Coevolution of patch-type dependent emigration and patch-type dependent immigration

Helene C. Weigang

Department of Mathematics and Statistics, University of Helsinki, P.O. Box 68, FI-00014 Helsinki, Finland

ARTICLE INFO

ABSTRACT

The three phases of dispersal - emigration, transfer and immigration - are affecting each other and the former and latter decisions may depend on patch types. Despite the inevitable fact of the complexity of the dispersal process, patch-type dependencies of dispersal decisions modelled as emigration and immigration are usually missing in theoretical dispersal models. Here, I investigate the coevolution of patch-type dependent emigration and patch-type dependent immigration in an extended Hamilton–May model. The dispersing population inhabits a landscape structured into many patches of two types and disperses during a continuous-time season. The trait under consideration is a four dimensional vector consisting of two values for emigration probability from the patches and two values for immigration probability into the patches of each type. Using the adaptive dynamics approach I show that four qualitatively different dispersal strategies may evolve in different parameter regions, including a counterintuitive strategy, where patches of one type are fully dispersed from (emigration probability is one) but individuals nevertheless always immigrate into them during the dispersal season (immigration probability is one). I present examples of evolutionary branching in a wide parameter range, when the patches with high local death rate during the dispersal season guarantee a high expected disperser output. I find that two dispersal strategies can coexist after evolutionary branching: a strategy with full immigration only into the patches with high expected disperser output coexists with a strategy that immigrates into any patch. Stochastic simulations agree with the numerical predictions. Since evolutionary branching is also found when immigration evolves alone, the present study is adding coevolutionary constraints on the emigration traits and hence finds that the coevolution of a higher dimensional trait sometimes hinders evolutionary diversification.

1. Introduction

Dispersal is a widely studied life-history trait that evolved because of many selective pressures (Ronce, 2007). Although it has been studied for decades, only recently studies have emphasised that dispersal has three phases: emigration or departure, transience or movement and immigration or settlement (Bonte et al., 2012; Clobert et al., 2009; Jacob et al., 2015; Metz and Gyllenberg, 2001; Travis et al., 2012) and that all phases interact on different levels. Whereas transience or movement happens usually during a continuous time phase, emigration and settlement choices are instant - discrete time - decisions. Understanding the complex dispersal behaviour is becoming increasingly more important as the vast majority of species experiences threats by global warming and climate change. Timing (Cote et al., 2016), costs (Bonte et al., 2012), patch-type dependent conditions, e.g., host plants or resource availability (Matter and Roland, 2002;

Schneider et al., 2003), or various other cues (Bowler and Benton, 2005), e.g., indirect information (Clobert et al., 2009; Cote and Clobert, 2007), all influence the non-random decisions to move and stop moving in heterogeneous environments. In turn, individuals have evolved ways to perceive and assess the local conditions of the environment (Doyle, 1975; Ehlinger, 1990; Garant et al., 2005; Matter and Roland, 2002; Schooley and Wiens, 2003; Zollner and Lima, 1999) and base their dispersal decisions on the cues and signals they encounter (Hanski, 2011; Hanski et al., 2002; Hey and Houle, 1987; Jaenike and Holt, 1991; Mitchell, 1977; Myers et al., 1981; Rees, 1969).

The empirical literature is jaded with condition dependencies at the three different dispersal stages, but mathematical models seldom incorporate such complexity. The only relative well-studied dependency is density-dependence. Many theoretical studies have investigated density-dependent emigration (Hovestadt et al., 2010; Kun and Scheuring, 2006; Poethke and Hovestadt, 2002; Poethke et al., 2007; Travis et al., 1999), or predator- or prey-density-

dependent emigration (Sjödin et al., 2015; 2014), whereas only very few have touched upon the evolution of density-dependent emigration and immigration (Metz and Gyllenberg, 2001; Parvinen et al., 2012; Poethke et al., 2011; Saether et al., 1999), or on density-dependent immigration (Nonaka et al., 2013; Parvinen and Brännström, 2016). These studies focused on density dependency, but did neglect other characteristics of the patch. Some studies allowed emigration decisions based on density and on the number of immigrants (immigrant-dependent dispersal; see Chaine et al., 2013), or on body-condition and patch-type (Bonte and De La Peña, 2009; Gyllenberg et al., 2011a; 2011b), but ignored dependencies of immigration decisions.

Studies that modelled immigration patch-type dependently, implemented it as a mechanistic settlement probability upon encounter (Baker and Rao, 2004; Doyle, 1975; Gyllenberg et al., 2016a; in prep.; Stamps et al., 2005; Ward, 1987), or as a phenomenological habitat choice trait (Beltman and Metz, 2005; Castillo-Chavez et al., 1988; Levins, 1963; Rausher and Englander, 1987; Ravigné et al., 2009), but disregarded the coevolution with patch-type dependent emigration.

Splitting up the dispersal process in a model will improve our knowledge on the coevolutionary forces and costs and benefits at each phase. It will inform us on how selection acts on the different life stages from a theoretical point of view. Hence, the multi-causal effects of patch-type dependency are studied in this paper. Dispersal is decomposed into its three stages and the joint evolution of emigration and immigration when both decisions depend on the physical characteristics of the patch, the patch types, is investigated. Emigration is handled as the natal dspersal probability of leaving a patch of certain type in the beginning of the dispersal season. Immigration is modelled as the settlement probability (Bonte et al., 2012; Clobert et al., 2009; Travis et al., 2012) of an individual into a patch upon encounter during a continuous-time dispersal season, i.e., in a mechanistic way. With the analytic methods of adaptive dynamics and complemented by numerical investigations and simulations I analyse the eco-evolutionary model to investigate how the selection pressures shape the dispersal decisions.

I find four qualitatively different evolutionary outcomes, including strategies that do not differentiate between the habitat types at settlement, and a strategy that fully emigrates from patches of one type in the beginning of the dispersal phase but nevertheless settles in the patches of equal type with full probability during the dispersal season. I highlight that when emigration is allowed to coevolve with immigration evolutionary branching can occur and the two emerging subpopulations remain coexisting after diversification. Stochastic simulations agree with the theoretical predictions and show evolutionary branching. The coevolutionary constraint that is induced through an additional evolutionary trait, the patch-type dependent emigration probability, sometimes hinders evolutionary diversification as compared to scenarios where only immigration is evolving (see Gyllenberg et al., 2016a).

In Section 2 I set up the ecological model deriving the next-generation operator. Section 3 derives the fitness proxy of the model. In Section 3.1 I derive the monomorphic singularity, explain how to derive the stability conditions (Section 3.2) and analyse the 4 qualitatively different evolutionary outcomes (Section 3.3), before investigating the effects of some parameters on the evolutionary outcome (Section 3.4). In Section 4 the implementation and results of the stochastic simulations are presented, followed by Section 5 where I discuss the novel results.

2. The model

Here, the life cycle of the annual, asexual and semelparous population is described (see equivalent setting in

Table 1
Notation.

Variable	Definition
B	number of offspring
β_i	relative fecundity in patch of type i
$d = (p_1, p_2, f_1, f_2)$	dispersal trait vector (evolving)
f_i	settlement probability into patch of type i (evolving)
M	number of patches
μ_i	death rate in patch of type i (patch safety)
ν	death rate in dispersal pool
p_i	emigration probability from patch of type i (evolving)
ϕ_i	relative frequency of patch of type i
ρ	patch encounter rate
s_i	survival until reproduction in patch of type i
T	length of dispersal season

Gyllenberg et al., 2016a). The landscape is structured in M patches of two types with frequencies ϕ_1 and $\phi_2 = 1 - \phi_1$, respectively. Each individual carries a heritable dispersal trait $d = (p_1, p_2, f_1, f_2)$, a *vector-valued* strategy, where p_i is the (natal) emigration probability from and f_i the settlement probability into a patch of type i for $i = 1, 2$. I sometimes write $f = (f_1, f_2)$. So for instance, individuals with strategy $(p_1, p_2, f_1, f_2) = (1, 0.5, 0.4, 1)$ always disperse from patches of type 1, emigrate from patches of type 2 with 0.5 probability, settle in patches of type 1 with probability 0.4 and always settle into the patches of type 2.

In the beginning of the year each patch is inhabited by one individual. It survives until maturation in a patch of type i with probability s_i. If it survives in the patch of type i it produces $B\beta_i$ offspring, where B is the offspring number and β_i denotes the relative fecundity in a patch of type i. After reproduction all mothers die. Then, the life cycle is continued by a dispersal decision and a continuous-time season during which individuals encounter patches. In the beginning of the season, individuals instantaneously emigrate from a patch of type i with probability p_i and join the dispersal pool. During the season the dispersing individuals (the individuals that joined the dispersal pool) die at a rate ν. Dispersers encounter, i.e., arrive at, a patch of type i at a rate $\phi_i \rho$, where ρ is the patch encounter rate and ϕ_i is the frequency of patches of type i. Upon encounter individuals immigrate into, i.e., settle in, a patch of type i with probability f_i. If the individual does not settle in the patch it has encountered, it moves back into the dispersal pool, where, if the dispersal season has not ended yet, it may encounter another patch during the next time step, or may die. Once an individual has decided to settle, it cannot change its decision later on. Non-dispersed individuals die during the season sedentary in a patch at a rate μ_i (patch safety), as do the newly settled immigrants in the patch of type i during the remainder of the season. I assume that the death rate in the dispersal pool is higher than in any of the patches, i.e., $\nu > \mu_i$ for $i = 1, 2$. The dispersal season ends at time T and dispersers that are still in the dispersal pool die. Then competition takes place with one individual surviving per patch (fair competition). To end up with a deterministic model, I assume that the number of patches M and the offspring number B are infinitely large. All parameters are summarised in Table 1. Note that the present model is an extension of the Hamilton–May model (Hamilton and May, 1977) and the model of Gyllenberg et al. (2016a).

I keep track of the population dynamics via a next-generation map of the dispersers. The next-generation operator $\mathcal{G}$ maps the number of dispersers N with strategy $d = (p_1, p_2, f_1, f_2)$ of one disperser generation to its next during the lifetime of the *family*, that is, all kin and kin's kin of the dispersing individuals in the natal patch (Diekmann et al., 1998; 1990). Hence, the disperser generations are not measured in real time, but operate during years the focal individual's kin and descendants remain in the na-