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Ecotone formation induced by the effects of tidal flooding: a conceptual model of the mud flat-coastal wetland ecosystem

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Abstract

The boundary between mud flat and coastal wetland ecosystems is highly productive and a haven of considerable biodiversity. It is also embedded in a highly dynamic environment and can be easily destabilised by environmental changes, invasive species, and human activity. Thus, understanding the processes which govern the formation of this ecotone is important both for conservation and economic reasons. In this study we introduce a simple conceptual model for this joint ecosystem, which demonstrates that the interaction between tidal flooding and habitat elevation is able to produce an ecotone with similar characteristics to that observed in empirical studies. In particular, the transition from mud flat to vegetated state is locally abrupt, occurring at a critical threshold elevation, but, on broader spatial scales can occur over a range of elevations determined by the variability in high tide water levels. Additionally, the model shows the potential for regime shifts, resulting from periods of unusual weather or the invasion of a fast growing, or flood resistant, species.

Keywords: ecotone structure, intertidal ecosystem, ecosystem engineering, competition, stochastic perturbation

1 Introduction

The transition between intertidal mud flat and coastal wetland ecosystems is of great ecological and economic importance. These habitats are found around the world, with salt marshes forming in temperate regions, e.g. the German Wadden Sea and New England

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coast, and mangrove swamps forming in subtropical regions, e.g. Florida and south east China, but, regardless of climate, are characterised by the highly productive communities of benthic invertebrates and plants that they support (Alongi, 1990; Barnes et al., 1997; Erftemeijer and Lewis, 1999; Zedler and Kercher, 2005). While these basal communities may be relatively homogenous (less so in subtropical environments), the biomass produced supports a wide range of higher organisms and thus these habitats as a whole represent a haven of biodiversity (Erftemeijer and Lewis, 1999; Zedler and Kercher, 2005). In addition to their ecological importance, many of the species in these communities are harvested, producing significant economic yields (Barbier et al., 1997) and the transition to a vegetated state protects the coastline from erosion, a significant problem in sub- tropical communities (Thampanya et al., 2006). These transitional ecosystems are threatened by a variety of factors and, despite their importance, are in decline globally (Zedler and Kercher, 2005). For example, human harvesting activities often damage the wetland community leading to a regime shift to mud flats (Thampanya et al., 2006). On the other hand, invasive grasses (such as Spartina species) can rapidly convert mud flats to vegetated meadows (Hacker et al., 2001; Zhang et al., 2005). The loss of either community naturally reduces biodiversity and productivity of the joint ecosystem, and thus understanding the population dynamics underlying this transition is important for both conservation and economic reasons.

Transition zones where one community gives way to another, also referred to as ecotones, have been studied extensively, see (Cadenasso et al., 2003; Strayer et al., 2003; Yarrow and Marín, 2007) and the references contained therein. Naturally occuring ecotones often form in the presence of an environmental gradient, such as temperature (Shugart et al., 1980) or salinity (Jiang et al., 2012; Basset et al., 2013), which induces a transition between similar communities, e.g. grassland or forest succession, with different tolerances to that gradient, e.g. see (Walker et al., 2003). Alternatively, periodic disturbances, such as storms (Dollar and Tribble, 1993) or fires (Hoffmann et al., 2012), can allow species to coexist in a long term transitional community which would otherwise be dominated by one species type, e.g. savanna ecosystems (Hoffmann et al., 2012). We note that the transition in wetland communities, from mangrove swamp to coastal wetland, results, in part, from a combination of these factors, as decreasing temperatures with latitude increases the frequency of winter freezes, a disturbance that mangroves are less able to tolerate (Guo et al., 2013; Saintilan et al., 2014).

Mathematical modelling has been used successfully in a variety of frameworks to describe features of ecotone formation (or more generally pattern formation) (Shugart, 1990; Gilad et al., 2004; Kondo and Miura, 2010; Gastner et al., 2011). In general, boundary formation in these models is a consequence of the interactions between species or a species and its environment. A particular focus of this research has been the important role of ecosystem engineers, that is species which significantly modify their habitats, in this process. For example, Jiang and DeAngelis (2013) show that an abrupt ecotone forms between species that have opposed engineering effects; in their case, halophytic mangroves and glycophytic hardwood hammocks compete to influence soil salinity. These engineering effects also create the potential for regime shifts in response to severe system disturbances, e.g. tropical storms, which create an opportunity for mangroves to invade hardwood hammock habitat. The role of more moderate disturbances in maintaining transitional communities has also been explored, for example in savanna ecosystems see (Thonicke et al., 2001; Hanan et al., 2008; Scheiter and Higgins, 2009).

However, even when incorporating such moderate disturbances, the systems considered in most studies are relatively stable compared to that of the mud flat to coastal wetland ecotone. This habitat is subject to daily tidal flooding, which causes a variety of effects, including soil erosion and sedimentation, fluctuations in salinity and, of course, direct changes in the populations of the two communities (Mahall and Park, 1976; Balke et al., 2014). The result is a highly dynamic environment which is known to have significant effects on the biodiversity and functioning of this ecosystem (Brose and Hillebrand, 2016; Fischer et al., 2016) and which, furthermore, can reasonably be expected to influence ecotone formation.

In addition to these interesting ecological effects however, the complexity of this environment represents a considerable source of uncertainty to be addressed in any model seeking to describe this system. In particular, a mechanistic approach, e.g. (Thonicke et al., 2001; Scheiter and Higgins, 2009), must determine an appropriate mathematical description for each of the many processes that make up the system behaviour. The parameters for each of these descriptions must then be determined by experimental data, which may not be available. Moreover, the more closely a model describes a particular set of environmental conditions, the greater the risk that the insights it provides are unique to that setting and that general phenomena cannot be readily identified or explained. On the other hand, a conceptual approach, e.g. (Holling , 1966; Hanan et al., 2008), represents the underlying physical processes only abstractly, and thus ignores these uncertainties, but cannot claim to represent a particular physical system. Instead, such models can be used to connect aspects of (abstract) processes to particular phenomena.

These considerations are, of course, inherent to any mathematical model and debate over which approach to use, and under what circumstances, is ongoing (Evans et al., 2013). We mention them here to provide some context regarding our modelling approach in this study. In particular, in contrast to existing models of the mud flat to coastal wetland ecosystem which are primarily mechanistic, e.g. (van de Koppel et al., 2001; Marani et al., 2010), we develop a minimal conceptual model in order to explore the key mechanisms producing and defining this ecotone. We assume that each of these habitat types mud flat and coastal wetland is characterised by a particular community, one benthic and the other terrestrial, which are affected differently by tidal flooding. We then model the dynamics of these communities as species competing for a common resource, which we regard as space, with the terrestrial "species" being assumed to act as an ecosystem engineer. The underlying dynamics of these populations is given by a simple system of differential equations. The tidal flooding process is modelled as a series of discrete stochastic events, representing differences in the high tide water level in relation to a fixed habitat elevation, which may negatively affect one or other of the populations. Using this model we seek to determine: 1) under what circumstances an ecotone can form and 2) how the spatial characteristics of that ecotone are affected by model parameters. In particular, we note that the mud flat to coastal wetland ecotone is known to occur over a relatively narrow range of elevations in a given habitat (Balke et al., 2014), however on a broader spatial scale, the position of this switch can vary significantly (Simenstad et al., 1997). Thus, we investigate how these characteristics can be reproduced in the model framework described.

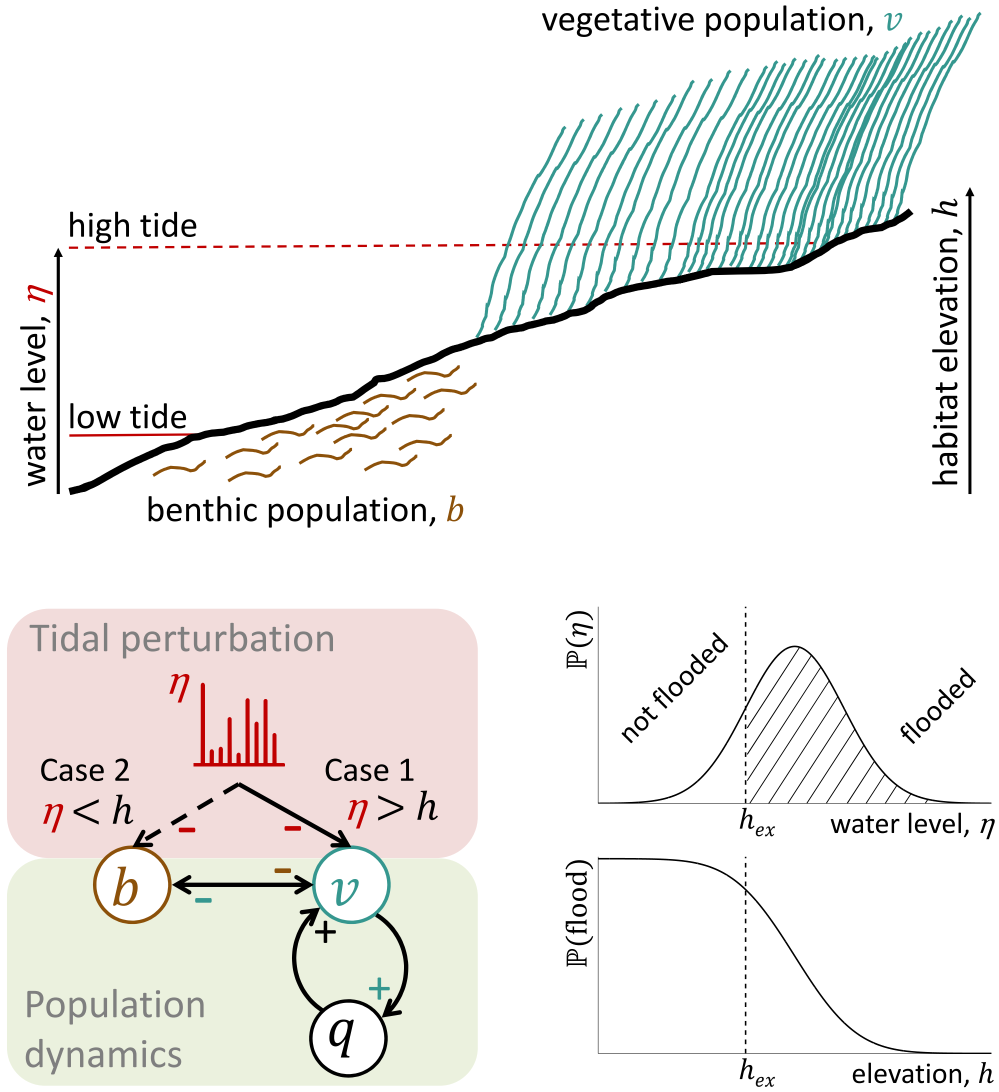

Figure 1: **top**: Sketch of the transition from mud flat to coastal wetland. The vegetative and benthic populations, v and b respectively, compete for space on an elevation gradient, h. The water level at high tide η varies. **bottom left**: Schematic diagram of the model components showing the qualitative interactions between populations, habitat quality q and the tide. Further details can be found in the text. **bottom right**: The probability of a particular high tide water level $\mathbb{P}(\eta)$ (top) and the corresponding probability that a habitat at a given elevation h will be flooded $\mathbb{P}(\text{flood})$ (bottom).

2 Model

We describe the combined mud flat and coastal wetland ecosystem, and its environment, using a simple conceptual model consisting of two components. A series of sketches, providing an overview of this model, can be found in Fig. 1. The first sketch, Fig. 1 top, is a cross-section through the ecosystem, showing the benthic b and vegetative v communities dominating at low and high elevations h respectively. The water level at high tide η, which determines how much of the habitat is flooded, varies on a daily basis. The underlying structure of the model is presented in a schematic diagram, Fig. 1 bottom left. The two communities compete, negatively affecting each other and the vegetative population improves the habitat quality q to its own benefit creating a positive feedback loop. These dynamics are described determistically. Tidal perturbations negatively affect either the vegetative population alone (Case 1) or both populations (Case 2). High tide occurs at regular intervals, period τ, but whether a perturbation is applied to a population depends on the high tide water level (which is generated stochastically) and the elevation of the habitat, see Fig. 1 bottom right. These two model components, deterministic population dynamics and stochastic tidal perturbations, are described in more detail below.

Mathematical description of the population dynamics

We approximate the two communities in our model as competing species using the classical Lotka-Volterra competition model (Murray, 2002). Additionally the vegetative species is assumed to act as an ecosystem engineer following the model developed by Cuddington et al. (2009). The resulting system of (deterministic) differential equations describes the population dynamics in this system:

$$\frac{dv}{dt} = a_v(q)v\left(1 - \frac{v + \gamma_b b}{K_v(q)}\right), \tag{1}$$

$$\frac{db}{dt} = a_b b\left(1 - \frac{(\gamma_v v + b)}{K_b}\right), \tag{2}$$

$$\frac{dq}{dt} = -cq + fv. \tag{3}$$

The population density of the vegetative and benthic species are represented by v and b respectively. The carrying capacities for each species are given by $K_v(q)$ and K_b respectively and their initial growth rates are $a_v(q)$ and a_b. To reduce the number of parameters we normalise the system such that the benthic population's initial growth rate and carrying capacity are both equal to one. As a result, the other variables v and q are measured in terms of the carrying capacity of the benthic population, while rates are given in terms of the initial growth rate of the benthic population.

The vegetative species is assumed to be a non-obligate ecosystem engineer (Cuddington et al., 2009), in that it improves the habitat quality, q, at a rate proportional to its density (fv) but does not require these improvements to survive. As the quality of the habitat increases it can sustain a higher population of the vegetative species and this species can grow faster, i.e. $K_v(q)$ and $a_v(q)$ increase. In order to ensure that the vegetative population remains finite, we assume that there is a limit to the habitat quality that can be maintained by the vegetative population (formal conditions are given in Appendix A.1). For numerical purposes we take $a_v(q) = a_0 + a_1 q$ and $K_v(q) = K_0 + \Delta K q/(1+q)$. The habitat quality decays exponentially with decay constant c representing the fact that the vegetative population is required to maintain any improvements.

Mathematical description of tidal perturbation process

The second component of our model describes the effect of flooding of the habitat at high tide. We assume that high tides occur with period τ and that the water level at high tide η is random drawing it from a normal distribution with mean $\mu = 0$ and variance

σ^2. (While the mean is arbitrary, simply setting the midpoint of the distribution, the variance has an ecological interpretation; a small variance corresponds to a system where water levels are very consistent and a large variance the opposite.) If η is greater than the habitat elevation h then the habitat is flooded, Fig. 1 bottom right. As noted above, we consider two possible effects of a flood event. In Case 1, when a flood occurs a fraction ρ of the vegetative population dies, i.e.:

$$v_+(i\tau) = \psi_v(v(i\tau)) = \begin{cases} v(i\tau) & ,\eta < h \\ (1-\rho)v(i\tau) & ,\eta \geq h \end{cases} \tag{4}$$

where i is a positive integer corresponding to the number of high tides that have occured and $v(i\tau)$ and $v_+(i\tau)$ are the populations before and after application of the tidal perturbation. In Case 2, in addition to this effect on the vegetative population, when a flood does not occur, the benthic population is affected in the same way, i.e.:

$$b_+(i\tau) = \psi_b(b(i\tau)) = \begin{cases} (1-\rho)b(i\tau) & ,\eta < h \\ b(i\tau) & ,\eta \geq h \end{cases} \tag{5}$$

with $b(i\tau)$ and $b_+(i\tau)$ being defined in the analogous way.

Typical system parameters

In order to solve this system numerically it is necessary to choose suitable parameters. Recalling that we consider time relative to the growth rate of the benthic species we take the period between high tides $\tau = 0.1$. This means that, in the absence of the vegetative population, 100 high tides (or about two months) will occur in the time required for the benthic species to grow from a near zero density to its carrying capacity. We assume that the initial growth rate and carrying capacity of the vegetative species are lower than those of the benthic species in an unimproved habitat ($q = 0$) taking $a_0 = 0.75$ and $K_0 = 0.5$. In the majority of our simulations we take $a_1 = 0$ and $\Delta K = 1.0$, meaning that the growth rate of the vegetative species is unaffected by habitat quality and that an improved habitat ($q \gg 0$) can support a vegetative population half again as large as the maximum benthic population. We set $f = 0.25$ and $c = 0.0625$ corresponding to relatively slow improvement of the habitat by the vegetative species. The effects of varying these, and the competition, parameters are dicussed in Section 3.2. We consider a representative range of different perturbation strengths ρ and high tide water level variances σ^2 in Sections 3.3 and 3.4. If these values are not stated their default values are $\rho = 0.04$ and $\sigma^2 = 5.0$.

3 Results

3.1 Mechanism for the formation of an ecotone

We begin by considering how an ecotone might form within the model described in Section 2. We note that an ecotone is a transition in space and, as such, the primary process underlying the formation of an ecotone must be spatial. In our model, the tidal perturbations are the only spatial process; since the frequency of flooding is moderated by habitat elevation h, while the population dynamics are completely non-spatial. It is

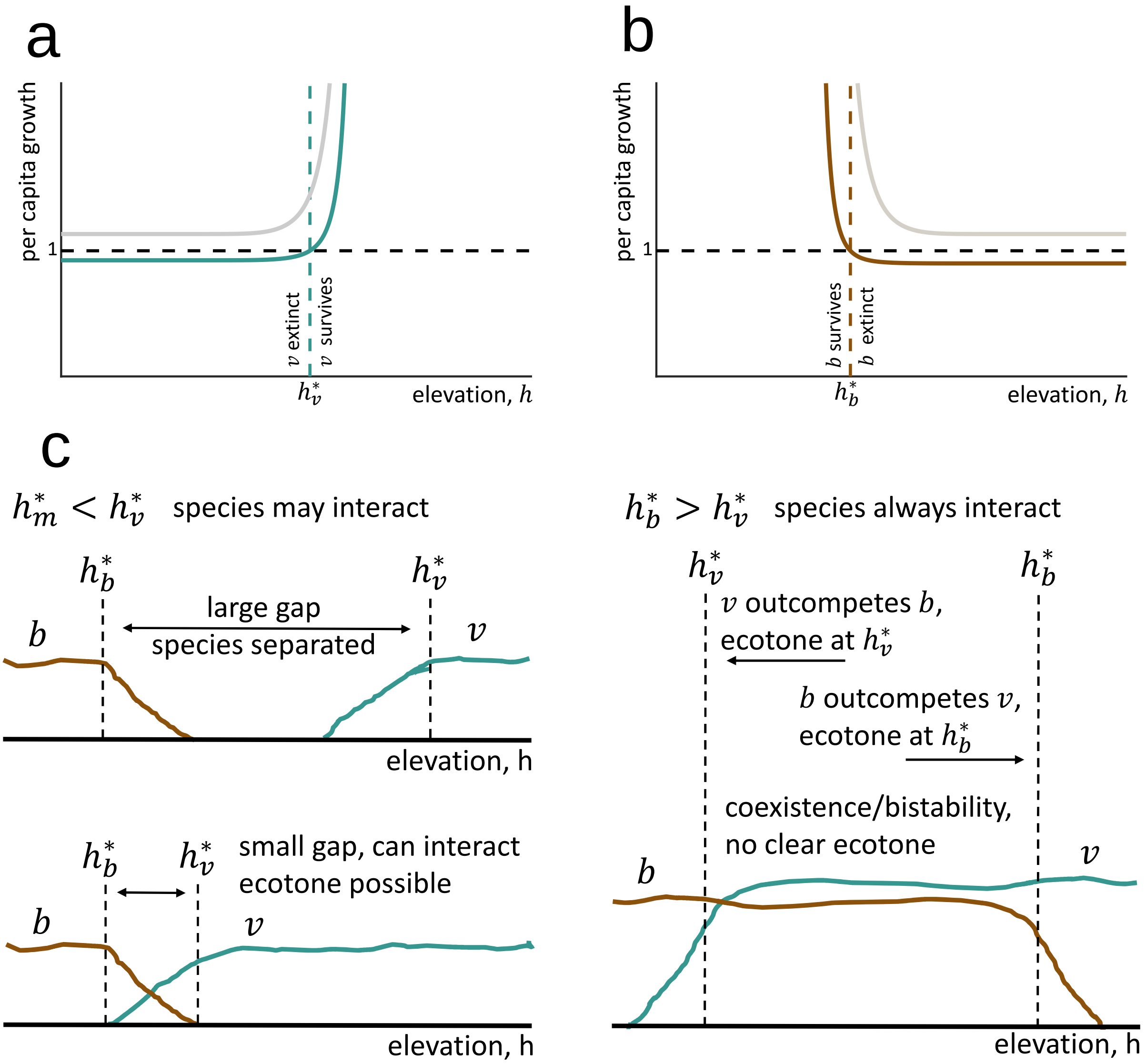

Figure 2: Effect of habitat elevation on species survival. **a**: Change in the per capita growth of the vegetative population (green curve) with habitat elevation h resulting from the change in the average time between floods $T(h)$ (grey curve). The population survives if the per capita growth is greater than 1. **b**: Change in the per capita growth of the benthic population (brown curve) with habitat elevation h resulting from the change in the average time between high tides that do not flood the habitat (grey curve). Again, the population survives if the per capita growth is greater than 1. **c**: Sketch of possible scenarios when both species are affected by tidal perturbations. The relative size of h_b^* and h_v^* and the outcome of the deterministic population dynamics determine whether an ecotone can form. (By a "clear ecotone" we mean a transition that occurs at a consistent elevation across multiple habitats.)

intuitively clear that, if the perturbations are sufficiently frequent and severe, they can drive a species to extinction. However, as the frequency drops, the population will be permitted to grow undisturbed for longer periods, compensating the perturbations and allowing the species to survive. This splits the habitat into two regions, one where the species can survive and another where it cannot, a necessary condition for the formation of an ecotone.

We formalise the intuitive mechanism described above by constructing and analysing a simplified single species system. Note first, that the mechanism suggests that whether or not a species is able to survive is determined by its growth between consecutive flooding events, which we denote $T(h)$. During this period the population grows according to Eqs. (1)-(3); however, it is clear that whether or not a species survives is typically determined at low densities of that species. At low densities the population will grow approximately exponentially (Malthus, 1809; Murray, 2002) since the effect of density dependence is small. Furthermore, we note that the density of the competing species is approximately constant when $T(h)$ is small and thus its effect on the species of interest can be included in the growth rate a. Thus we arrive at the following equation for the growth of the (vegetative) species:

$$v\left((i+1)T(h)\right) = v_+\left(iT(h)\right)\exp\left(aT(h)\right), \tag{6}$$

where $v_+\left(iT(h)\right)$ and $v\left((i+1)T(h)\right)$ are the populations immediately after the previous perturbation i and immediately before the next perturbation $i+1$ respectively. The surviving population after the perturbation is then given by Eq. (4) yielding:

$$v_+\left((i+1)T(h)\right) = v_+\left(iT(h)\right)(1-\rho)\exp\left(aT(h)\right), \tag{7}$$

which is simply the discrete form of the exponential growth equation (Murray, 2002). The per capita growth rate is given by:

$$\Delta v(T(h)) = \frac{v_+\left((i+1)T(h)\right)}{v_+\left(iT(h)\right)} = (1-\rho)\exp\left(aT(h)\right), \tag{8}$$

and we know that if it is greater than one the population is increasing and thus can survive, while if it is less than one the population is decreasing and will go extinct (Murray, 2002).

The period between flooding events $T(h)$ is dependent on the distribution of water levels at high tide and the habitat elevation. In particular, since we assume that water levels are distributed normally (with $\mu = 0$) the probability that they exceed h on a given tide is given by:

$$\mathbb{P}(\eta > h) = \frac{1}{2}\left(1 - \operatorname{erf}\left(\frac{h}{\sqrt{2\sigma^2}}\right)\right), \tag{9}$$

cf. Fig. 1 bottom right. The average time between floods at a given elevation is thus:

$$T(h) = \frac{\tau}{\mathbb{P}(\eta > h)} = \frac{2\tau}{\left(1 - \operatorname{erf}\left(\frac{h}{\sqrt{2\sigma^2}}\right)\right)}, \tag{10}$$

where τ is the time between high tides. We see that the minimum period between floods is τ, and that $T(h)$ increases as h increases, see the grey curve in Fig. 2a. Eventually

$T(h)$ goes to infinity, which corresponds to elevations that high tide can never reach. This increase of $T(h)$ with elevation means that, if the per capita growth for τ is less than one, e.g. $\Delta v(\tau) = (1-\rho)\exp(a\tau) < 1$, there is some elevation h_v^* below which the vegetative species will be driven to extinction and above which it may be able to survive, dependent on the deterministic population dynamics, see Fig. 2a.

Consider now Case 1 of the complete model described in Section 2, i.e. where the vegetative species is affected by tidal perturbations and the benthic species is unaffected. The argument above shows that there exists a threshold elevation h_v^* below which the vegetative population will go extinct. On the other hand, the benthic species can survive at any elevation. Thus, in order for an ecotone to form, i.e. for there to be a transition from a region dominated by the benthic population to a region dominated by the vegetative population, v must outcompete b in the (unperturbed) deterministic system. Then b will survive below h_v^* where v is driven to extinction, and v will survive above h_v^* and competitively exclude b.

In Case 2 of the complete model, where the benthic species is negatively affected when floods do not occur, a similar argument shows that there is some h_b^* above which it will be driven to extinction and below which it may survive, see Fig. 2b. In this case, the formation of an ecotone depends on the relative positions of h_b^* and h_v^* and, in some cases, the competition between the two species, refer to Fig. 2c for a summary of the possible outcomes.

3.2 Behaviour of the deterministic population dynamics

In the previous section we noted that the outcome of competition between the benthic and vegetative species affected whether or not an ecotone could form within the system. In this section we present a summary of the behaviour of the deterministic system in order to identify parameter ranges suitable for ecotone formation. A more detailed analysis can be found in Appendix A.1. In the case of classical Lotka-Volterra competition (Murray, 2002), the parameter space divides into four regions: a coexistence region, C, where the species are both able to survive; two regions where one species always survives and the other becomes extinct, B and V; and a bistable region, VB, where either of the two species can survive (and the other become extinct) dependent on initial conditions. In our system, a fifth region, CB, may emerge, depending on the parameter values, in which either only b survives or a coexistence state is reached. This fifth state arises from the ecosystem engineering effect of the vegetative species, a more detailed explanation can be found in Appendix A.1. An example map of the possible outcomes, relative to the competition parameters γ_b and γ_v, is presented in Fig. 3b.

The boundaries of the C, V and VB regions can be found analytically by standard techniques, phase plane sketches in Fig. 3a and Appendix A.1, and are given explicitly in the figure. The condition determining the position of the CB-B boundary is complex, depending on all system parameters and the form of $a_v(q)$ and $K_v(q)$, and as such we determine it by numerical analysis of the system Jacobian. This region expands as f/c and ΔK increase. The vegetation growth rate appears to have little effect on the position of this boundary. However, we note that this may be a limitation of the numerical investigation undertaken, as terms relating to this rate can be found in the expression governing this

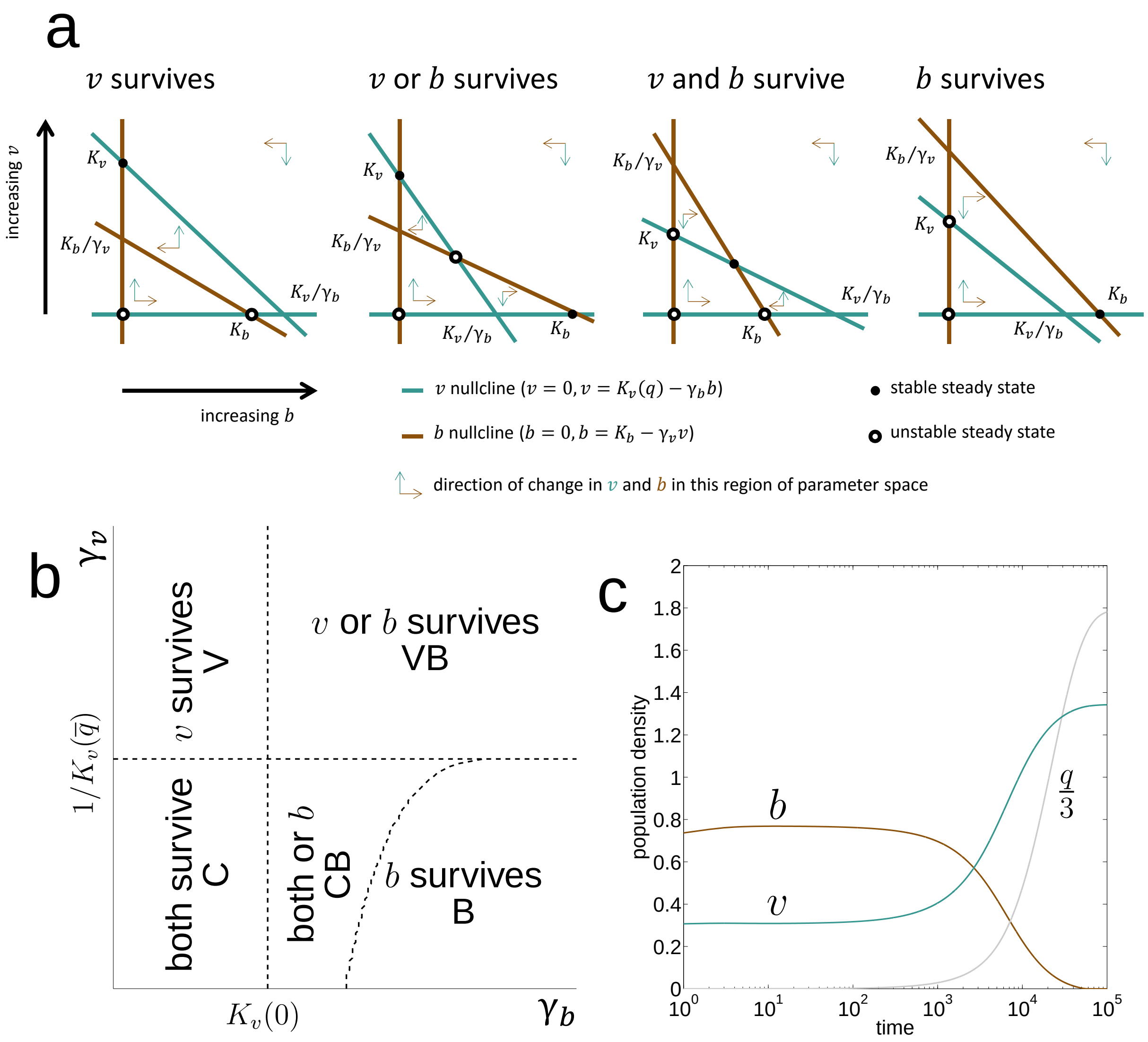

Figure 3: Behaviour of the deterministic system. **a**: Zero isoclines for v and b for constant habitat quality q. Note that q only affects the stability of the coexistence steady state (see Appendix A.1 for details). The relationships between the labelled intercepts determine the stable outcomes of the system, see **b**: Stable outcomes of the system relative to the competition parameters, γ_b and γ_v, taking $K_b = 1$ and $\bar{q}$ to be the steady state value of the habitat quality in a system where $b = 0$. In the bistable CB region there are two coexistence steady states whose stability depends on q, its boundary was found by numerical analysis of the system Jacobian. **c**: Example of the dynamics of v, b, and q with very slow ecosystem engineering dynamics ($f = 2.5 \times 10^{-3}$, $c = 6.25 \times 10^{-4}$) near the V-C boundary. Unless otherwise stated the standard parameter set given in Section 2 was used.

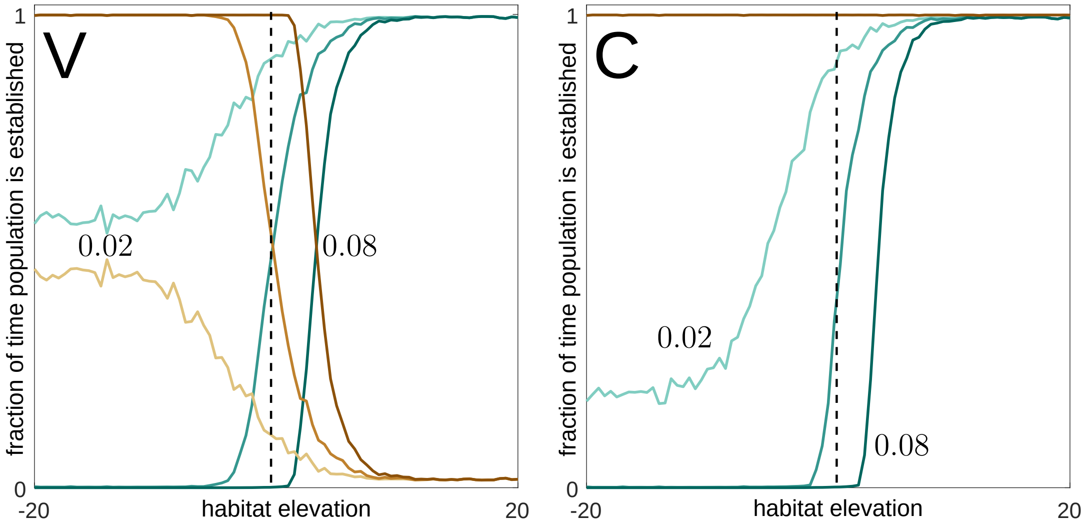

Figure 4: Transitions in system state as habitat elevation changes for a range of perturbation strengths. The average fraction of time for which each species is established in the habitat is plotted against habitat elevation. A species was considered established if its population density was greater than 0.1. The average was calculated from an ensemble of 1000 systems with small uniformly distributed initial populations ($\sqrt{v_0^2 + b_0^2} < 0.1$) which were run for 1000 time units. Brown and green curves correspond to the benthic and vegetative species respectively. Each subplot corresponds to a different outcome of the deterministic population dynamics, see labels in Fig. 3. The competition parameters (γ_b, γ_v) used were: **V** - $(0.5, 1.5)$ and **C** - $(0.5, 0.5)$. The strength of the perturbation ρ was one of 0.02, 0.04 and 0.08, see labels in the plots. Otherwise the parameters were as stated in Section 2. The dashed lines provide a guide for the position of h_v^* for $\rho = 0.04$.

boundary. The growth rate of the vegetative species $a_v(q)$ does not otherwise affect the steady states of the system, which is an unrealistic byproduct of the classical formulation of the Lotka-Volterra equations (Mallet, 2012). This rate does play a role in determining which outcome is most likely in the bistable regions (results not shown).

Finally we note that, if the dynamics of the engineering process are sufficiently slow, i.e. f and c are small, the two species can coexist for considerable time for competition parameters in the V region, Fig. 3b. This occurs when $\gamma_v < 1/K(0)$ but $\gamma_v > 1/K(\overline{q})$, where $\overline{q}$ is the steady state value of the habitat quality q in a system where $b = 0$. In such cases, the habitat quality continues to improve in the apparent coexistence state, allowing v to increase and thus forcing b to decrease. This eventually results in the benthic species becoming extinct. Note that the same process occurs for higher values of f and c, but the apparent coexistence state is not observed due to the faster dynamics.

3.3 Ecotone formation when flooding affects only the vegetation population

In Section 3.1 we laid out a mechanism by which tidal flooding can cause the formation of an ecotone in a habitat with varying elevation. We now use numerical simulations to confirm this theoretical understanding, beginning with the first type of flooding perturbation (only vegetation is affected by flooding). We begin by considering how likely it is that a given species is able to establish a population in the habitat. We estimate this by calculating the fraction of a time course (length 1000 units) for which each species is able to maintain a population density above 0.1 (the maximum density of a species at colonisation). An average (calculated from an ensemble of 1000 systems with small uniformly distributed initial populations, $\sqrt{v_0^2 + b_0^2} < 0.1$) of these fractions is plotted against habitat elevation in Fig. 4 for typical examples from the V and C regions of the competition parameter space. Note that, while this is an indirect measure, it captures most of the behaviour of the system. Some of the more complex outcomes that are missed by this measure are discussed in Appendix A.2.

In the V and C regions there is a transition from a state where only b survives (resulting from the tidal perturbations) to the state obtained in the deterministic system, Fig. 4V,C, for sufficiently large ρ (≥ 0.04 for the parameters considered). Thus, as we expect, in the V region, the benthic species typically survives at low elevations and the vegetative species survives at high elevations, producing an ecotone. In the C region a coexistence state exists at high elevations. This might, in practice, give the appearance of an ecotone since the benthic invertebrate population may not be readily discernable in a sufficiently vegetated habitat. For weaker perturbations $\rho < 0.04$, v is sometimes able to survive on low lying habitats if its initial population is sufficiently large and/or the time series begins with a sequence of low water levels at high tide. The result is effectively a flooding induced bistability (of type VB or CB respectively) which transitions back to the deterministic state as habitat elevation increases.

The bistable regions VB and CB also produce transitions from a benthic species dominated state to the underlying bistable state, but these transitions are less well defined due to the randomness inherent in bistable states. An example of such a transition can be found in Appendix A.2. In the B region, where the vegetative species is outcompeted by the benthic species, elevation has no effect, since b is able to establish itself at any elevation driving v to extinction (not shown).

We observe that these transitions from one state to another appear to take place over a range of elevations. It is important to note that the system does not reach some intermediate transition state in this range. Instead, any given realisation of the model produces an abrupt switch from one state to the other, see Eq. (7) and Appendix A.2. However, the position of this switch varies due to the particular initial conditions and high tide levels used. By averaging over multiple realisations we obtain the typical behaviour that can be expected in a collection of habitats, e.g. along a coastline. Thus, while the ecotone in any particular habitat is abrupt, in a spatially extended community the ecotone position will vary. We now consider how the characteristics of the flooding process affect the shape of this spatially extended ecotone.

3.3.1 Factors affecting the shape of the spatially extended ecotone

Firstly, as the variability in the water level at high tide σ^2 increases so does the range of elevations over which the transition between states occurs, see Fig. 5. This can be explained by referring to Eqs (7-10). In particular, we recall that while the expected time

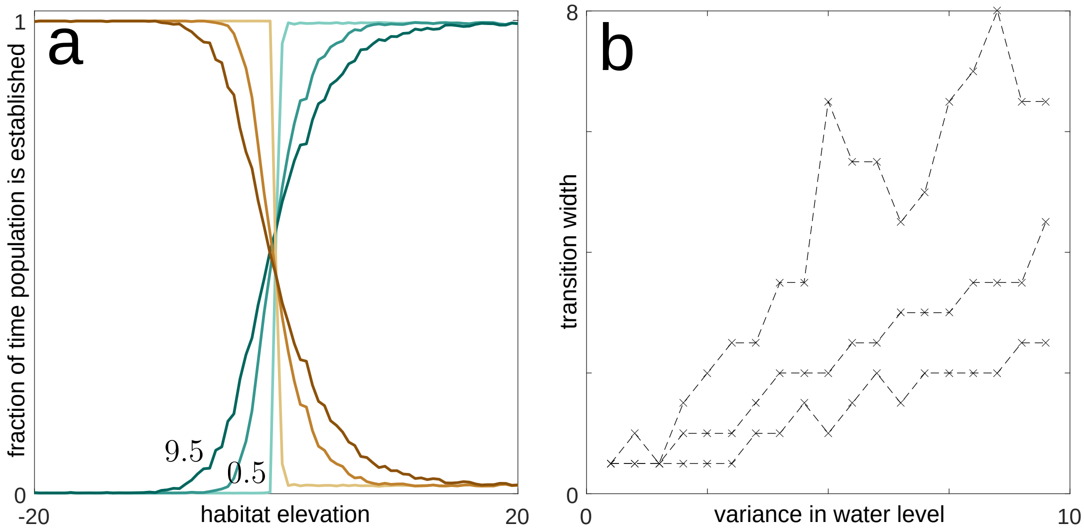

Figure 5: Effect of variance in high tide water level σ^2 on ecotone shape. **a**: Plot of the average time for which a population is established as in Fig. 4, variances of 0.5, 4.5 and 9.5 are plotted, see labels in the figure. **b**: Plot of the range of elevations containing the central 40% of the transition against variance. Three example curves are plotted using competition parameters from the V and C regions (Fig. 3). All other parameters were as stated in Section 2.

between floods $T(h)$ gives a sharp transition from extinction to survival, the true water level at any given high tide, and hence the interval between successive floods, is random. Thus as σ^2 increases the variability in water level between successive floods gets bigger, creating the possibility that, in a particular habitat, a sequence of low water levels will allow the vegetative species to establish itself at an elevation where it cannot usually survive. This increases the range of elevations over which the transition occurs on this broader spatial scale, increasing the effective width of the ecotone.

Since the probability of a flood, given by Eq. (9), is symmetric, the centre point of the ecotone, approximately h_v^*, is determined by the expected time between floods and so is only weakly affected by σ^2. In systems where the population dynamics have a more complex effect on the transition, for example when a state dominated by b becomes a bistable state, the transition is not necessarily symmetric. This can result in the midpoint of the transition changing with variance, see Appendix A.2 for further details.

Perturbation strength, on the other hand, affects both the position and width of the ecotone, see Fig. 6. We see that as ρ increases the midpoint of the ecotone shifts to higher elevations (Fig. 6a). These changes slow as ρ increases, a trend which arises from the non-linearity of Eq. (10). In general, a stronger perturbation decreases the growth between floods shifting h_v^* (and thus the ecotone position) to higher elevations. However, the steep increase in the time between consecutive floods, see Fig. 2a, means that, beyond a certain point, a very large increase in ρ is required to have any effect. We also note that there are two distinct curves with the same shape in this plot. This results from differences in the strength of competition between the species. When the benthic population is a weak competitor, a stronger perturbation effect is required to drive the vegetation extinct and thus induce a transition.

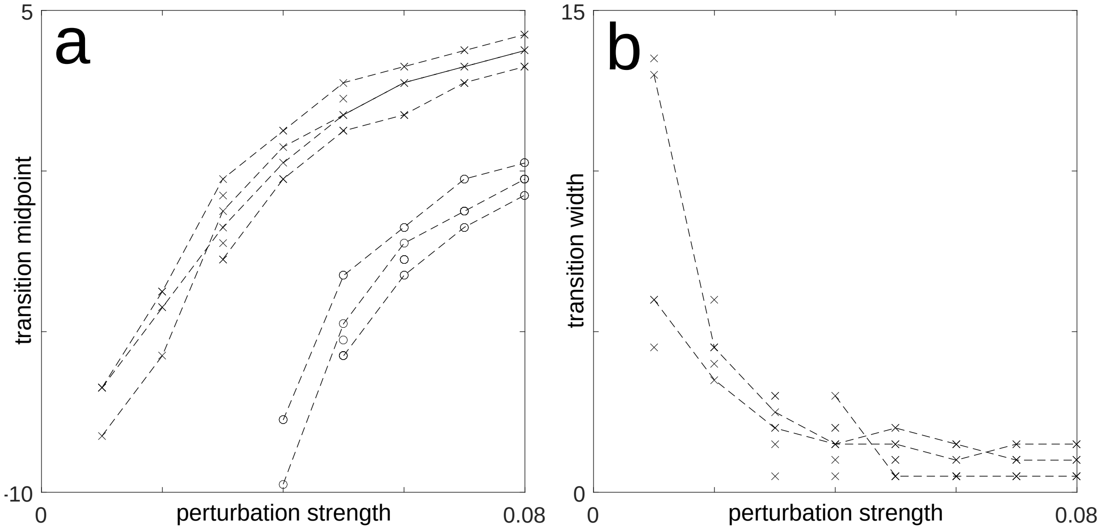

Figure 6: Effects of perturbation strength ρ on ecotone shape. **a**: The elevation at the midpoint of the transition and **b**: the range of elevations containing the central 40% of the transition, are plotted against perturbation strength. Curves are plotted for a range of competition parameters from the V and C regions, dashed lines connect curves for some parameter combinations to guide the eye to the general trend (Fig. 3). Otherwise the parameters were as stated in Section 2.

As discussed above the width of the ecotone increases as σ^2 increases. However in addition we see that this width decreases as ρ increases (Fig. 6b). This is because increasing the perturbation strength decreases the chance for the vegetative species to survive a single flood, reducing the importance of variability in the time between successive floods.

3.3.2 Effect of allowing the growth rate of the vegetative species to increase with habitat quality

Allowing the growth rate of v to increase with the habitat quality q ($a_1 > 0$) has no significant effect on the typical system state when initial populations are small (i.e. for colonisation scenarios), see Appendix A.3. However it does allow larger, established, vegetative populations to endure substantially more severe perturbations, Fig. 7. We consider a baseline case where $a_1 = 0$ (dashed curves) and a second case where $a_1 = 1$ (solid curves). As before, we plot the average fraction of the time course for which each species survives for two values of the perturbation strength ρ. When growth rate is not affected by habitat quality, a ρ of 0.05 is sufficient to drive the vegetative species to extinction at low elevations, resulting in an ecotone. However when growth rate is affected by habitat quality, v is able to survive at all elevations for this ρ, excluding b. In order to create an ecotone in this case ρ must be twice as large, i.e. 0.1, and, even then, v persists at lower elevations than it could when the growth rate was unaffected by q.

This effect is not observed in colonisation scenarios since, at low elevations, v is generally driven to extinction before it can significantly improve the habitat quality ($q \approx 0$). Further implications of this ability of the ecosystem engineer to enhanced its resilience

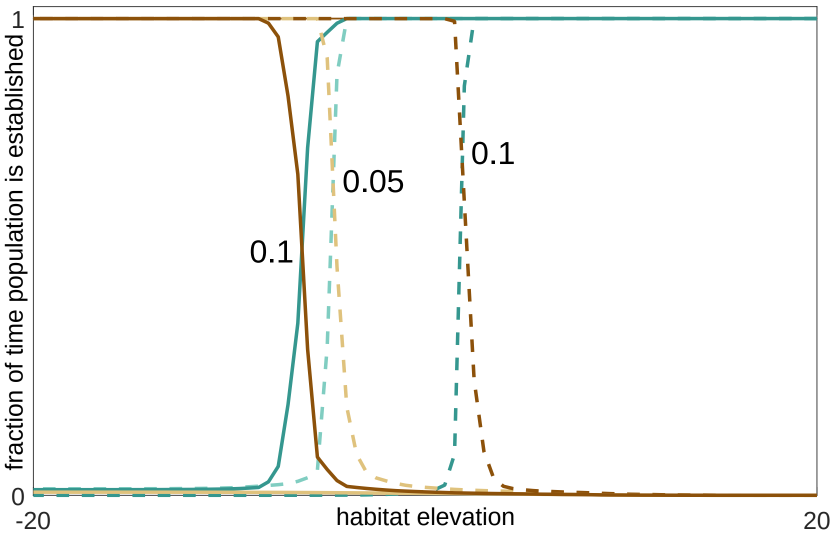

Figure 7: Effect of vegetation growth rate increasing with environment state. Dashed curves correspond to the case when $a(q)$ is constant with respect to q, solid curves to the case when $a(q)$ increases with q. Curves are plotted for perturbation strengths ρ (see values in plot) where each system first displays a transition. The initial system state was set to $(v_0, b_0, q_0) = (1.5, 0.1, 1.0)$ for all runs, competition parameters were $(\gamma_b, \gamma_v) = (0.5, 1.5)$, all other parameters were as in Fig. 4.

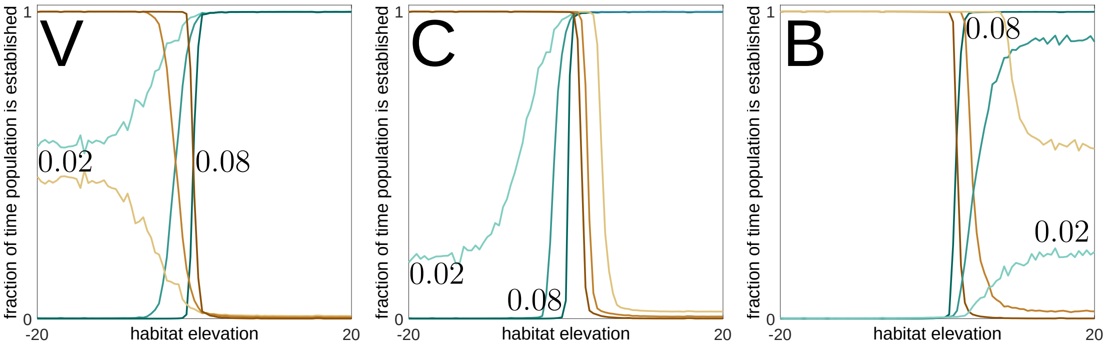

Figure 8: Transitions in system state as habitat elevation changes when tidal perturbations affect both species. We plot the same measure as used in Fig. 4 for different outcomes of the deterministic population dynamics. The competition parameters (γ_b, γ_v) used were: **V** - $(0.5, 1.5)$; **C** - $(0.5, 0.5)$; and **B** - $(1.0, 0.5)$. The strength of the perturbation ρ was one of 0.02, 0.04 and 0.08, see labels in the plots. Otherwise the parameters were as stated in Section 2.

to tidal perturbations will be discussed in Section 4.

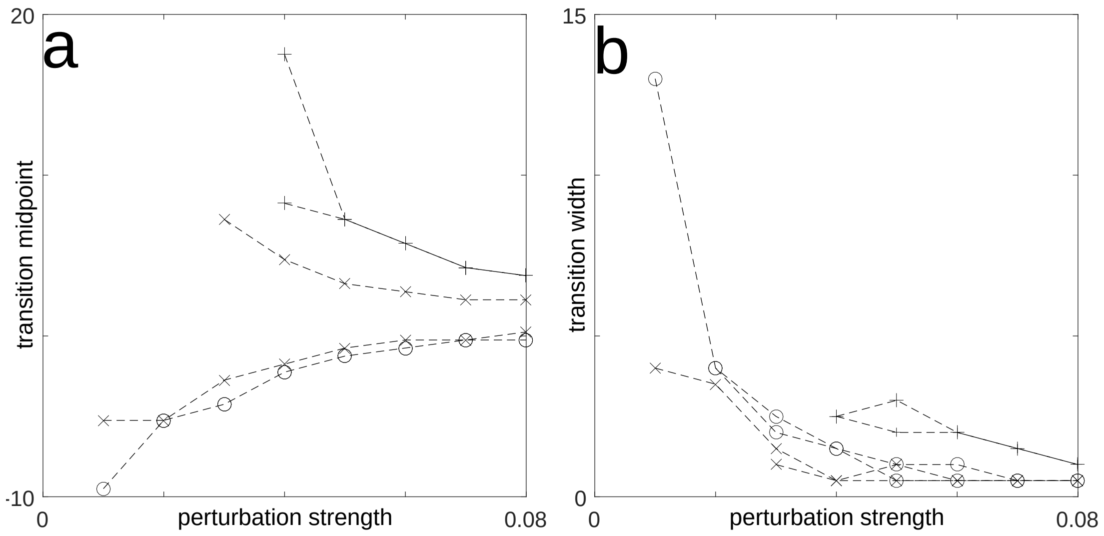

Figure 9: Effect of perturbation strength on transition shape with inundations affecting both populations. Plots and parameters are as in Fig. 6a-b. Symbols correspond to specific regions of parameter space: × – C, ○ – V, and + – B.

3.4 Ecotone formation when tidal perturbations affect both populations

We now consider ecotone formation in the second case, where tidal perturbations affect both species, see Section 2. The same indirect measure, average fraction of time for which each species is established in the habitat, is plotted against habitat elevation for three possible outcomes of the deterministic system, Fig. 8. We take the perturbation strength ρ to be the same for both species, and as a result obtain an almost symmetric system, the only difference being that the benthic species has a higher growth rate at low densities ($a_b = 1$, $a_v(0) = 0.75$). Consequently the two transition elevations, h_b^* and h_v^* lie close together, and thus, as long as the perturbation strength is sufficient, an ecotone is obtained regardless of the dynamics of the two populations (see Fig. 2c, lower left). In particular, note that there is now a transition in the case where the benthic species outcompetes the vegetative species Fig. 8B, which was not the case when only v was affected by flooding. For weaker perturbations we obtain various forms of flooding induced bistability, for example in the C region we have a transition from a CB state to a CV state.

On the extended spatial scale, the effect of perturbation strength on the transition midpoint depends on the competition parameters, see Fig. 9a. In the V region, the midpoint moves to higher elevations as perturbation strength increases, reflecting the change in h_v^*. Similarly in the B region, the midpoint moves to lower elevations with ρ reflecting the change in h_b^*. In the C region, the v and b transition midpoints move in opposite directions towards 0. In fact, the direction of the shift depends on the dominant species in the deterministic system, that is the species which the perturbation must control to create an ecotone. Thus the ecotone shifts to higher elevations if the vegetative species dominates, and to lower elevations if the benthic species dominates. If the species can coexist the ecotone midpoint shifts towards zero, since this is the elevation at which the tidal forcing has equal probability to affect either species.

The width of the transition always decreases with perturbation strength (Fig. 6), as in the first case, and we note that high perturbation strengths always result in an abrupt ecotone. The effects of variance on transition shape are very similar to those observed for Case 1 and are not shown here.

4 Discussion

In this study we present a simple model which describes the transition from mud flat to coastal wetland communities. We consider the two community types as competing species which are negatively affected by regular environmental disturbances, tidal flooding. These disturbances are moderated by an environmental gradient, the elevation of the habitat. In this system, ecotones form if one species can outcompete the other in the deterministic system but is unable to survive when subjected to frequent perturbations. An ecotone can also form if one species is driven to extinction by regular floods, while the other is unable to survive in the absence of floods. In contrast to previous studies of ecotones in related ecosystems Jiang et al. (2012); Jiang and DeAngelis (2013), the mechanism for ecotone formation in this system is not the interaction between species but instead the effect of the tidal forcing; in particular, the change in the average period between floods as habitat elevation increases. As such, the parameters which most strongly affect the formation of an ecotone, and its resulting shape, are characteristics of the tidal perturbation process rather than the population dynamics.

In any particular habitat, our model produces an abrupt switch from one community to the other in good agreement with empirical observations of mud flat to coastal wetland ecotones in temperate, e.g. (Simenstad et al., 1997; Balke et al., 2014), and subtropical, e.g. (Woodroffe, 1995), zones. In other models of wetland ecotones such sharp transitions are a consequence of competition between two communities and, in particular competing ecosystem engineering effects, e.g. (Jiang et al., 2012; Jiang and DeAngelis, 2013). However, in our model, this characteristic of the ecotone arises instead from the regular tidal flooding to which the system is subjected. These perturbations create a critical transition elevation, see Section 3.1, which divides the habitat into two regions, each conducive to colonisation by one of the species. This mechanism for control of the vegetative population has some empirical support in both saltmarsh and mangrove systems (Balke et al., 2011; Friess et al., 2012), and has an obvious analogue in the role fires play in maintaining boundaries between grasses and trees in savanna ecosystems (Thonicke et al., 2001; Hanan et al., 2008; Scheiter and Higgins, 2009). While increasing model complexity could allow this mechanism to form a more gradual ecotone, in this study, we focus on the shape of the ecotone on a broader spatial scale encompassing multiple habitats, such as may be found along a coastline.

On this extended scale we find that the abruptness of the ecotone depends on the properties of the flooding process. In particular, if the forcing is either very regular, i.e. the high tide level is consistent, or the perturbation is severe, i.e. a relatively large fraction of the population dies as a consequence of flooding, the transition from one community to the other occurs in a narrow range of habitat elevations. On the other hand, if the high tide level is irregular and the perturbation is not too severe the transition becomes spread out across a wide range of elevations, producing a broad ecotone. Thus, in areas where the tides are dominated by the predictable lunar cycle, on sheltered coasts for example, we would expect the transition from mud flat to coastal wetland to occur at a consistent elevation. In contrast, if weather conditions, which are inherently irregular, have a large effect on tide levels we would expect greater local variation in the transition elevation. Indeed, this provides a mechanism by which the ecotone position in a particular habitat might vary throughout the year, a phenomenon that has been observed empirically (Simenstad et al., 1997).

In our model, the ecosystem engineering capabilities of the vegetative species have little influence on the structure of the ecotone in scenarios where both species are introduced to an unoccupied habitat. However, the advantage provided by these capabilities is most significant for established populations. We show in Section 3.3, Fig. 7, that an established population can survive floods of significantly greater severity in an improved habitat if its growth rate is increased by this improvement. This creates the potential for regime shifts in response to periods of unusually weak or intense flooding. For example, a transition zone which experiences low tides for an extended period sees a spread of the coastal wetland community to lower elevations. Due to the stabilising effect of ecosystem engineering, a return to the typical tidal pattern does not affect this altered system. Instead a period of unusually intense flooding (such as might occur during a storm) is required to restore the previous balance between the two communities. A similar pattern has been observed in mangrove colonisation of mud flats (Balke et al., 2011), although here the effect is not strictly related to ecosystem engineering but instead to a threshold level of seedling maturity that must be attained in order to survive regular tides.

Similarly, the introduction of an invasive species, e.g. (Hacker et al., 2001; Zhang et al., 2005), can also result in a regime shift. From Eq. (7), Section 3.1, we can see that higher growth rates and lower sensitivity to flooding increase the range of elevations at which a species is able to survive. Either characteristic would also allow an invasive species to outcompete the native species at its normal elevations. Due to the exponential term in Eq. (7) a quite small change in growth rate can be sufficient to allow a species to survive throughout the entire habitat resulting in a shift to a single community system.

We have made two major simplifying assumptions in formulating this model, in particular: 1) that the benthic species does not act as an ecosystem engineer, and 2) that high tide water levels are random. We justify the first assumption by noting that, in this system, the two communities do not appear to have opposing effects on their environment. Instead, they both appear to stabilise the soil (Austen et al., 1999; Hacker et al., 2001), thus reducing tidal erosion. Moreover, clearance of coastal wetland is known to result in increased soil erosion (Thampanya et al., 2006), suggesting that this community has a stronger stabilising effect. We can interpret the assumption that only the vegetative species is an engineer in this context, by saying that our model describes further habitat improvement by this species beyond the level that can be achieved by the benthic species.

The assumption that high tide water levels are random has potentially greater implications for our results. Tide patterns certainly contain a very strong periodic component arising from the lunar cycle (Hendershott and Munk, 1970) which is ignored in our model. However, we argue here that the effects of predictable variation in the tides can still be captured in the framework we describe. In particular, we show in Section 3.1 that the survival of a species is determined by its growth between consecutive flooding events, Eq. (7). While the intervals between floods at a particular elevation will be affected by variations in high tide water level, for a predictable tidal pattern these intervals can be calculated and thus incorporated into an analysis similar to that performed in Section 3.1. Thus, the effects of periodic variation in tides can be dealt with relatively straightforwardly, justifying our focus on more unpredictable variations such as may be introduced by changes in the weather. Of course, weather conditions are not entirely random, a given weather pattern may affect a habitat for several days. We suggest that the effects of this can be readily modelled using autocorrelated, rather than white, noise, in future work. Extreme events, such as storms, could be represented by a long period of higher water levels, however we note that this limits the maximum effect of such events. A separate random process, which has a more severe effect on the populations than normal tidal flooding, would provide a more realistic representation of such events.

We might also expect that habitats which are close together would experience similar flooding patterns. This could be represented by introducing a second spatial dimension, i.e. distance along the coastline, and assuming a degree of correlation in high tide levels which decays with this distance. While it is clear that such a model will reduce local ecotone variability, on larger spatial scales, sufficient for this correlation to decay, the results presented here will be largely unchanged. Thus, this appears to be a primarily technical refinement which does not necessarily provide any new insights into the fundamental behaviour of the ecotone. However, it would allow this model to be fitted more accurately to a particular empirical system given suitable experimental data.

Finally we note that, in our model, flooding has no impact on habitat quality. Given the known role of tidal flooding in soil erosion (Hacker et al., 2001; Thampanya et al., 2006), and the countervailing effects of sediment trapping by coastal vegetation, we might expect this omission to have a significant effect. In practice however, since we assume that the vegetative species is able to survive in an unimproved environment, allowing flooding to affect habitat quality does not change the fundamental behaviour of this model. In particular, reducing habitat quality does not drive either species to extinction and thus floods that affect only the habitat quality cannot result in ecotone formation. Alternative formulations of the model could address this in one of two distinct ways. Firstly, the vegetative species could be treated as an obligate ecosystem engineer Cuddington et al. (2009), that is one that requires improvement of the environment in order to survive, would allow ecotone formation in response to soil erosion. A number of studies show an Allee effect in coastal grass populations which could be attributed to this mechanism (Davis et al., 2004; Taylor et al., 2004). Secondly, the currently abstract habitat quality could be interpreted as habitat elevation, thus more directly coupling the effects of ecosystem engineering and the perturbation regime. The first case may be more technically representative of the reality of the system but it is not clear that it would produce any new insights into its fundamental dynamics. In contrast, the second case introduces a new feedback into the system and thus is likely to have more significant effects. This then presents an additional area for further research.

In conclusion, despite the relative simplicity of this model, we are able to reproduce phenomena that are observed in empirical systems and to make predictions about what factors will change the way such systems will behave. Of course, our modelling approach limits the scope of these predictions (and comparisons) to the typical dynamics that would be found on a broad, landscape, scale, rather than providing a detailed understanding of individual habitats. On the other hand, we are able to make predictions without first characterising each individual habitat of interest experimentally. Moreover, while our approach is relatively insensitive to local variation, it can readily take into account large scale changes in the environment, such as might be caused by ongoing climate change. Thus, we suggest that, in the highly uncertain environments that are so often encountered in ecology, it may be better to focus on relatively crude models that are robust to this uncertainty, instead of more detailed, and consequently more costly, models which may not be able to account for these changing environments.

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A Supplementary material

A.1 Analysis of the steady states of the deterministic population dynamics

The steady states of the Lotka-Volterra competition equations:

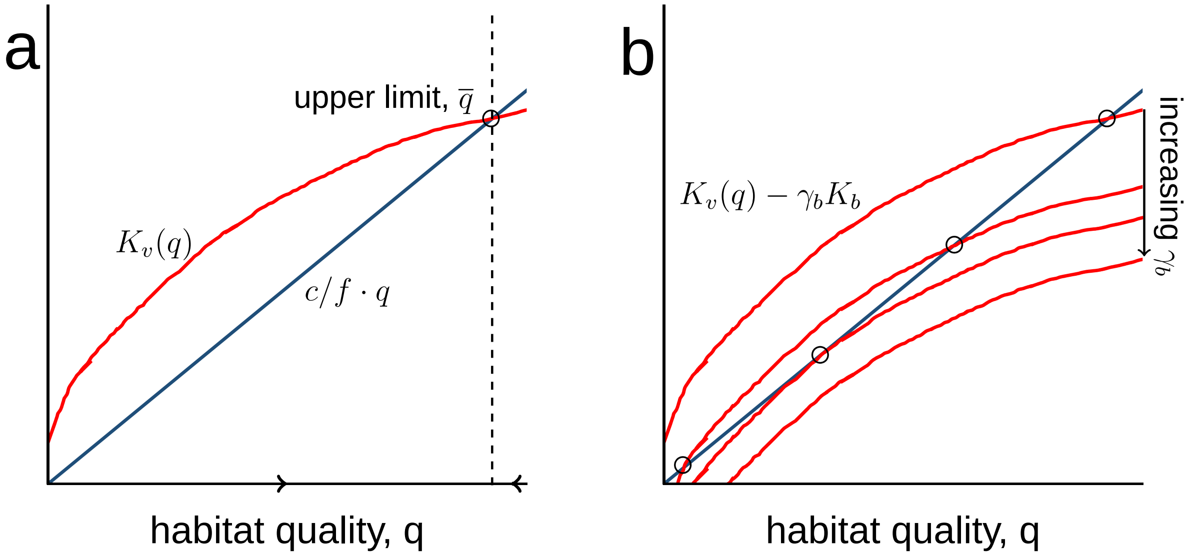

Figure A.1: **a**: Sketch of the vegetative carrying capacity with respect to habitat quality q. Curves and fixed point are labelled in the sketch. Arrows indicate the change in q on either side of the fixed point. **b**: Sketch of the bifurcation induced by changing γ_b in the recurrence relation $q = f/c \cdot (K_v(q) - \gamma_b K_b)$. Red curves represent $K_v(q) - \gamma_b K_b$ at different values of γ_b, blue line represents $c/f \cdot q$ as in **a**. As γ_b increases the number of fixed points (black circles) changes from 1, to 2, to 1 and finally to 0.

$$\frac{dx}{dt} = a_x x \left(1 - \frac{x + \gamma_y y}{K_x}\right), \tag{A.1}$$

$$\frac{dy}{dt} = a_y y \left(1 - \frac{y + \gamma_x x}{K_y}\right), \tag{A.2}$$

are well known, see for example Murray (2002). In particular they are: an extinction state $(0, 0)$; a state with only x $(K_x, 0)$; a state with only y $(0, K_y)$; and a coexistence state

$$(1 - \gamma_x \gamma_y)^{-1} \cdot (K_x - \gamma_y K_y, K_y - \gamma_x K_x).$$

The signs of the following expressions determine whether the coexistence state exists and which of the states are stable:

$$1 - \gamma_x \gamma_y, \tag{A.3}$$

$$K_x - \gamma_y K_y, \tag{A.4}$$

$$K_y - \gamma_x K_x. \tag{A.5}$$

In particular, the states with only x or y are stable if Expression (A.4) or (A.5) respectively is less than zero. The coexistence state is only biologically reasonable, i.e. with two positive populations, if all three expressions have the same sign, and is stable when expressions (A.4) and (A.5) are greater than zero. The extinction state is always unstable.

Our model is based on these dynamics, but incorporates a third system variable, habitat quality q, see Eqs (1-3) repeated below for reference:

$$\frac{dv}{dt} = a_v(q)v\left(1 - \frac{v + \gamma_b b}{K_v(q)}\right), \tag{1 repeated}$$

$$\frac{db}{dt} = a_b b\left(1 - \frac{(\gamma_v v + b)}{K_b}\right), \tag{2 repeated}$$

$$\frac{dq}{dt} = -cq + fv. \tag{3 repeated}$$

Habitat quality is improved by the ecosystem engineering activity of the vegetative species and, in turn, increases the carrying capacity (and growth rate) of that species. To reflect this we assume that both $a_v(q)$ and $K_v(q)$ are positive and increasing for $q \geq 0$. In order to ensure that the vegetative population remains finite we also assume that there is a limit to the habitat quality that can be maintained by the vegetative population. To ensure this we must impose an additional condition on $K_v(q)$ derived as follows. We note first that the maximum attainable vegetative population at a given q is given by $K_v(q)$ by definition. Then, from Eq. (3), the maximum rate at which q can increase is $fK_v(q) - cq$. Thus, if $K_v(q)$ intersects the line $c/f \cdot q$ for some $\overline{q} > 0$ with gradient less than c/f then $\overline{q}$ is an upper limit on the habitat quality that can be maintained by the vegetative population, see Fig. A.1a. (Note that, for a complex $K_v(q)$, there could be more than one $\overline{q}$ satisfying this condition. In such cases we can take the smallest such $\overline{q}$ since the system dynamics will not allow v and q to increase past $K_v(\overline{q})$ and $\overline{q}$ respectively. These higher limits could only be reached if we start with a large initial v and q.)

With this condition we are now ready to analyse the steady states of our deterministic population dynamics, Eqs (1-3). The steady state value of the habitat quality is determined by the density of the vegetative population. In particular, the only value of q such that Eq. (3) is equal to zero is $f/c \cdot v$. Substituting this into the steady states obtained for the Lotka-Volterra system we obtain: $(0, 0, 0)$, $(K_v(q), 0, f/c \cdot K_v(q))$, $(0, K_b, 0)$, and

$$(1 - \gamma_v\gamma_b)^{-1} \cdot \big(K_v(q) - \gamma_b K_b, K_b - \gamma_v K_v(q), f/c \cdot (K_v(q) - \gamma_b K_b)\big),$$

where we must solve the following recursive equations:

$$q = f/c \cdot K_v(q), \tag{A.6}$$

$$q = f/c \cdot (K_v(q) - \gamma_b K_b), \tag{A.7}$$

for the second and fourth states respectively.

Eq. (A.6) is exactly the condition we solved to ensure finiteness of v and thus we know this equation has one (relevant) solution, $\overline{q}$. Without explicitly stating $K_v(q)$ we cannot find explicit solutions for Eq. (A.7). However, referring to Fig. A.1b, we see that γ_b acts a bifurcation parameter: for $\gamma_b = 0$ we have a single solution $\overline{q}$; as it increases a second (unstable) solution emerges; and as γ_b increases further these two solutions eventually collide and then disappear leaving no solution. (Alternative choices of $K_v(q)$ can produce no bifurcation or a more complex bifurcation but this is the case that applies to our choice of $K_v(q)$.) Where Eq. (A.7) has two solutions, the system has five steady states, since two coexistence solutions are possible. However, one of these coexistence solutions is always

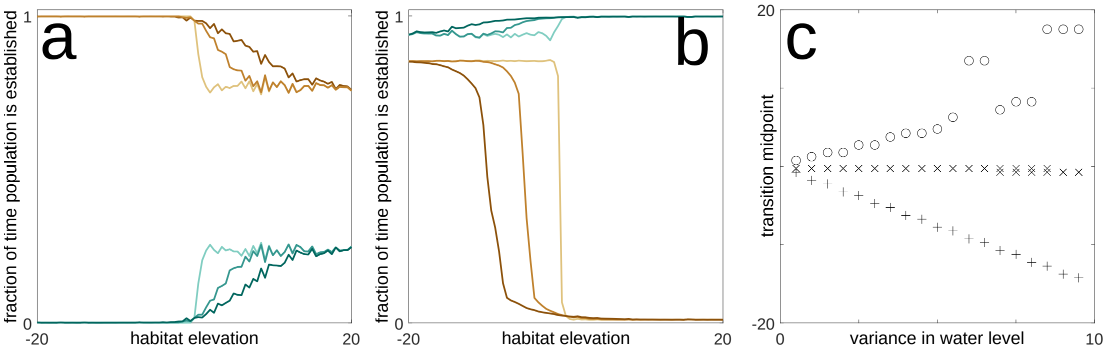

Figure A.2: Examples of the effect of variance on transitions involving a complex state. Plots are as described in Fig. 4. **a**: The deterministic system is bistable with competition parameters $(\gamma_b, \gamma_v) = (1.0, 1.5)$. **b**: The effect of the perturbation allows coexistence of the two species with competition parameters $(\gamma_b, \gamma_v) = (0.25, 1.5)$. **c**: Plot of the transition midpoint against variation in high water level for: a typical ecotone transition - $\times$; the case plotted in **a** - $+$; and the case plotted in **b** - $\circ$. The default parameters were used, variance ranged from 0.5 to 9.5 with lighter curves corresponding to lower variances.

unstable, which allows the existence of the CB bistable region observed in Section 3.2. Where Eq. (A.7) has no solutions there is no (biologically reasonable) coexistence steady state (similar to the case where Expressions (A.3-A.5) do not all have the same sign).

Finally, we note that the stability criteria for the states where only v or b survive are unchanged from the Lotka-Volterra model (although Expression (A.4) is dependent on q), since, in these states, the habitat quality is automatically stable. For the $(K_v(\overline{q}), 0, \overline{q})$ state this is clear from Fig. A.1a, while for the $(0, b, 0)$ state, Eq. (3) shows that q will decrease to zero if $v = 0$ and we know from the Lotka-Volterra system that v will decrease to zero for any small perturbation. As such the C-V and B-VB boundary is given by $\gamma_v = 1/K_v(\overline{q})$ (taking $K_b = 1$ in Expression (A.4)). Similarly the region in which $(0, b, 0)$ is stable starts at $\gamma_b = K_v(0)$ (taking $K_b = 1$ and $q = 0$ in Expression (A.5)). As a consequence only the boundary between CB and B cannot be determined analytically.

A.2 Transitions between more complex states

When tidal forcing results in a transition from or to a complex state, such as bistability or coexistence, the effect of variance changes. Fig. A.2a shows a case where the deterministic system is bistable. At low elevations, the benthic species is heavily favoured since, while either population can survive, any additional mortality in the vegetative population allows the benthic species to become dominant. Variability in the flood magnitude has little effect in this region, but, at high levels, creates cases where the vegetative species is driven to extinction at high elevations. Thus the transition midpoint shifts to higher elevations as variance increases in this case, see Fig. A.2c.

Fig. A.2b shows a case where flooding allows coexistence of the species at low elevations, by reducing the effective carrying capacity of the vegetative population to a point where it does not exclude the benthic population. At the same time, the effect of the benthic

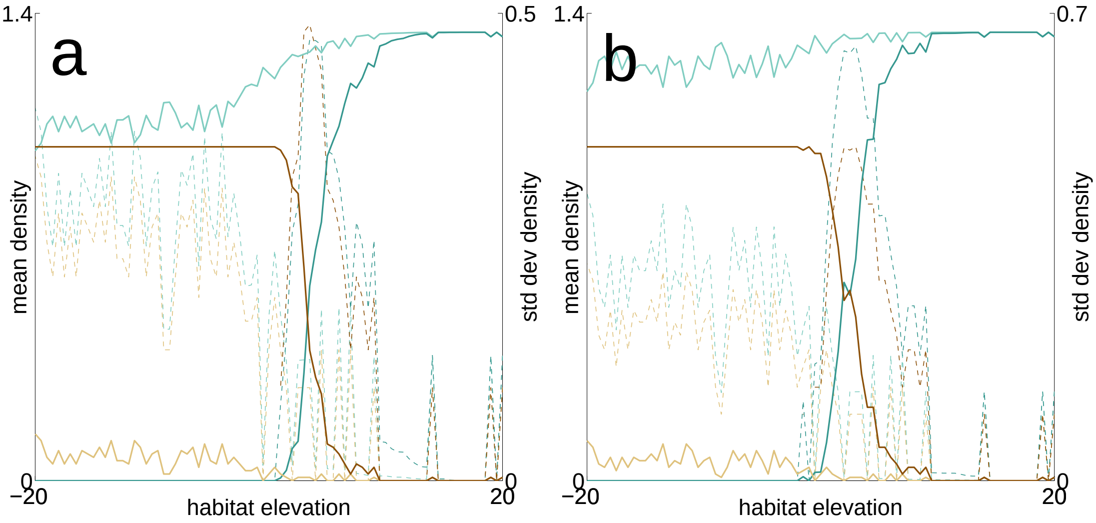

Figure A.3: Examples of the effect of flooding on population densities. Average density (solid curves) and standard deviation (dashed curves) were calculated from the system state after 1000 time units for 100 realisations of the system with random initial populations as described in Fig. 4. **a**: Parameters were the same as in Fig. 4V. **b**: Parameters were the same as in Fig. 4V with the exception that $a_1 = 1$. The lighter curves and darker curves correspond to perturbation strengths of 0.2 and 0.8 respectively.

population is too weak to drive the vegetative population to extinction even with flooding. In this case, variability in the flood magnitude has little effect at high elevations, where the vegetative species always outcompetes the benthic species, but at low elevations increased variability creates periods where the vegetative population becomes large enough to eliminate the benthic population. Consequently the transition midpoint shifts to lower elevation as the variance increases in this case see Fig. A.2c.

Fig. A.3c and d show the effect of flooding on average population densities rather than colonisation outcomes. Weak perturbations induce a bistability at low elevations indicated by the high variability in density (standard deviation). At elevations above the transition average densities approach the equilibrium densities obtained in the deterministic model and standard deviations go to zero, indicating that these densities occur in most realisations. Strong perturbations result in the average b and v going to 1 and 0 respectively at low elevations, indicating that the vegetative species is always driven to extinction by flooding. At high elevations, the deterministic equilibriums are re-established. Note that in this case, standard deviations are highest during the transition, indicating that the transition zone is effectively bistable, with habitats supporting one of the two species rather than a coexistence state.

When a increases with q, Fig. A.3d, the average density of the vegetative species increases at low elevation for weak perturbations. Given that the average density of the benthic species does not decrease, and thus that there are a similar number of states where it survives as when a does not increase with q, Fig. A.3c, this indicates that a higher density of v is reached, i.e. that the vegetative species is more resilient to the effect of flooding.

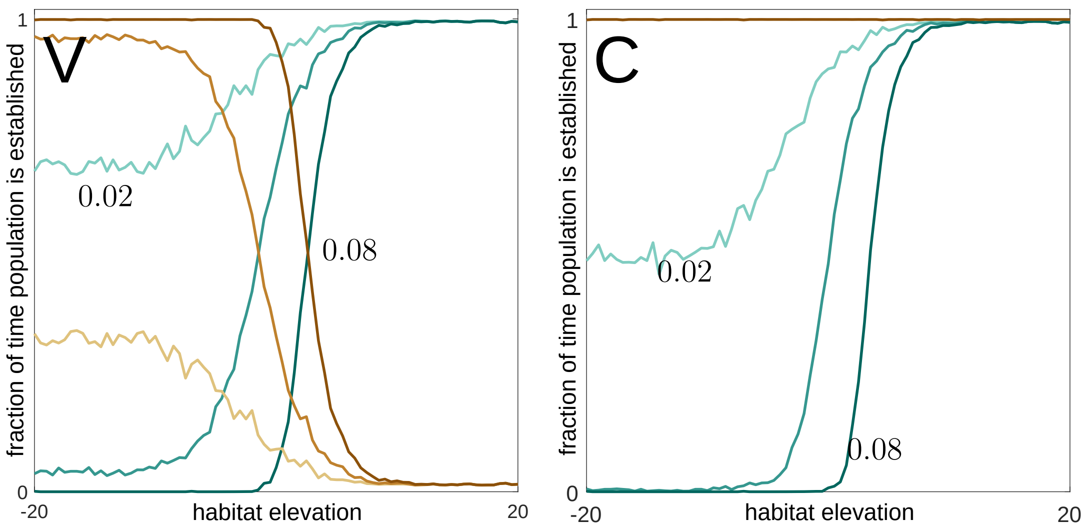

Figure A.4: Typical system states obtained for a range of habitat elevations and perturbation strengths. Plots and parameters are as in Fig. 4 with the exception that $a_1 = 1$.

A.3 Transitions with engineering affecting growth rate

Fig. A.4 is an analogue of Fig. 4 with a allowed to increase with q. The plots are almost indistinguishable indicating that this has little effect on colonisation outcomes.