Original research article

Traveling waves and spatial patterns from dispersal on homogeneous and gradient habitats

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A B S T R A C T

Models of dispersal for response to global climate change can refer to theory on traveling waves developed for invasions. The relevance of this theory may depend on its density- versus habitat-dependence, but it has not considered environmental gradients nor related feedbacks. An agent based simulation model (ABM) for a plant species or vegetation type is developed here, focusing on properties of traveling waves. The ABM simulated no-tailed, thin-tailed, and fat-tailed dispersal kernels (random uniform, Gaussian, and Cauchy kernels, respectively). Probabilities were based on either population density or habitat, and for the latter as homogeneous or on a gradient, and if a gradient positive feedback from populations to the habitat was added to represent process at ecotones such as a positive feedback switch or the stress gradient hypothesis (SGH) feedback. The uniform and Gaussian kernels produced traveling waves with constant speed, but the fat-tailed Cauchy kernel produced traveling waves that accelerated and also flattened as the low-probability portion of wave accelerated fastest. On a gradient, when populations approached the limit of habitability the waves steepened and stopped traveling. The effect of SGH feedback on traveling wave slopes depends on the dispersal kernel. With strong facilitation on the gradient, greater variety of spatial patterns were able to develop among the replicate simulations of the fat-tailed kernel when it flattened to a greater spatial extent of low probability presence. In addition to the heterogeneity of the habitat and its modification by facilitation, the details of dispersal can also affect the feedback between spatial pattern and the establishment process that will affect the rate of advance of a species or an ecotone into new territory.

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1. Introduction

1.1. Ecological response to climate change

The migration of species is the primary response of species to climate change as seen during the past 20,000 years. Migration in response to ongoing and future climate change has been modeled in various ways (Pitelka, 1997; Thuiller et al., 2008; Travis et al., 2013; Ferrarini et al., 2014). Although the importance of spatial processes have long been recognized (e.g., Hanson et al., 1989), many models are not sufficiently spatially explicit (among other simplifications; cf. Ferrarini et al., 2017). Statistical species distribution models, mechanistic models, and their occasional combination usually do not include the process of dispersal across or into landscapes of varying habitat or do so phenomenologically (Heikkinen et al., 2006; Cabral et al., 2017). The primary reason for this shortfall is weak parameterization of dispersal kernels. The tails of the kernels determine the spatial process, but these tails, representing long distance dispersal, are difficult if not impossible to determine empirically (Horn et al., 2001; Bullock et al., 2017). Some mathematical models using reaction-diffusion equations skip over the step of creating dispersal kernels and instead imbed a diffusion rate (Leroux et al., 2013). Theoretically, however, dispersal kernels from jump processes, as opposed to birth-jump processes studied here, are relatively well understood (e.g., Bates et al., 1997; Coville, 2007; Berestycki et al., 2009) and are background to other ecological processes (e.g., Banerjee and Volpert, 2017).

New research is exploring various elements of the dispersal process contribution to response to climate change (Garcia and Borda-de-Agua, 2017). We aim to develop a narrative on how

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dispersal kernels might affect the advance of a species, and an ecotone, on an environmental gradient.

Ecotones are the focus of much research on responses to ongoing climate change: in forest-savanna (Staver et al., 2011; Oliveras and Malhi, 2016), forest-grassland (Whitesides and Bekker, 2011; Dee and Palmer, 2017) and forest-tundra (Dullinger et al., 2004; Malanson et al., 2011; Boisvert-Marsh et al., 2014; Camarero et al., 2017) among others. At such boundaries the spatial patterns appear to be in a feedback loop with processes (Harsch and Bader, 2011), but linkage is problematic. Malanson and Zeng (2004) found that a model with evolutionary algorithms quickly converged on patterns from different initial conditions. Zeng and Malanson (2006) developed a model-based narrative of advance-coalescence-advance for alpine treeline ecotones in which spatial advances were linearly associated with spatial patterns created by nonlinear feedbacks; they described the result as a self-organized system. Bourgeron et al. (2015) described similar patterns as multiscalar. The problem has the hallmarks of nonlinear complexity (Loehle et al., 1996; Malanson, 1999; Li, 2002; Burkett et al., 2005).

Attention has focused on these contrasts because it is likely that biotic interactions, competition and/or facilitation, could occur. The related conceptual frameworks of a positive feedback switch (Wilson and Agnew, 1992) and the stress gradient hypothesis (SGH) (Maestre et al., 2009) have developed and been applied to such ecotones. The positive feedback or facilitation that would occur at the advancing ecotone of a biome should increase its rate of advance, but this advance is dependent on the continually changing spatial pattern. Other work has emphasized the spatial nature of the facilitation (e.g., Malanson 1997; Malanson and Resler, 2015; Malanson et al., 2017), but competition is an alternative (e.g., Hernandez-Garcia et al., 2015). These relations have consequences for the continued existence of species, the diversity of areas at multiple scales, ecosystem function, and resulting ecosystem services. Most work has focused on the heterogeneity of the abiotic environment as the source of spatial pattern (e.g., Holtmeier, 2003; Resler et al., 2005; Butler et al., 2007; Elliott and Cowell, 2015) or on the spatial feedback, including directional effects (e.g., Alftine and Malanson, 2004; Smith et al., 2003; Bader et al., 2008). Some have suggested that evolving spatial patterns at ecotones could be interpreted through the lens of complexity theory (Malanson, 1999; Mills et al., 2006; Zeng and Malanson, 2006).

These and other studies of feedback between spatial patterns and ecotones have not adequately addressed the role of dispersal (but see Brooker et al., 2007; Ferrarini et al., 2014), although the pattern of seedling recruitment is sometimes observed (Rehm and Feeley, 2013; Johnson et al., 2017). For the movement of a species or an ecotone, dispersal is a prerequisite. We follow a line of modeling initiated by Kot (1992) and expanded, critiqued, and reiterated by Kot et al. (1996, 2004) and Clark et al. (2001), with new insights from Potapov and Lewis (2004) that led to the recent work by Leroux et al. (2013). In these papers Kot and colleagues found that the advance of a species into new territory could accelerate, but acknowledged that in extremis this would be unrealistic. Clark et al. (2001); Clark Lewis et al., 2003 proposed biological restrictions that would lead to non-accelerating advances. Kot et al. (2004) faulted this approach (somewhat cryptically) for including density dependence. While seeming to apply only to general constraints, the assessment of traveling waves remains a useful approach, however, because they remain a link between more generalizable formal theory and landscape-specific applications models. Most of that work addressed the ecological issue of invasion of an area by a new species; therein, the habitat of the area was homogenous for the species. Others have addressed dispersal in the advance of a species or biome in the context of climate change; therein, the habitat could be a gradient, otherwise heterogeneous, and/or changing (Malanson and Armstrong, 1996; Malanson, 1997; Malanson and Cairns, 1997; He and Mladenoff, 1999; Lischke et al., 2006).

1.2. Traveling waves

A related literature on advancing biological fronts has also examined traveling waves. Observation and modeling of traveling waves of expanding patterns of bacteria in Petri dishes have considered sharp waves (Kawasaki et al., 1997; Satnoianu et al., 2001; Mansour, 2008; Jalbert and Eberl (2014). Normally, the waves studied have some regularity (usually continuously differentiable) and are strictly positive in the domain. However, sharp waves have an abrupt limit at the low-probability end and are exactly equal to zero in parts of the domain.

Generally, these patterns have been modeled with reaction-diffusion equations rather than a birth-jump dispersal process. However, recently birth-jump processes have been introduced to describe a population or trait for which dispersal cannot be decoupled from birth. These types of models were introduced recently (Hillen et al., 2015}) as a generalization to integro-differential equations that arise from a position-jump process (a stochastic process that generalizes random walks (Hutson and Martinez 2003; Othmer et al., 1988) in that individuals can make spatial jumps with a given probability) and reaction-diffusion equations (Cantrell and Cosner, 2003).

Motivated by these studies, Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), however, introduced a birth-jump processes leading to a degenerate reaction-diffusion equation (in the diffusion-limit), which produced sharp waves. Working in parallel, here we develop an agent based simulation to explore some details of traveling waves. Beyond demonstrating their existence, however, we begin consideration of their consequences for spatial pattern-process feedbacks. We examine traveling waves that arise from differences in specific density-versus environmental-dependence, dispersal kernels, and environmental gradients, with and without positive feedback. Although motivated by outcomes in PDE Rodriguez and Malanson, 2017(Rodriguez and Malanson, in review), those are not a prerequisite. We use agent based simulation models (ABM) because it allows realistic spatially explicit representation of these processes and constraints (some of which were noted by Lewis and Pacala, 2000). ABM are a group of models that focus on individuals and derive from models created for practical application, not theoretical development (Grimm and Railsback, 2005). In their most extended form, agent based models have been used to examine the interactions of individuals responding to climate change across complicated landscapes (Dey et al., 2017; Redmond et al., 2017) and in more abstract or stylized scenarios (Smith-McKenna et al., 2014; Mohd et al., 2016). However, theory can be explored using ABM, at some cost of tradeoff of ABM strengths (e.g. Malanson, 2015).

1.3. Questions addressed

We asked: Can traveling waves represent the relevant processes? Do waves have characteristic shapes? Do waves accelerate, and under what circumstances? We also search for conditions that would give rise to, or approximate, distributions for sharp waves.

We hypothesize:

- Traveling waves produced from density-dependent seed production do not differ qualitatively from those produced from