are averages over the individual runs. Black line shows time dependence of the average frequency of occupied patches. Remaining parameters used: \( \beta = 1.25, N = 4000, \alpha = 3, d = 0.1, c = 0.5 \), 100 stochastic realizations in d–f.
wave', be retrieved in areas initially occupied by clones, as explained above. Hence, after the colonization of an empty habitat is completed, the asexual wave is brought to a halt and the sexual wave starts to catch up and progressively erode the clonal colonies. However, this process is slow when individuals are long-lived (d is small), because the sexual wave can only progress when already occupied patches at the expansion front are
emptied. In fact, the speed of the sexual wave is roughly proportional to \( d \) (compare slopes of blue curves in the post-colonization phase in Fig. 3b–c).

For most combinations of death rate (\( d \)) and clonal reproduction (\( c \)), asexual reproduction at the expansion front forms clonal colonies (Figs 2–3, 6–7). This is true for highly perennial populations (\( d \ll 1 \)) even when sexual recruitment is much more successful than asexual recruitment in the long run (\( c \ll 1 \)). For shorter lived perennial organisms (\( 0.01 < d < 1 \)), the minimum value of \( c \) above which clonal colonies are formed is higher, but still such that sexual recruitment is more successful than asexual recruitment in the long run (\( c \ll 1 \)). For annual species, circumstances under which an asexual wave is formed are much more restrictive; that is, in the long run, asexual reproduction should be slightly more successful than sexual reproduction for an asexual wave to be established (\( c > 1 \)). This somewhat contrasts the expectations in a metapopulation scenario with low migration, and/or high extinction rates of local populations, as investigated by Pannell & Barrett (1998). In their study, uniparental (e.g. asexual) reproduction in annual species provided higher reproductive assurance than bi-parental (e.g. sexual) reproduction, whereas conditions were less restrictive in perennial species. This finding, however, is based on a comparison of the capacity for colonization of empty patches by annual or perennial bi-parental species, as compared to uniparental species. In this case, perennial bi-parental immigrants benefit from a longer waiting time to find mates and establish colonies and are thus more successful than annual bi-parental species. The model presented here, however, considers species with capacity for both asexual and sexual reproduction. As explained above, in this case colonization typically occurs by means of an asexual wave. During the colonization of a new habitat, the first wave (the asexual wave) more persistently prevents colonization by the second wave (the sexual wave) if individuals are long-lived.

In our model, an annual population with a poor asexual capacity may fail in colonizing a new habitat altogether. However, with individuals of a long lifetime, or a high per-season per-individual rate of production of sexually recruited offspring, risk of failure diminishes (results not shown), as also pointed out by Pannell & Barrett (1998) but for obligate sexual species.

Adding occasional long-range dispersal in our model to a species with mostly restricted dispersal has both short-term and long-term effects. Primarily it facilitates colonization of new habitats by already established dominant clones so that they appear in multiple sites. In this way, and in line with what was originally suggested by Baker (1955), long-range dispersal increases the spatial separation of sexual and clonal recruits. By this mechanism, occasional long-range dispersal also increases the number of dominant clones. The reason for this is that new genotypes produced in areas with sexual activity occasionally disperse and establish in new areas and from here initiate new asexual waves. Secondarily, occasional long-range dispersal also promotes the introduction of individuals of opposite sex into established clonal areas, thereby facilitating the erosion of existing clonal colonies.

Our finding that the expansion occurs in the form of an asexual wave even when an asexually reproducing population is not expected to grow faster than a sexually reproducing population during the expansion (Figs 6, 7), is akin to earlier findings of ‘allelic surfing’ (Edmonds et al., 2004; Klopfstein et al., 2006; Excoffier & Ray, 2008; see also Berestycki et al., 2013; as well as a discussion on ‘area effects’ in, e.g. Goodhart, 1963). In both allelic surfing and under area effects, neutral stochastic processes rather than selection for or against particular genotypes determine the structure of populations during transient stages. These transient stages may be short or long. In our model, perennials of average lifetimes of 5–10 or more reproductive seasons, form dominant clones that persist for thousands to tens of thousands of reproductive seasons (Figs 3, 6). This timescale is relevant not only for very recent species invasions but also for post-glacial colonization of northern habitats.

**Comparison of model results with empirical data**

In our model, the mechanism by which some genotypes come to dominate the new population is neutral, that is it does not invoke selection for or against particular genotypes. Indeed, the genotype dominance arises simply because it gains an access to a larger available habitat than the other individuals. In this respect, our model offers an alternative, or a complement, to models of the expansion process in situations when dispersal is predominantly short-ranged, in combination with stochastic demographic effects at the expansion edge that additionally promote clonal reproduction locally and hinder the expansion of sexual recruits even so a population reproduces by both mechanisms. Once the asexual wave takes over the expansion front, one of the individuals at the expansion front obtains a reproductive advantage over the other individuals in the habitat, simply because it gains an access to a larger available habitat than the other individuals. In this respect, our model offers an alternative, or a complement, to models that suggest structural patterns after colonization to be a consequence of selection on genotype variation (e.g. Parker et al., 1977; Vrijenhoek, 1984; Peck et al., 1998; Kearney, 2005). To illustrate how the two types of models may be contrasted and compared, we first examine the predictions of our neutral model if parameterized by data from the seaweed *Fucus radicans*. In the next step, we outline predictions of our neutral model and of the selection-based model and compare qualitative patterns observed in *F. radicans* with model predictions.
As already described, *F. radicans* is dioecious and both females and males are capable of sexual and asexual reproduction. Although it is known to be long-lived and perennial, to our knowledge, there is no direct estimate of individual lifetime in this species. We have instead used data from the related fucoid species (*Ascophyllum nodosum*) that lives in similar habitats as *F. radicans* in the Atlantic. Measuring survival rates of marked individuals Aberg (1992) estimated maximum lifetime in *A. nodosum* to be 50–60 years. With this as a guideline we assume an average lifetime in *F. radicans* of at least 10 years, corresponding to \( d \leq 0.1 \) in our model. Under this assumption, the minimum clonal-reproduction parameter \( c \) for which we expect clonal dominance at the expansion front in *F. radicans* is around 0.3 (for \( d = 0.1 \), see Fig. 6), or smaller (for \( d < 0.1 \), see Fig. 7). As we find large areas where clones are rare (e.g. Estonia, see Fig. 1), we expect that asexual reproduction is, in the long run, either less or equally successful as sexual reproduction. Thus, assuming that \( d = 0.1 \), we conclude that \( 0.3 < c \leq 1 \) in *F. radicans*. For \( c = 0.5 \) and \( d = 0.1 \), and with occasional long-distance dispersal (as observed in *F. radicans*, see Fig. 1), our neutral model generates two asexual waves, one in each of the two expansion fronts, resulting in large areas dominated by single clones. Due to occasional long-distance dispersal, additional clones dominating relatively large areas get established during the expansion phase (Figs 4–5). We note that this model result is in agreement with the empirical finding of a few widespread (and very old) clones in *F. radicans* (Fig. 1). After about 1000 years (Fig. 4b) the model predicts that the new area becomes completely filled up, but it takes additionally 10 000 years before the sexual wave finally erodes the large clones. Note that these estimates are based on our model results with \( N = 4000 \). In reality, however, the total number of patches (individuals) is likely much larger. Increasing the number of patches, while keeping all other parameters the same, the time to the completion of colonization, and the persistence time of clonal colonies is expected to be even larger than the estimates given above.

Five specific predictions from our neutral model can be compared with empirical data retrieved from earlier studies of *F. radicans*.

**Prediction 1**
The neutral model predicts a strong distributional bias in sex ratio in recently colonized areas dominated by one sex and single clones, whereas the sexual wave has eroded this bias near the original area. Under selection, asexual recruitment is expected in ecologically marginal habitats (Vrijenhoek, 1984; Peck *et al.*, 1998). Unfortunately, these predictions are difficult to separate in practice, as the younger habitats may also be the more ecologically marginal habitats. This seems true in *F. radicans* where colonization presumably started in central Baltic and proceeded towards younger and more marginal areas in the north. This model comparison thus remains inconclusive in this case.

**Prediction 2**
The neutral model predicts that the few clones that happen to be at the front at start of the expansion will efficiently spread by the asexual wave and become widely distributed. Under selection, it is more likely that different environmental conditions will favour different local clones recruited from local sexual events. In *F. radicans*, the largest clone has an extensive geographic distribution that dominates most populations sampled over 550 km of shore line spanning latitudinal gradients in, for example, salinity and temperature (Fig. 1). It seems unlikely that selection is uniform over the wide ecological and geographic ranges occupied by this large clone, and its distribution is more compatible with predictions of the neutral model.

**Prediction 3**
Following the arguments above, the neutral model predicts the most dominant clones to be the same as those established at the front of the asexual waves when these waves were initiated. The dominant clones are thus, most likely, the oldest clones. Under selection, by contrast, it seems likely that, over time, earlier dominant clones are replaced by new and more competitive ones, potentially introduced by long-range dispersal. In *F. radicans*, the dominant clones are indeed very old. The most widespread clone, for example, has accumulated numerous somatic mutations that suggests this clone may be thousands of years old (Ardehed *et al.*, 2015). This observation is therefore more compatible with a neutral mechanism.

**Prediction 4**
Under selection, fitness of a locally dominant clone is expected to be higher than fitness of other genotypes present in the same area, whereas a neutral model makes no such predictions. Empirical tests of genotype fitness are limited by what aspects of fitness are actually tested, and in what context. Keeping this in mind, experimental tests of performance of some dominant clones (including the most widely distributed clone) in *F. radicans* show that none of them are more tolerant to physical stresses than sexually recruited genotypes from the same area (Johannesson *et al.*, 2012). Moreover, the most widely distributed clone has a similar growth rate and similar capacity for asexual reproduction as two less widely distributed clones (Johansson, 2013). This far, there is thus no support for a positive correlation between clonal dominance and fitness. This prediction is, therefore, also more compatible with a neutral than a selection-based mechanism.
Prediction 5

Under a neutral scenario, there is no selection among genotypes with different capacities for asexual and sexual reproduction. Under selection, on the other hand, successful genotypes maintained by asexual reproduction will be favoured in ecologically marginal areas. As there will be a trade-off between investing in sexual and asexual propagules, sexual reproduction is likely to be locally lost, or reduced, by selection in marginal, as compared to central areas. In particular, old dominant clones are most likely to have lost (or significantly reduced) their sexual function. In *F. radicans*, members of the large clones remain sexually active and produce gametes at similar rates as other individuals (Forslund & Kautsky, 2013), supporting a neutral model over a selection-based model.

Model relevance – other species

Sex ratios are biased in many species that have invaded new territories (see Introduction), but even more interesting is that in several of these species a few large clones dominate the new area despite a mix of genotypes being present in the native area (Ting & Geller, 2000; Eckert, 2002; Saltonstall, 2002; Reitzel et al., 2008; Halling et al., 2013). For some of these species, it has also been observed that members of the dominant clones have the potential to be sexually active (Green & Noakes, 1995; Kliber & Eckert, 2005; Johnson et al., 2010). This suggests that the reason for cloning in these cases is not primarily selection against sexual recruitment.

We have modified our model to test its relevance for some additional life-history strategies. Thus, for a dioecious species where only one sex is able to reproduce both sexually and asexually (e.g. water fleas and aphids, Yin et al., 2012; Gilabert et al., 2015), the model outcome does not change significantly. Our model of long-range dispersal of adults or vegetative parts is relevant for macroalgae, aquatic invertebrates, and some aquatic plants (Ingólfssoon, 1995; Rothäusler et al., 2015) but many terrestrial plant species disperse long
distances by sexually produced seeds. The model results show that long-distance dispersal by sexually produced seeds leads to formation of local clones that are unlikely to spread to multiple distant areas. Empirical data support this model prediction as widely distributed dominant clones are found in species dispersed by adults or fragments living in aquatic environments (Freeland et al., 2000; Ting & Geller, 2000; Eckert et al., 2003; Kliber & Eckert, 2005; Darling et al., 2009; Pettay et al., 2009; Koenders et al., 2012), whereas aquatic and terrestrial plants dispersed by sexual seeds tend to have local clones (Waycott et al., 1996; Carino & Daehler, 1999; Reusch, 2001; Paun et al., 2006; Wilk et al., 2009).

Conclusion

A geographic sexual bias with large and dominant clones in some areas and mostly sexual recruitment in other areas can be generated under two different but not mutually exclusive mechanisms, namely (i) selection for fixation of the most fit genotype (Fig. 8, right) and (ii) neutral processes (i.e. random dispersal and demographic stochasticity) in an expanding spatially structured population where all genotypes have the same fitness (Fig. 8, left). In what follows we do not consider species in which asexual recruitment is overall more efficient than sexual recruitment, as such species are expected to be highly asexual over their complete distribution (Fig. S1). Furthermore, we focus on a post-colonization stage that is transient but long-lasting. We find that whether the prevailing mechanism for establishing a clonal bias is neutral or selection-based depends on the individual’s life span and the relative rate of asexual and sexual reproduction. (The more detailed pattern depends on the rate of long-distance dispersal and if this is by adults, vegetative parts or seeds.) For species with a longer life span, expansion is dominated by the asexual wave of colonization. Consequently, genotype distribution is largely neutral, even when the rate of sexual reproduction is relatively high compared to the rate of asexual reproduction (Fig. 8, left). Notably, under the asexual expansion wave, selection is efficiently eliminated by the absence of genotype variation. For an annual species, by contrast, neutral mechanisms during expansion are weak, and instead, it expands by a sexual wave (Fig. 8, right). Sexual reproduction is here a major source of new genotypes, and this provides an opportunity for selection for generally or locally fit genotypes that may be fixed under selection against sexual recombination. Indeed, selection has widely been invoked as a general mechanism behind dominance of asexual recruitment in recently, and relatively recently (post-glacial) invaded areas (Parker et al., 1977; Vrijenhoek, 1984; Peck et al., 1998; Kearney, 2005). Our conclusion, however, is that under circumstances of long-lived (perennial) dioecious and mainly locally recruited species, a fully neutral model is more likely to explain clonal dominance and sexual bias in recently, or relatively recently colonized areas. The clonal dominance is transient, but even so it persists over time periods relevant for most human-mediated and post-glacial invasions. Eventually, following the sexual wave, the transient stage will be replaced by an equilibrium-like stage during which genotype variation will recover. Notably, our model considers one-dimensional habitats, such as a shoreline, but we expect that the main conclusions obtained in this study will be retained in two-dimensional habitats, although local clonal structures are likely to be more complex than described here (e.g. the establishment of more clones during the expansion process). However, a more detailed investigation of a model involving a two-dimensional habitat would potentially allow for assessing the conditions under which genotypes are distributed in a guerrilla-like or a phalanx-like pattern (Ardehed et al., 2015).

As illustrated here for the seaweed Fucus radicans, a modelling approach can provide predictions that can be compared with empirical data on age and distribution of single clones, annual or perennial life-styles, estimates of average life span, mechanisms and rate of dispersal, and (if available) relative per-individual investments in asexual compared to sexual reproduction. Such a qualitative comparison of empirical data and model prediction is a necessary step to argue for a neutral or a selection-based explanation for clonal bias in individual species.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article: Figure S1 Spatial sexual patterns in annuals.
Figure S2 Frequency of asexual recruits as a function of time.
Figure S3 The importance of the short-range dispersal parameter *α*.
Figure S4 The importance of the habitat size.
Figure S5 The importance of the habitat size for the distribution of dominant clones.
Figure S6 Sexual patterns in the model with males reproducing only sexually, and females reproducing both sexually and asexually.
Figure S7 The effect of long-range dispersal of sexually produced seeds on the sexual structure.
Figure S8 The effect of long-range dispersal of sexually produced seeds on the dominant clones.
Appendix S1 Implementation of the model.
Appendix S2 Simulations with males reproducing only sexually.
Appendix S3 Simulations with long-range dispersal of seeds instead of adults.

Data deposited at Dryad: https://doi.org/10.5061/dryad.02c47.

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