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

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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.

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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

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.

1.4. Previous models

The role of hydrochory for population distribution and abundance has been explored using individual-based models previously. Campbell et al. (2002) simulate landscape-scale plant invasions mediated through hydrochory. Through computationally generating drainage networks and introducing 'seed agents' that each disperse through a random-walk, they were able to closely reproduce empirical observations. This model was the first, to our knowledge, to show the importance of water-mediated dispersal in a riparian environment.

As the model focuses on the complexity of hydrochory itself, Campbell introduces a pre-defined number of seed agents into the headwaters of their river network. Each seed begets one adult, which in turn produces one seed, in effect abstracting out the population dynamics involved in a real system. In contrast, in our model, while using a dispersal mechanism similar to that of Campbell et al. (2002), we represent the full life cycle of SJV to generate population dynamics. In addition, we are considering a tidal stream and therefore include bi-directional dispersal.

Soomers et al. (2013) developed a model that contrasts air and water dispersal of different types of seeds, achieved through drainage ditches in agricultural zones. They find that water dispersal transported more seeds over longer distances than wind dispersal and reiterated the importance of connectivity for plants that rely on water dispersal. Soomers et al.'s treatment of hydrochory focused on a mechanistic understanding of how seeds disperse through drainage ditches. While this complexity is important for an analysis that focuses on precisely quantifying the dispersal of different types of seeds, we argue that, in a landscape-scale simulation of one type of plant, much of this complexity can be reduced.

Levine (2003) uses multispecies Markov Chain models to describe the demographic changes between populations upstream and downstream. By omitting a mechanistic model of hydrochory and replacing it with a series of grid-neighborhoods, connected through probabilistic dispersal, focus was on the local interactions of plants and their consequences on local biodiversity. Through simulated dispersal, upstream neighborhoods' compositions would in turn influence biodiversity downstream. Levine concludes that hydrochorous seed input would only increase a population's size and diversity if that population was seed limited, and also that most of a site's seed input would come from nearby patches upstream. He further argues that the relationship between water dispersal and population size and diversity is more complicated than ecologists' intuitive understanding of it. Only under certain conditions will such dispersal affect a population's size and a patch's species diversity patterns.

2. The model

The model description follows the ODD protocol for describing individual- and agent-based models (Grimm et al., 2006, 2010). The model was constructed in Java, using MASON simulation toolkit (Luke et al., 2005). The source code is available for download from Github, and can be found at https://github.com/mscrawford/jointvetch.

2.1. Purpose

The model was created to investigate the interplay between environmental stochasticity and hydrochory in a tidal-wetland ecosystem, and particularly their influence on metapopulation dynamics of an annual plant species, *A. virginica*.

2.2. Entities, state variables, and scales

The model contains the four entities: plants, mobile seeds, plots, and the environment. Plants are described by the state variables lifestage and location. The lifestage is either seedling or adult, where seedlings compete to become adults and adults reproduce. A plant's location is represented via continuous x- and y-coordinates. Mobile seeds are characterized by their location as well and their "maximum float time," which indicates how long they can drift on the river.

Our simulated area is broken into a grid of $1\,m^2$ plots, which are each characterized by their discrete x- and y-coordinates, and a propensity. *Propensity* is a quantitative estimate of a given plot's habitability for SJV. It is a baseline average for a plot over time, and will be adjusted by environmental stochasticity in a given year, as described below. A plot's propensity determines the fecundity and survival probability of the plants that are located on it, and therefore directly impacts the plot's intrinsic rate of increase (r). Propensity also affects the plot's carrying capacity, as described in Section 2.7.5. Because of the intricate complexity of the real habitat, and because there is relatively little plot-by-plot empirical data available, propensity is our attempt to synthesize numerous (mostly unknown) interplaying factors into a single variable. We derive the propensity based on the Nature Conservancy's GIS data, as described in Section 2.7.3.

The "environment" entity controls the environmental stochasticity of the simulation; i.e., the yearly, overall (not plot-specific) level of favorableness for the species' reproduction and survival. A simulation's time step corresponds to 1 h while seeds are dispersing. During the rest of the year there are only three other time steps: (1) in which every plant "survives" to adulthood, and (2) in which the adult plants reproduce, and (3) at the end of the year to advance time, cull existing plants, and record observations.

2.3. Process overview and scheduling

At the beginning of each simulation year, the environment first sets the "environmental quality" for that year. Last year's germinated seeds then survive to adulthood and then reproduce. Both survival and reproduction are asynchronous processes. However, because plants do not interact except at the plot level, this asynchrony has no effect on the simulation. Plants only interact when carrying capacity is being measured, at which point every surviving plant has the same probability of being removed stochastically.

After reproduction, each seed may germinate immediately, where their maternal plant dropped it, or disperse through the river. Secondary dispersal, via hydrochory, transports seeds up- or down-stream according to the tides; new positions are synchronous and calculated by the hour. After each mobile seed either implants into the river's edge or drowns, the year ends, and the model's state is recorded. Last year's adult plants are then removed from the landscape, and the process begins anew.

Competition, seen in the conceptual diagram, Fig. 1, is the multiplicative result of the propensity, carrying capacity, and environmental stochasticity submodels. These three submodels affect adult plants' reproductive capacities, as well as germinated seedlings' growth into adult plants.

2.4. Design concepts

2.4.1. Emergence

All individual-level processes are imposed via vital rates and other parameters. Population dynamics, structure, and distribution emerges from these processes and their interaction with landscape structure and dynamics and dispersal via hydrochory.
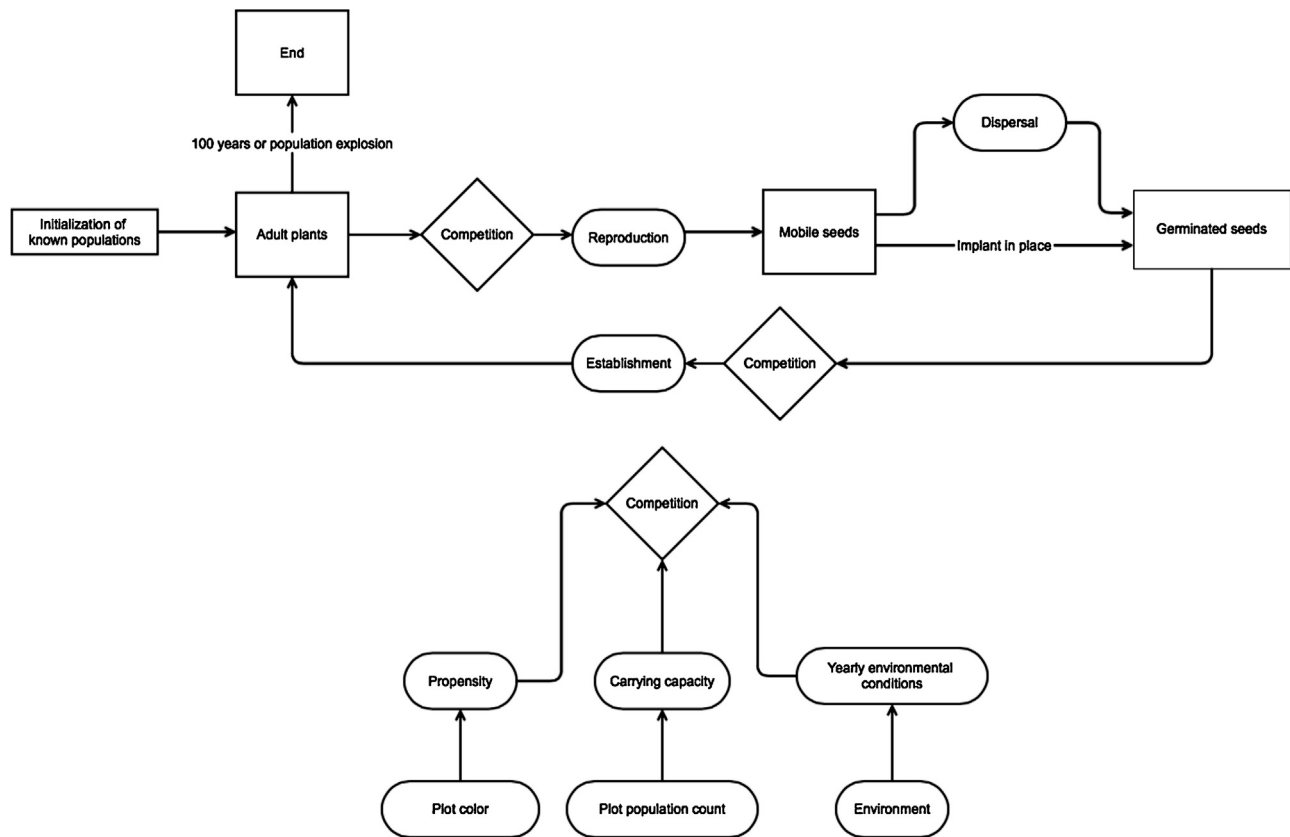
Fig. 1. A conceptual diagram of the model processes and their schedule. Propensity, carrying capacity, and environmental conditions all factor into competition, which in turn affects both reproduction and establishment.

2.4.2. Interaction

Plants interact with each other via intraspecific competition within a plot (see carrying capacity submodel).

2.4.3. Stochasticity

To represent natural variation as well as factors the model does not account for explicitly, various parts of the model are stochastic. During hydrochory, the decision of which tributary to choose is governed by both the currents' direction and certain probabilities. Stochastic environmental variation is imposed on the plants' vital rates.

2.4.4. Observation

Data is collected at the end of each simulation: the total number of SJV plants after the simulation finishes, the year the simulation ended (which could be less than 100 if SJV goes extinct or its population increases higher than 150,000 individuals, a phenomenon further described in Section 4.2), and the number of geographically isolated clusters of SJV.

2.5. Initialization

The simulation is initialized with a configuration based on the current state of the Holts Creek SJV populations. Each simulation is initialized using historic SJV population locations, stored as geospatial coordinate points (Division of Natural Heritage, 2011). Each population point, a coordinate pair, has that population's count attached to it. Each individual is treated as an adult plant and is dropped within a radius of 2 m around the center point, as determined by a uniform random distribution. For example, The Nature Conservancy ecologists may have found a population at (37°32.971′, −76°58.992′) with 26 individuals. In the simulation,

then, 26 individuals would be placed within a circular spread with a radius of 2 m, centered on that coordinate pair.

The simulation uses several types of geospatial input data as well as The Nature Conservancy population point and count data. From the USDA, we obtained orthoimagery of Holts Creek from the summer of 2013. From the USGS, we used the hydrography dataset to model the marsh, and the river network in Holts Creek (Fig. 2). These datasets are included in the source package provided.

While SJV populations have been found at, at least, seven other locations in Virginia, we chose to simulate Holts Creek based on the extensive records of SJV population sizes (The Nature Conservancy, 2010) and locations on Holts Creek (The Nature Conservancy, 2010; Division of Natural Heritage, 2011). Fig. 3 shows the history of SJV population sizes on Holts Creek. Beyond simulation initialization, these records inform our understanding of the realism of the data collected from our model.

2.6. Input data

The model does not include any external input of driving environmental variables.

2.7. Submodels

2.7.1. Hydrochory

The dispersal of seeds by water is modeled through the mobile seed entity traversing a directed graph, hereafter called the river network, obtained through the USGS hydrography dataset. Because over 90% of SJV populations are within 4 m of the stream edge and 34% of those populations' seeds are taken up by the tides (Griffith and Forseth, 2006), we make the simplifying assumption that if and only if the maternal plant is less than 4 m from the river edge can
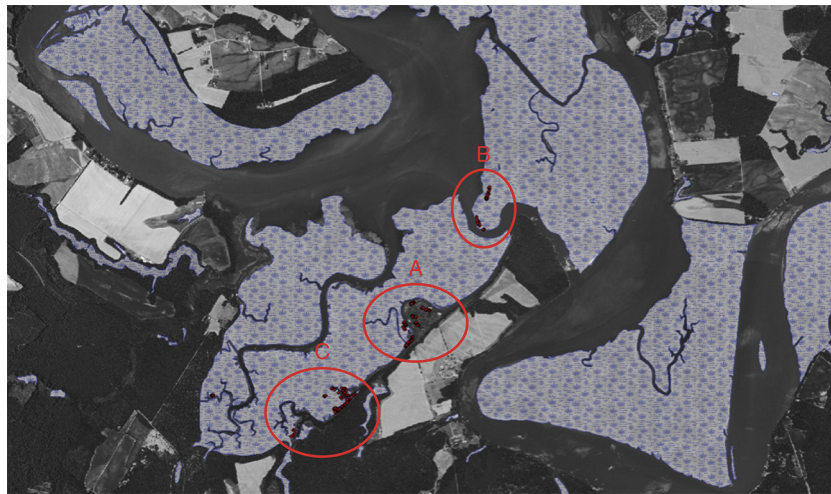
Fig. 2. Holts Creek, VA with known SJV populations in red and the tidal marsh in light blue. The Nature Conservancy catalogs the Holts Creek metapopulation of SJV through three "zones," A, B, and C. Data courtesy of: The Nature Conservancy (SJV population), USGS (Hydrography dataset waterbody), USDA (aerial photography).

a seed disperse, and that all such seeds have a .34 probability of doing so.

To move the seed from its maternal plant to the river network, the seed is translocated to the point on the river network that it is closest to. Once there, the simulation probabilistically decides how many hours that seed will float based on an empirical distribution, derived from seed floatation data detailed in Griffith and Forseth (2002). Roughly half of the seeds that disperse will drown within the first 28 h they are on the river. Empirical evidence has shown that propagules that drop below the water's surface are usually not able to germinate (Griffith and Forseth, 2002).

In traversing the river network the seed is subject to the tidal forces that govern Holts Creek. Each propagule moves up and down the graph based on a sine curve, derived from Griffith and Forseth (2002), which mirrors the flow rates of the incoming and outgoing tides. The distance traveled by a seed at time t is defined as:

$$distance(t) = r \cdot \sin\left(t \cdot \frac{\pi}{p}\right) + s$$

where r, the range between highest flow rates upstream and downstream, is 769.5 m/h, t is the time in hours, p, the tidal period, is 13 h, and s, a linear shift, is 13.5 m/h. The shift is necessary because data has shown that the tides, at their respective fastest speeds, move upstream slightly slower than downstream.

To avoid all seeds moving in lockstep, each seed begins its dispersal at a random point during the first tidal period. Each time step, or hour, the seed is moved upstream or downstream according to the tidal equation.

Seeds disperse realistically through the river network. As the tides move out, toward the York River, the propagules will in turn be carried downstream. When the tides reverse, they will move upstream. At junctions that contain more than one possible path, depending on the tides, the seeds will randomly chose one of them to follow.

An important, imposed, variable involved in the hydrochory submodel is the probability that a propagule will be caught and implanted into the riverbank on any given time step. At the start of a seed's "turn," it first decides whether or not it will implant based on the parameterized implantation probability. If the propagule implants into the riverbank, it is translocated to the nearest marsh edge and dropped inland 0–4 m at a (uniformly) random angle. It then decides whether or not it will germinate based on the quality of its plot. If it does, it can then transition to the adult life stage and reproduce.
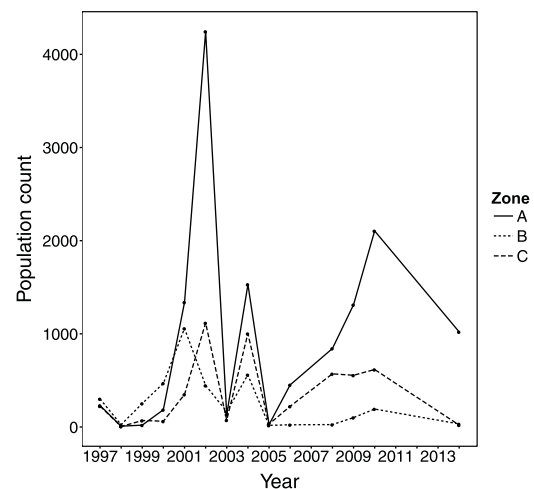

Fig. 3. SJV plant counts on Holts Creek, VA 1997-2014. No data shown for 2011–2013 and straight line connects 2010 and 2014. Zones A–C are sub-sections of all locations on Holts Creek. Data courtesy of The Nature Conservancy.

If it does not implant into the berm, it will check to see if it has been floating for longer than its pre-calculated maximum floatation time. If so, it will drown; if not, it will continue to float with the tides.

The implantation probability obeys a geometric distribution, because most seed input to a riparian site comes from nearby patches upstream (Levine, 2003). A geometric distribution is the probability distribution of the number χ of Bernoulli trials needed to get one success. In other words, a seed will continue to float down the river until it either drowns or is successfully caught by the riverbank and implanted into the soil. Interestingly, because a higher implantation rate will result in more seeds being caught by the riparian edge closer to their original population, a low implantation rate counter intuitively has a comparatively higher chance of successful long distance dispersal.

Hydrochory could be either "on" (H_{on}) or "off" (H_{off}). The implantation probability is as discussed above, parameterized with values calculated such that 0%, 1%, 3%, 5%, 13%, 24%, 43%, 57%, 76%, and 94% of seeds successfully implant into the berm.

The hydrochory boolean variable reflects whether seed transport will actually occur. If hydrochory is "on" (H_{on}), then some seeds (as described above) will predictably float on the river. With hydrochory "off" (H_{off}), seeds will automatically implant

into their primary dispersal location. Whether or not they get a chance to germinate, however, depends on the value of a precomputed geometric distribution that mirrors the process used with H_{on}. Therefore, with an identical implantation probability, approximately the same number of seeds will successfully implant, regardless of whether H_{on} or H_{off}.

2.7.2. Life cycle

SJV's life history is modeled through the vital-rate transition matrix, derived in Griffith and Forseth (2005), and modified by the propensity submodel. We converted the raw data Griffith used to compose the matrix into probability distributions rather than fixed rates. Since there is no agent behavior in between germination and survival, we combined the two vital rate distributions into a single multiplier hereafter called survival.

Transitions between the stages are modeled probabilistically, though the specific probability is controlled by the propensity of the 1 m^2 "plot" the plant is on (see Section 2.7.3). The propensity of a "plot" is designed to approximate the landscape's influence on SJV's intrinsic rate of increase (r). In other words, each 1 m^2 plot inside the simulation's representation of Holts Creek has its own r. The probability is further modified by the carrying capacity of the plot and the environment's quality that year.

2.7.3. Propensity

Unfortunately, there is no foundation of data to build from to simulate an area's habitability for SJV. There is little data to show what conditions SJV can grow under beyond the presence or absence of competitor plants (Griffith and Forseth, 2003), but it is necessary to approximate this variable to investigate how SJV's metapopulation dynamics change with hydrochory and environmental stochasticity.

We define the "propensity" of a plot as its average suitability to grow and sustain SJV over time. To estimate this quantity, we take advantage of the Nature Conservancy's extensive record of SJV population data on Holts Creek (Figs. 2 and 3; The Nature Conservancy, 2010), a raster derived from 2013 aerial photography of the marsh, plus the empirically derived vital rate distributions for SJV (Griffith and Forseth, 2003). The basic idea is to correlate the frequency of actual SJV occurrence on plots with different levels of visible light reflection to specific vital rates. In this way, we can predict which color band intensities tend to correspond to plots with more favorable conditions. We limited our analysis to the red band, as it is most correlated with biomass.

To derive an approximation of a plot-based propensity for SJV to grow inside Holts Creek, we used the following process: (1) Using the USGS hydrography dataset's waterbody polygon, isolate all raster squares from the USDA orthophoto within the marsh (Fig. 4). Then (2) isolate all raster squares within 3 m of SJV populations on Holts Creek (Fig. 5). Finally, (3) for each reflection level, divide the SJV frequency by the Holts Creek frequency and normalize the result, creating a *propensity* for each level of reflection to have SJV found near it. For example, the SJV frequency at reflection level 135 is 38 and the Holts Creek frequency is 7045. On other hand, the SJV frequency at reflection level 100 is 89 and the Holts Creek frequency is 178,460. After dividing to get the propensity, one discovers that value 135 is 11 times more likely to contain SJV than value 100 (*propensity*[135] = 0.041, *propensity*[100] = 0.0038).

To transform our new data on relative propensity into specific vital-rate transitions, we composed a cumulative distribution function (Fig. 6) by extrapolating the propensity distribution to all the plots in Holts Creek. In other words, we transform the data such that we can query it to answer questions such as, "what percentile of Holts Creek has a propensity less than .02?" The answer in this case turns out to be 94%. By querying the vital rate distributions at each color's percentile of propensity, we can derive a new distribution
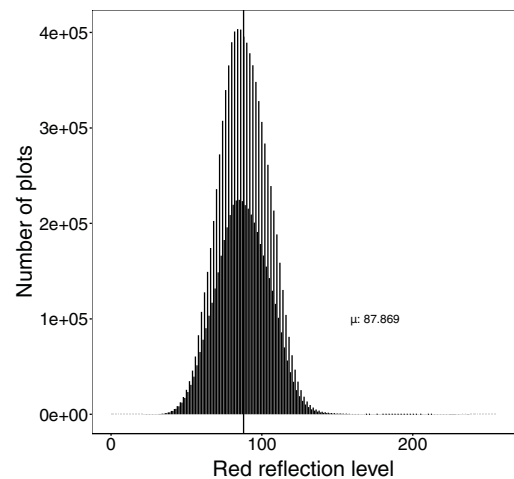

Fig. 4. Left: The frequency distribution of the intensity of red light reflected by all 1 m^2 plots in Holts Creek. There are a total of $13,591,050 \text{ m}^2$ plots in Holts Creek. Red wavelength reflection is a proxy for standing biomass in a plot.
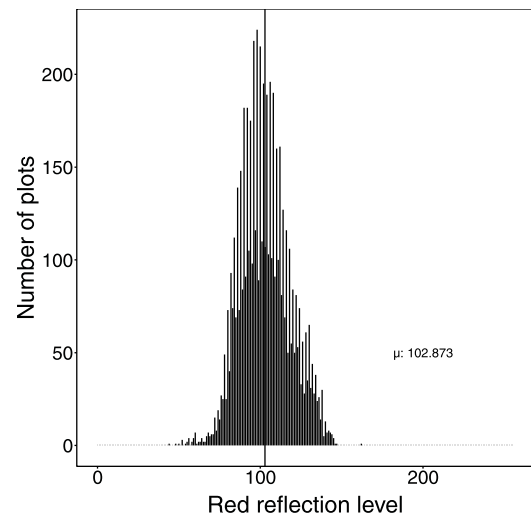

Fig. 5. Right: The frequency distribution of the intensity of red light reflected by all 1 m^2 plots within 3 m of a population of SJV. There are 6065 m^2 plots in total. The mean is statistically significant in its difference from Holts Creek as a whole. Mann–Whitney test was used to calculate statistical difference. $U = 56,057$, and $p < 0.001$.

for both vital rate distributions that reflects an approximate vital-rate based on our measure of how good each geographic location is (Fig. 7).

To integrate this measure of propensity into the model, a plant uses its plot's vital rate transitions. The vital rates are static throughout the simulation, so plots that have SJV on them with a positive rate of growth will continue to grow unless environmental stochasticity negatively influences them. As seen in Fig. 8, the application of this methodology onto Holts Creek will classify the landscape into areas that can sustain SJV and areas that cannot.

Note that a plot's propensity represents its average quality over time; due to environmental stochasticity, some good plots will have bad years and some bad plots good years. Also, we understand that rivers and floodplains are dynamic ecosystems that vary over time due to disturbance events and erosion; however, simulating such macroscopic changes to the propensity profile, however, is beyond the scope of the current study.
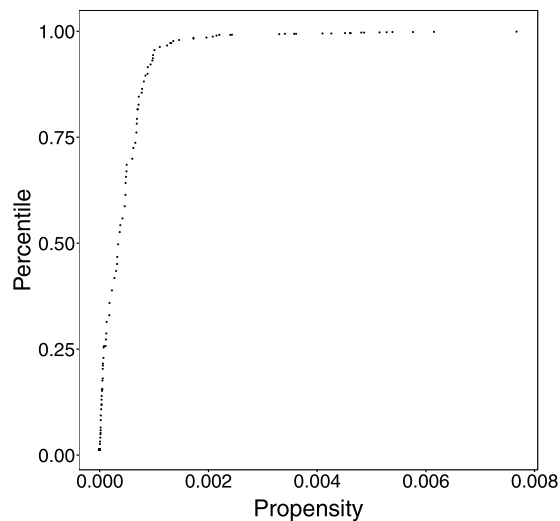
Fig. 6. Left: Cumulative density function of propensities in Holts Creek. Notice that the range of the *x*-axis is identical to the minima and maxima values of the normalized propensities. Using this CDF, we can conclude that almost all of the squares in Holts Creek have a propensity less than 0.01.

Fig. 7. Right: Survival rates for each red reflection level. For very good absorption levels, the survival rate is quite high. For more common reflection levels, the survival rate is very low.

2.7.4. Environmental stochasticity

Environmental stochasticity is imposed by multiplying all vital rate transitions by a yearly adjustment. As with propensity, this is an attempt to simplify innumerable real-world dynamics – in this case, most of them weather-related – into a single quantity that can affect the simulation.

Each simulated year, we draw a value for the environmental stochasticity from a reciprocal distribution. We use a reciprocal distribution rather than a Gaussian because the former preserves the geometric mean. This distribution is described by its maximum (its minimum is the reciprocal), termed Environmental Stochasticity Maximum (ESM). Consider a Gaussian distribution with a $\mu = 1$ and $\sigma = 0.5$. A variate with a value of 0.5 is equally likely as a variate of 1.5, one standard deviation away. Halving a rate is not counterbalance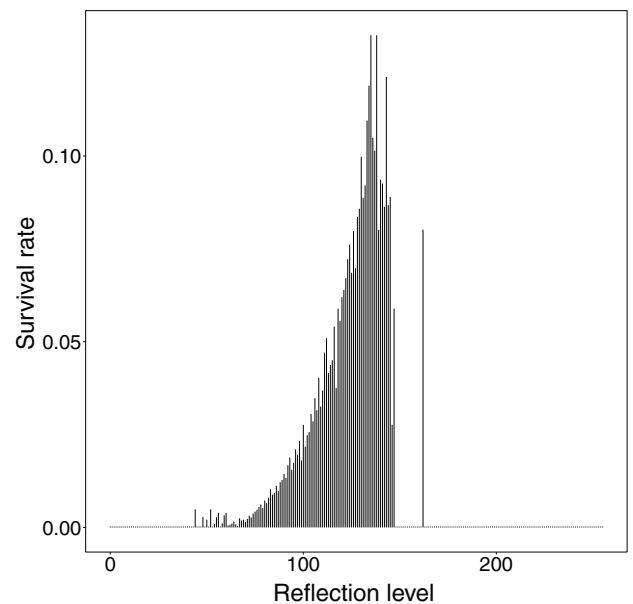d by multiplying it by 1.5. Instead, to remain faithful to a geometric mean of 1, we need halving the number to be as likely as doubling it.

For simplicity, we assume that the abiotic and biotic factors that affect SJV's yearly variation in population count are uniform across the entire landscape (there are no local disturbances). Furthermore, this model assumes that the mechanisms behind environmental stochasticity do not depend on prior years' variates, In other words, the environmental stochasticity in year *n* does not influence that of $n + 1$. While this assumption reduces the complexity in the simulation, it is consistent with the likely independence of major drivers of environmental stochasticity (e.g. local weather) from year to year.
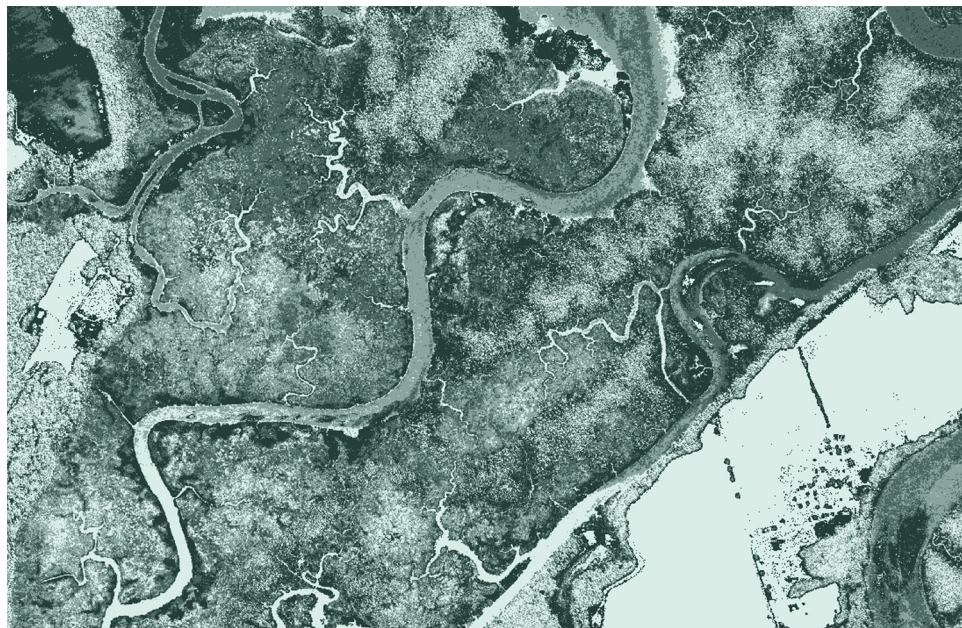

Fig. 8. Reclassification of each 1 m^2 in Holts Creek based on its propensity. The darker shades have more propensity for SJV. Therefore, one can conclude that agricultural areas, white areas in lower right quadrant, have very low propensity for SJV, as do the higher biomass areas inside the marsh. Notable for being high in propensity are the borders of the creek, which is consistent with empirical evidence (Griffith and Forseth, 2002).

We parametrically test how different variations in environmental stochasticity affect the survivability of SJV in Holts Creek. The value used to control this variation is the reciprocal distribution's maximum value, referred to as the environmental stochasticity maximum. The distribution's minimum value is defined as the reciprocal of the maximum. To illustrate, a maximum yearly multiplier of 3 corresponds to a minimum yearly multiplier of 1/3. Therefore, the best possible year for the plant would see 3X the vital rates and the worst would see 1/3.

2.7.5. Carrying capacity

Carrying capacity, like competition, is measured on the plot scale. Griffith's observations (Alan Griffith, personal observation) suggest that there is a carrying capacity for SJV of about 50 plants/m^2.

Initially, we investigated two methods to implement carrying capacity: (1) using the square 1 m^2 plots, and (2) using circular fields each with an area of 1 m^2. Running the simulation and testing its output with a Pearson's Chi-squared test, we saw that there was no statistically significant difference between the total number of plots reached using the two algorithms ($p = 0.9745$). However, we did observe a statistically significant difference in the total number of plants ($p < 0.0001$) of around 3.5%. Because the radial carrying capacity algorithm was prohibitively slow, we accepted the small discrepancy in the total number of plants and used a plot-based carrying capacity.

We imposed the carrying capacity by removing the proportion of plants that exceeds a plot's carrying capacity. Because we cannot know the theoretical growth of SJV a priori, we chose to limit the number of plants able to grow in a m^2 area after the current year's cohort progresses to reproductive age. If the plot's population size, P, exceeds the carrying capacity K at the end of time step t, we randomly remove individuals from the plot. Therefore we calculate $prob_{survival} = K/P_t$. We then apply this probability of survival to every plant on that specific plot, thus removing all the plants that "died because of competition during the year." We furthermore multiply this carrying capacity coefficient by surviving plants' reproductive rates as they produce seeds, to reflect the cost of a highly competitive environment (Griffith and Forseth, 2003).

3. Calibration

Using initial parameterization, many aspects of the simulation's behavior were qualitatively consistent with the species as empirically observed, but the number of individuals was too high. This was uniformly true, despite thoughtful cross-checking of all the quantitative empirical data we used. To scale the simulation down - and to prevent SJV's population from exploding regardless of parameter settings - we needed to introduce a multiplicative factor (of

less than 1) on each of the plant's vital rates. Producing reasonable metapopulation sizes required a reduction of the vital rates by almost 84 percent. This parameter, which uniformly decreases every plot's r, is termed the *calibration factor* (CF).

4. Results

4.1. Environmental stochasticity

As the yearly environmental conditions of Holts Creek become more variable (ESM is raised above 2), then regardless of the rate of implantation during hydrochory, the 100-year survival chance of the metapopulation begins to fall significantly (Fig. 9). When ESM is 3, there is a 50-50 chance SJV populations will be extirpated from Holts Creek after 100 years. When environmental stochasticity is set to reproduce observed levels of variation in population size, the model predicts a 100-year extinction risk of only 2%.

At ESM greater than 3, a large proportion of simulation runs end in extinction (about 87% with an ESM of 5). In these cases of high stochasticity, a small minority of simulation runs produces explosive growth, wherein the population reaches above 150,000 individuals. This phenomenon occurred only once with an ESM of 2.5 (out of over 3000 distinct simulation runs) and is relatively more common with the higher stochasticity levels: 11 times with an ESM of 3.5 and 16 times with values of 4.5 and 5. Because each stochasticity level has slightly fewer than 3200 distinct runs, the odds of this explosive scenario are exceedingly low.

Though there are anomalous population explosions in several runs with higher levels of environmental stochasticity, as seen in Fig. 10, even with a low ESM and implantation rate, populations of SJV in the high 10,000s are not uncommon.

Additionally, these explosive scenarios only occur in simulations with unrealistic levels of successful post-dispersal implantation. This implies that a confluence of factors is required to produce explosive growth: both a very high ESM and also a large minority of dispersing seeds successfully implanting in new parts of the marsh. This confluence of factors may be necessary because, with a realistic amount of water dispersal, there are very few distinct population patches and thus the metapopulation is restricted by carrying capacity. With a high level of hydrochory but low environmental stochasticity, the patches where successful seeds implant are often transient, since they are inhospitable for population establishment and become locally extirpated after a few years. Both of these factors together, however, result in the metapopulation circumventing the restriction of carrying capacity by having many "good" patches available for successfully dispersing seeds. There is no local population restriction.

Note that because of memory and computing time limitations on the Stampede computer, an explosive population that
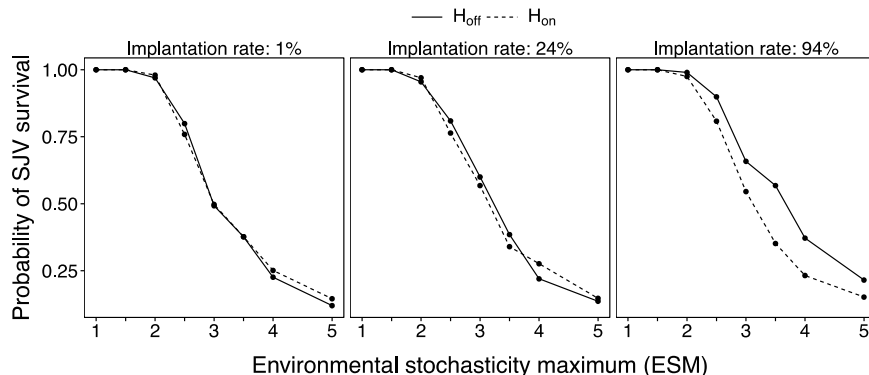

Fig. 9. Probability of metapopulation survival for SJV, as a function of the hydrochory boolean, the rate of implantation, and the ESM. Environmental stochasticity greatly influences the 100-year survival probability of SJV. The hydrochory boolean, H_{on} or H_{off}, as well as the level of hydrochory play a smaller role.
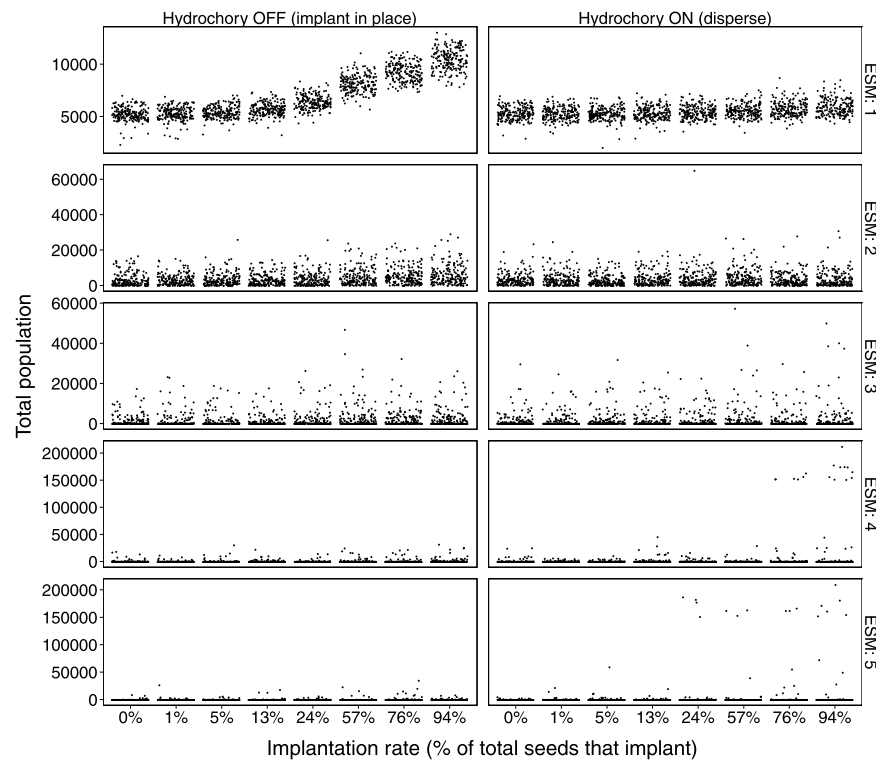
Fig. 10. Population counts of SJV after 100 simulated years, varying the hydrochory boolean, rate of implantation, as well as ESM. With higher environmental stochasticity levels as well as more than 24% of total seeds successfully implanting, there is a small chance that the population will "take off" to over 150,000 individuals. Note that very high populations, greater than 20,000 individuals, are rare but do exist even with moderate environmental stochasticity and low implantation rates. Each facet's scales are independently generated.

reached 150,000 individuals was terminated, and counted as an end scenario in the simulation. It is possible that with extreme environmental stochasticity, a few of these runs, had they continued, would have collapsed as quickly as they arose when a particularly bad year or years was generated.

4.2. Hydrochory

With H_{on}, i.e. seeds successfully dispersing, the average number of plants after 100 years increases as implantation rate increases. This increase in average number of plants is dampened with H_{on}. But the incidence of very large populations is higher with H_{on} than with H_{off}.

As seen in Fig. 11, the total population count after 100 years increases as CF increases, with both hydrochory boolean values. Comparing the two, the rate of increase is about the same. For any given value of CF, the total population count after 100 years also increases as implantation rate increases. But the rate of increase is quite different when comparing H_{on} and H_{off}, which leads to the following interesting dynamic.

As implantation increases, H_{off} produces a much greater increase in total population count than H_{on}. This effect is due to dispersal mortality as well as a lack of high propensity sites for dispersing seeds to implant in. At CF values above 0.175, however, this difference between H_{on} and H_{off} disappears. Above CF 0.19 hydrochory greatly increases the population's size. Our interpretation of this phenomenon is that when the habitat as a whole is friendlier to SJV, the key factor that constrains population growth changes: it is no longer limited by a lack of available low-competition patches, but rather by carrying capacity. Hydrochory allows for a carrying capacity limited population to "export" seeds and therefore greatly

increase population size. However, if the calibration factor is low those seeds will likely die if they implant.

4.3. Clustering analysis

After each simulation we used the DBSCAN algorithm (Ester et al., 1996) to obtain the number of clusters of SJV in Holts Creek, where a cluster is defined as a geographically isolated group of plants. Because the runtime of DBSCAN increases exponentially with the number of plants in the simulation, we only calculated this statistic for simulations that ended with fewer than 25,000 plants. Though this behavior was rare, this cutoff resulted in the higher environmental stochasticity levels having slightly fewer data points than the lower ones. Of the 19,000 simulations run with an ESM > 2, 136 completed with over 25,000 plants and could not be processed.

As seen in Fig. 12, with H_{off} and averaging across all levels of environmental stochasticity, increasing the implantation rate leads to a higher number of clusters after 100 simulated years. More environmental stochasticity leads to more variability in the cluster counts though an overall decrease in the average number of clusters, due to added extinction risk. Ultimately, at ESM > 2, an increasing number of simulations end with metapopulation extinction.

4.4. Rescue effect

The data derived from this iteration of the model indicates that, while external seed input from robust populations could re-establish a dead patch, it is very unlikely that the number of immigrating seeds could sufficiently bolster a weak, transient population. In other words, when environmental factors lead a
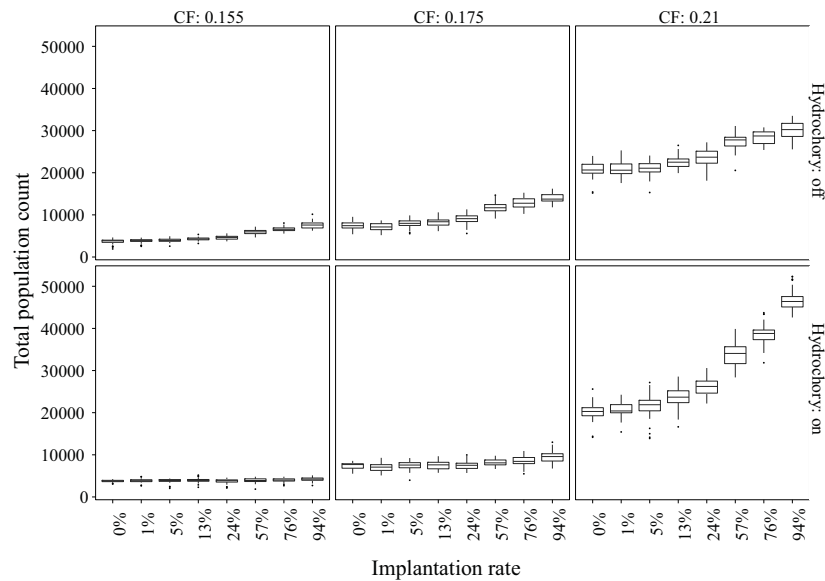
Fig. 11. Number of plants after 100 years varying the hydrochory boolean and calibration factor. Environmental stochasticity was kept at a constant "1" during this time, resulting in no environmental influence during the simulation.
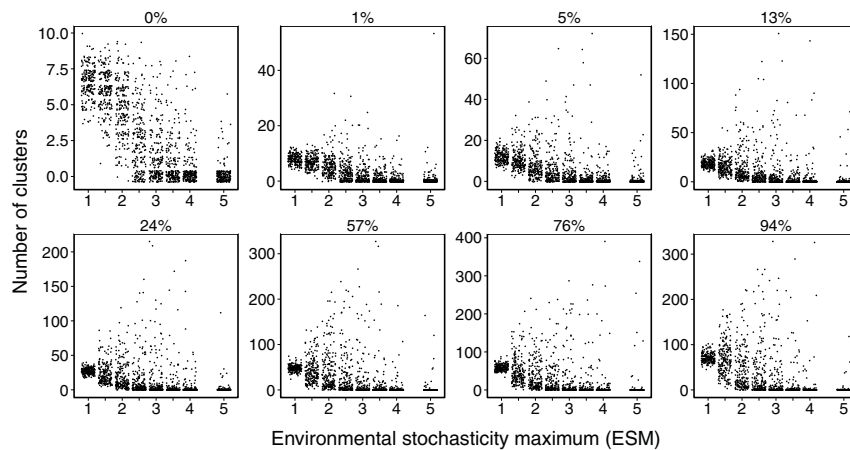

Fig. 12. Cluster dynamics varying ESM, implantation rate and H_{on}. With more seeds dispersing successfully and implanting, more clusters are present in Holts Creek. As more environmental stochasticity is added into the system, the number of clusters present after 100 years shows a greater spread. Each facet's scales are independently generated.

population toward extirpation, external seed input is moot to the longevity of a population.

Furthermore, it is unlikely that seed input into an already colonized patch would have any significant effect on that patch's overall population. If the patch characteristics are favorable for SJV and there is already some number of plants in the patch, it is likely that its success is assured, assuming there are no catastrophic environmental swings.

It is the case, however, that hydrochory enables new patches to be colonized, potentially repeatedly, given a relatively mediocre patch quality and a varying environment.

5. Discussion

5.1. Investigating the importance of hydrochory on metapopulation dynamics

With an adjustment rate that produces realistic population counts, the model indicates that SJV's secondary dispersal mechanism, hydrochory, will play little part in the long-term survival of the plant.

Indeed, if seeds were to implant in place rather than disperse, SJV would, in high-implantation rate scenarios, be better off. This is apparently because most areas of Holts Creek are inhospitable to the plant. Even with unrealistically high numbers of dispersing seeds successfully implanting into the berm, there are so few areas habitable for SJV that dispersing is almost a "doomed" endeavor; new populations will most likely be small and transient in nature. If a plant is able to grow to adulthood and produce seeds, it is probably already in a hospitable area. Those that implant locally are likely to successfully grow to adulthood, impeded only by carrying capacity.

With a higher adjustment rate, above .20, the opposite pattern emerges. Because there are so many hospitable plots (with an r above 1) SJV is limited only by dispersal and carrying capacity. If no effective dispersal mechanisms (such as hydrochory) exist, then the population growth rate is constrained *only* by carrying capacity. With H_{off}, the metapopulation can only grow as fast as the individual populations can expand, and no new populations are formed. With H_{on}, however, more new populations can be established, increasing the metapopulation growth rate significantly.

Note, however, that without an unrealistically high implantation rate (greater than 13% of the seeds successfully implanting

after dispersal) hydrochory makes very little difference no matter the calibration factor. The populations established by water dispersal, even under the most generous vital rates, are not numerous or large enough to make any substantial difference in metapopulation count.

With the model calibrated to reproduce observed population counts and fluctuation and a realistically low implantation rate, it appears that hydrochory can establish some new populations and could potentially, with beneficial environmental stochasticity, slightly increase the metapopulation size. However, generally these populations will be small and transient in nature, vulnerable to environmental fluctuations that could potentially extirpate them.

To summarize, the only way hydrochory could confer an overall metapopulation advantage is if (1) there were enough hospitable, but unreached, areas where water-bound seeds could establish new populations, (2) the carrying capacity was reached in areas where SJV already exists, limiting the utility of additional seeds implanting locally, and (3) the likelihood of successful water dispersal is high enough to ensure that seeds will actually reach these hospitable patches.

5.2. Environmental stochasticity's influence on metapopulation dynamics

When environmental stochasticity is set to reproduce observed levels of variation in population size, the 100-year chance of extinction for Sensitive joint-vetch is only 2%. Introducing more stochasticity into the system decreases significantly the probability that the Holts Creek metapopulation of SJV will survive for another 100 years.

Because our model does not incorporate some factors that are most concerning for ecologists studying the plant - such as habitat destruction and climate change - we can only associate these factors with higher levels of environmental stochasticity, and this leads to a precipitous drop in the 100-year survival chance of SJV. Furthermore, when incorporating higher levels of environmental stochasticity into the model, we did not observe hydrochory positively influencing the 100-year survival probability of SJV. Without directly managing new, weak populations, there is little chance that they establish for the long term.

It is also worth noting that climate change is not expected to be mean-reverting. While inside the simulation a bad year could be followed up by an equally good year, realistic systems influenced by climate change will not be so lucky. The overall mean quality of Holts Creek is likely to continually drop as the marsh becomes more inundated by sea level rise and more disturbed by intense weather events.

Lastly, our model casts doubt on the efficacy of the "rescue effect." Any seed input by other populations into a sink population would not necessarily "save" that population for more than a few years, depending on environmental factors. While these transient populations may be observed, without outside management they will inevitably fall to environmental variation with or without external seed input.

5.3. Is "propensity" a viable proxy for patch suitability?

The decision to use "propensity" to approximate patch suitability was a pragmatic one. It is important for future analyses, including future iterations of this model, to understand its limitations and benefits for marshland ecosystems.

Our measure of propensity and its approximation of patch suitability is a mixed picture. After calibrating the measurement, the largest populations of SJV in Holts Creek were preserved in silico, while some of the smaller though consistent populations disappeared. The populations preserved by our approximation fared

quite well, growing to sizes comparable or larger than those empirically observed. Their geographic footprint shrunk, however.

Using the red band to approximate biomass is admittedly imperfect, since different plants (and abiotic entities) absorb different levels of red light. Furthermore, even implementing a vegetation index such as the Normalized Difference Vegetation Index (NDVI) is precarious on a small scale. However, as the purpose of this simulation was not to predict exact population locations or sizes, we argue that it is effective in constructing a heterogeneous habitat for a subject species to exist within. By calibrating the model we can outline broad patterns that can only emerge by comparing extreme parameterizations with more realistic ones.

5.4. The calibration factor (CF) and thoughts for model revision

One finding revealed by the simulation is that the efficacy of water dispersal is highly dependent on a tidal plant's overall ability to thrive in its habitat. We happened upon this finding somewhat by accident, when we discovered the presence of as-yet unexplained factors that make SJV less plentiful overall than the uncalibrated model would suggest. The degree to which vital rates are calibrated is crucial in determining whether hydrochory is a benefit, a liability, or a non-factor.

As Fig. 11 illustrates, when the CF is low, water dispersal has a negative impact on the metapopulation. This is because fewer viable plots exist, and a newly dropped seed is better off implanting in place - on or near its maternal plot, which was good enough by definition to have supported the maternal plant - than in venturing downstream in a probably fruitless search for a distant viable plot. When the CF is raised, this negative effect disappears: a sufficient number of viable plots will be present throughout the habitat that seeking them is not a lost cause.

Eventually, as the CF is raised even higher, the likelihood of reaching a distant viable plot makes it more beneficial for seeds to leave their maternal plots than staying close to home and being subject to carrying capacity limits (see rightmost side of Fig. 11).

The idea of plot "propensity" was initially constructed to simply approximate the influence of a heterogeneous environment on SJV's vital rates, therefore enabling us to see how well it can utilize hydrochory to find suitable new patches. We made the simplifying assumption that empirical observations about which plot colors SJV does and does not inhabit in Holts Creek could be used to approximate this propensity. As it turned out, this (uncalibrated) propensity measure created far too many "good" areas for SJV. Recall Fig. 8, a reclassified raster indicating patch suitability for SJV in Holts Creek, presented in Section 2.7.3. The darkest green color on the map contains the color spectrum defined as most suitable for SJV, and there are tens of thousands of these appropriate squares. With so many good locations and no calibration, SJV does not need secondary dispersal to access new patches. It would only have to reach 2000 m^2 with a carrying capacity of 50 plants/m^2 to have 100,000 individuals in the metapopulation, which is more than possible in an excellent habitat over 100 years.

In calibrating propensity to achieve known population levels, we create an environment where very few plots are suitable for SJV and secondary dispersal is, for all intents and purposes, a death sentence. While this behavior is consistent with reality - ecologists have only rarely observed SJV colonizing new, long-term populations (Griffith, 2014) - it is also true that by introducing the CF we eliminated some known population centers of SJV. The most likely conclusions from all this are (1) there are additional factors, not accounted for by the above model, that impact SJV's vitality, and (2) our metric based on aerial imagery is an imperfect measure of a plot's true propensity.

Ecologists are currently gathering data on two variables that may impact the conditions under which SJV can thrive: tidal

inundation duration and depth (Griffith and Speray, unpublished data). The exploration of these two factors, and their incorporation into the suitability data, could provide a more precise measure of a plot's propensity. Only once we can more accurately predict where SJV can thrive can the model be used for geographic prediction. More accurate data about the propensity of Holts Creek plots, if it leads to a simulation which can more faithfully reproduce the actual locations of SJV populations, will also help us validate the other aspects of the model. Future work will include an analysis comparing the geographic positions of empirical and simulated plots, enabling an even more detailed, spatially explicit validation of SJV's geographical tendencies.

6. Conclusions

Our model represents two broad processes: secondary dispersal and environmental stochasticity. Both of these process results can inform us about potential active management of SJV populations. The model also addresses two potential outcomes of active management: total population size and the number of populations in the metapopulation. Model results allow us to think about these processes separately, as dispersal is not directly changed by environmental stochasticity changes and vice versa.

Increased dispersal could be implemented in the field by collecting seeds from existing populations and placing them at high quality sites, currently unoccupied by SJV. This action may produce results similar to the highest, simulated implantation rates, because we can ensure implantation and decrease the chances of seed death in transit. Furthermore, our simulation is consistent with the need to continue management of these established populations. Distributing seeds to new sites, in the simulated Holts Creek and in the real Holts Creek, will successfully increase the geographic distribution of SJV. But, the increase in the number of occupied patches will be short lived without ongoing management. Low rates of germination, establishment, and adult survival, explicit in our model as demographic parameters, would make most established sites sink populations. As a result, established populations will most often go extinct. In addition, naturally established populations will be small and very likely to succumb to competition or lower swings in environmental stochasticity. As a result, populations must be established with many seeds or the survival of small numbers of plants must be maximized through active management.

Environmental stochasticity cannot itself be managed, but individual SJV plants and seeds could be protected from swings in environmental quality from year to year. While some decreases in vital rates may be intrinsic to individuals, many of the causes of death or decreases in reproduction are environmental in nature. For example, a good year for SJV may be a year in which a population site is devoid of competitor species because of a winter's ice scour. If we remove SJV plants and seeds from the environment, we would remove SJV individuals from some of the environmental conditions that decrease vital rates. It is most practical to remove seeds from the environment to protect individuals from environmental stochasticity. Specifically, if we harvest seeds in the fall and hold them overwinter, overwinter survival will increase. This vital rate is one of the lowest of all vital rates for SJV (Griffith and Forseth, 2005, 2006).

Acknowledgements

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Geospatial data sources

[1] New Kent County, VA, 2012 National Ag. Imagery Program Mosaic, United States Department of Agriculture, 2012.

[2] New Kent County, VA, 2012 National Hydrography Dataset, The National Map, United States Geological Survey, 2012.

[3] Division of Natural Heritage, 2011. Element occurrence records – *Aeschynomene virginica*. Virginia Department of Conservation and Recreation, Richmond, VA.