Ecological Modelling 316 (2015) 217–229

Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Predicting metapopulation responses of a tidal wetland annual to environmental stochasticity and water dispersal through an individual-based model

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ARTICLE INFO

Article history:
Received 12 February 2015
Received in revised form 31 July 2015
Accepted 2 August 2015
Available online 15 September 2015

Keywords:
Hydrochory
Aeschynomene virginica
Metapopulation
IBM
Environmental stochasticity
Rare species

ABSTRACT

Freshwater tidal wetlands are a complex environment for annual plants. Seedling establishment and survival may be limited by a variety of factors, including competition with perennials and the twice-daily inundation of seeds and seedlings. Hence such species are often endemic and rare. Their observed population dynamics can be extraordinary, with individuals reappearing in certain patches where they had been absent for several seasons, and with total populations varying by orders of magnitude between years. Many interacting influences are thought to be at play here, including seed banks and water-based seed dispersal (hydrochory). So far it is not known (1) to what degree environmental stochasticity is likely to affect the population's survival in its natural habitat, (2) what role hydrochory plays in propagating and maintaining the species, and (3) how these two factors interact with one another. We therefore took the annual *Aeschynomene virginica* (Sensitive joint-vetch, SJV) as an example and developed an individual-based model in a geographically precise replica of its Holts Creek, Virginia, habitat. The model represents SJV's life cycle and is calibrated to data from a variety of empirical studies on the plant. Vital rates are partly calibrated from aerial imagery providing estimates of the biomass of specific patches. Simulated seeds enter the river network based on their proximity to the water's edge, and then travel upstream and downstream according to estimated flow rates, float times, and implantation probabilities. Additionally, random seasonal environmental conditions are imposed, depressing or inflating vital rates within prescribed ranges. We found that as environmental stochasticity increased to more than relatively modest levels, the long-term survival probability of the species precipitously declined. Hydrochory, though it may have played an important role in the past in allowing SJV to reach the regions in which it now thrives, had little impact on the plant's long-term likelihood of survival for our study population. Nevertheless, the model's performance indicates the existence of additional key factors at play in SJV's metapopulation dynamics that were not considered or quantified so far. These may include the varying elevation of habitat patches and the corresponding variability in submersion time, which should be taken into account in future modeling of annuals in freshwater tidal wetlands. We conclude that population models which include detailed representations of the spatial and temporal heterogeneity of environmental drivers can deliver important general insights even if they must be tied to specific study sites.

1. Introduction

Freshwater tidal wetlands are areas that are far enough upstream to be above the influence of saline waters, yet which are still within the influence of twice-daily tides. These wetlands are known for their high species diversity (Odum et al., 1984) and high biomass (Whigham et al., 1978), and are often dominated by a few perennial species (Simpson et al., 1983). Annual species find themselves in a complex environment where a variety of biotic and abiotic variables may impact growth, survival, reproduction and, as a result, population dynamics. As a consequence, annuals are often rare and endemic species in freshwater tidal wetlands (Ferren and Schuyler, 1980).

Several potentially important factors in the (meta)population dynamics of tidal wetland annuals have been identified. For example, seedling establishment may be limited by competition

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http://dx.doi.org/10.1016/j.ecolmodel.2015.08.019
0304-3800/

with perennials (Whigham et al., 1978; Odum, 1988; Griffith and Forseth, 2003) and longer inundation of seeds and seedlings (Simpson et al., 1983; Griffith and Forseth, 2003). Both seed banks and hydrochory have been observed and measured for some species and are thought to aid survival. However, the relative importance of these factors, and the ways in which they interact with each other, are largely unknown (Alexander et al., 2012).

The complex interplay of environmental factors in this habitat suggests that individual-based models (IBM) may be beneficial to gain more insight into the population dynamics of such species, as this modeling approach is most flexible (Grimm and Railsback, 2005). We developed a spatially explicit IBM, based on data from Geographical Information Systems (GIS), in which individuals of a particular tidal wetland species are simulated according to the available quantitative information about that plant. Such a model promises to reveal much about how a multitude of carefully observed behaviors would unfold in a complex habitat like freshwater tidal wetlands.

1.1. Sensitive joint-vetch

Aeschynomene virginica, or Sensitive joint-vetch (SJV), is a rare and endemic species of this kind. It is an annual plant in the family *Fabaceae* (Gleason and Cronquist, 1991). Populations of SJV are found on the coastal plain from New Jersey to North Carolina (U.S. Fish and Wildlife Service, 1995). They are often associated with the berm of the marsh and stream (U.S. Fish and Wildlife Service, 1995;Griffith and Forseth, 2003), but plants can also be found in "meadow populations" which are not associated with stream edges (Griffith, personal observation).

SJV population size can vary by two orders of magnitude among years (The Nature Conservancy, 2010) and plants can be absent from a patch for several years and then reappear (Bailey et al., 2006; Griffith, 2014). Patch re-establishment may be explained by seed banks or seed dispersal (Freckleton and Watkinson, 2002). Populations may re-establish in empty patches when seeds disperse from other populations in a metapopulation (Van der Meijden and Van der Veen-Van Wijk, 1997; Bullock et al., 2002). Seeds germinating from seed banks also may give the appearance of population re-establishment, when in fact seeds in a seed bank are simply plants that are difficult to see (Harrison and Taylor, 1997; Bullock et al., 2002).

SJV, in addition to being a representative, wetland endemic, is a federally threatened species (U.S. Fish and Wildlife Service, 1992).A primary concern in conservation ecology is deciding whether investing funds into the support of a rare species is worthwhile; can that species be successfully rehabilitated? What specific conservation methods have the greatest chance of success? Decades of research, monitoring, and conservation efforts have been invested into the maintenance of sensitive joint-vetch populations, but there is no consensus as to whether it is possible to save.

It benefits ecosystem managers to have a broad and multidisciplinary foundation of information to use in their decision-making. Therefore, investigating the baseline chance for SJV to persist, and seeking to understand the repercussions of conservations strategies are necessary and worthwhile. Furthermore, investigating SJV allows us an opportunity to study tidally driven hydrochory as a means of metapopulation persistence. Lastly, it may be possible to generalize these results to similar hydrochorous, rare species, however the efficacy of water dispersal for different species is quite variable and the results from a very species specific study should not be carelessly extrapolated to other species and habitats.

1.2. Hydrochory

A great deal of research has been done to investigate the influence of hydrochory on riparian systems, especially in terms of describing the impact of dispersal on riparian landscape biodiversity patterns and its ability to shape metapopulation dynamics of riparian vegetation (Nilsson et al., 2010). Researchers have sampled deposited sediment (Vogt et al., 2006), used nets to catch dispersing seeds (Gurnell et al., 2005; Andersson and Nilsson, 2002), and tested propagule mimics (Bång et al., 2007; Johansson and Nilsson, 1993) to learn how seeds interact with water to produce such spatially complex population patterns in a riparian environment. Bång et al. (2007) found that the majority of "seeds" stranded less than 300 m from their origin. Vogt et al. (2006) found that large flood events transport seeds, thus increasing riparian plants' dispersal range.

Other studies have shown that some hydrochorous species may have large geographic ranges compared to those that use other dispersal mechanisms (Kubitzki, 1991). Furthermore, because hydrochory is capable of long-distance dispersal (Cain et al., 2000; Sannikov and Sannikova, 2007), it can connect distant populations (Waser et al., 1982). Notably, floods, with a large water surface and high current velocity, may support extreme long-distance dispersal, as would calm weather that facilitates hydrochory through the central river current without interference by wind. Because SJV lives in a tidal marsh, it is highly susceptible to both these weather patterns (Cain et al., 2000).

Hydrochory can also potentially lead to recolonization of storm-disturbed sites, whether they are in riparian zones (Helfield et al., 2007) or tidal areas (Wolters et al., 2005). This "rescue effect" should in theory reduce extinction risk (Brown and Kodric-Brown, 1977), though no empirical evidence of it has been reported. By modeling a hydrochorous species in a heterogeneous landscape with large and small populations, and by introducing the influence of environmental stochasticity, we can test the rescue effect.

1.3. Metapopulation dynamics and patch quality

Long term observations of SJV populations on Holts Creek in Virginia suggest some populations may survive through source and sink dynamics. Populations on smaller patches may be absent in any given year (Division of Natural Heritage, 2011). Seeds are known to bank (Griffith and Forseth, 2006; Baskin et al., 2005), though empirical data suggests the seed bank is short-lived (Griffith and Forseth, 2006). Thus, "thriving" patches that exist consistently from year to year may, though their population size may fluctuate, either support mediocre patches or have little impact on them.

However, research also indicates that models that wish to properly simulate these regional patterns should not only consider features at the landscape-scale, such as patch size and isolation. Increasing evidence supports the hypothesis that local habitat quality is a driving factor in metapopulation dynamics and as such it must be incorporated into metapopulation models (Frey et al., 2012). Unfortunately, it is very difficult to quantify patch quality. While it is easy to measure patch characteristics, such as vegetation structure, elevation, or microclimate, it is difficult to transform this knowledge into vital-rates for a target species. Without knowing the precise connection between these variables, including it in metapopulation analyses is often guesswork (Mortelliti, 2010). Therefore, to test the influence of hydrochory and environmental stochasticity on the metapopulation, we seek to approximate the role of patch quality in SJV's life history through a simulation.