

## **Appendix C from I. Martínez et al., “Disentangling the Formation of Contrasting Tree-Line Physiognomies Combining Model Selection and Bayesian Parameterization for Simulation Models”** (*Am. Nat.*, vol. 177, no. 5, p. E136)

### **Overview–Design Concepts–Details Description of the Tree-Line Model**

#### **Overview**

##### *Purpose*

The purpose of the model is to identify the minimal set of processes involved in the formation and maintenance of *Pinus uncinata* tree-line ecotones, with the objective of disentangling how these processes interact to generate different tree-line physiognomies.

##### *State Variables and Scales*

Each individual tree was defined by four state variables: position ( $x, y$ ), height ( $h$ ), status (alive or dead), and age ( $a$ ; table C1). Individuals were classified in different growth forms according to  $h$  and  $a$ : seedling ( $h < 0.5$  m and  $a \leq 10$  years), sapling ( $0.5 \text{ m} \leq h < 1$  m), pole ( $1 \text{ m} \leq h < 4$  m), adult ( $h \geq 4$  m), and krummholz ( $h < 0.5$  m and  $a > 10$  years). Simulations were run in a partial torus (a  $60 \times 180$  grid with  $1\text{-m}^2$  cells), with periodic and absorbent boundaries on the lateral and longitudinal (i.e., altitude) sides, respectively. Individual trees within the plot had free coordinates; that is, each tree could occupy every possible position within the plot. However, for computation of competition and safe sites, we divided the transects into a grid of  $1\text{-m}^2$  cells. The model proceeds in annual time steps.

##### *Process Overview and Scheduling*

The model followed the fate of each individual tree throughout its life, and the basic schedule of the model includes the following processes and environmental constraints: individual growth and mortality, competition between adults, seedling establishment, and krummholz-to-seedling facilitation. Each model simulation was run until the coefficient of variation (CV) of simulated adult densities was below an arbitrarily set threshold ( $CV < 0.075$ , estimated over a moving window of 50 years) that we considered a steady state. Because of the internal stochasticity of the model, some variability was evident after this quasi-steady state was reached, although this process error was less important than variation derived from changes in parameter values or model structure. In this way, and given our interest in average model behavior, model outputs were averaged over 10 realizations captured from single simulations separated by 50 years.

#### **Design Concepts**

*Emergence.* The main features defining the tree line along the ecotone (the height of the vegetation and the densities of different growth forms) emerged from interactions among individuals. Individuals were defined by a set of rates defined a priori but dependent on the parameterization of the model.

*Adaptation.* Depending on the parameterization of the model, individual size determines adult fecundity, competition coefficients, and the rates of growth.

*Fitness.* Modeling individual fitness was not an objective of the model.

*Prediction.* Individuals had no decision abilities.

*Sensing.* Individuals had no decision abilities.

*Interaction.* Individuals compete for space at recruitment (preemption of space and creation of safe sites) and as adults. The model implements krummholz-to-seedling facilitation, which affects both growth and recruitment.

*Stochasticity.* Mortality was considered a stochastic process dependent on the age and position of the individual along the tree-line ecotone. The modeling of the recruitment process also included a certain degree of stochasticity. In both cases, probabilities were calculated on the basis of individual and/or environmental conditions, providing realism to both processes.

*Collectives.* Individuals were not grouped.

*Observation.* Four patterns were selected to assess the ability of different models to reproduce observed tree-line structures. They consisted of the density of different growth forms (seedlings, adults, and krummholz individuals) and the mean height of all individuals excluding krummholz. These quantities were estimated for 5-m-wide subplots covering 20-m altitudinal bands along the transect for both field data and model output. At each altitudinal band, we estimated mean densities and tree height over the subplots and the standard deviation of these properties.

## Details

### Initialization

As the initial condition of the simulation, we used a random distribution over the entire transect of 260 seedlings, 104 saplings, 78 poles, 52 adults, and 130 krummholz individuals. The initial condition was set so as to approximate densities observed in the field, in order to avoid the extinction of the population. Apart from this, the initial condition had no effect on the outcome of the different simulations, since they were run until a steady state was reached, which depended mainly on model parameterization.

### Input

Varying spatial conditions were included in some model configurations through the use of two independent environmental gradients that modified the rates of growth and mortality along the gradient.

### Submodels

*Rule 1: altitudinal-gradient response functions on growth and mortality.* To represent the dependence of demographic rates on the position of each individual along the gradient ( $y$ ), we formulated two independent response functions ( $g_g(y)$  and  $g_m(y)$ , for growth and mortality, respectively), considering a flexible, logistic functional form,

$$g_p(y) = \frac{1 + \exp(-a_p b_p)}{1 + \exp(-a_p (b_p - y))}, \quad (C1)$$

where  $p$  is an index for growth ( $g$ ) or mortality ( $m$ ),  $a_p$  and  $b_p$  are parameters to be fitted, and  $0 \leq y \leq 180$ . The parameter  $a_p$  ranges between 0 and 0.5 and influences the steepness of the gradient response, with higher values corresponding to steeper gradients. For  $a_p = 0$  we have  $g_p(y) = 1$  (i.e., no gradient response), and for  $a_p = 0.5$  the gradient drops within 20 m from values of near 1 to near 0. The parameter  $b_p$  shifts the gradient in the  $y$ -direction and ranges between 0 and 180 m. For model versions without gradient response, we set  $a_p = 0.0$ .

*Rule 2: competition.* We used a simple phenomenological competition index that was motivated by the zone-of-influence (ZOI) approach (Schwinning and Weiner 1998). We employed the parameterization given by Wiegand et al. (2006; see their appendix S1). Each tree  $i$  competed within a circular zone of influence  $ZOI_i$  with radius  $r_{zoi}$  proportional to its height  $h_i$  (i.e.,  $r_{zoi} = rh_i$ ). During the simulations, the overlap areas  $O_{ij}$  between the zones of influence of each pair of adult trees  $i$  and  $j$  were calculated. The competition index employed related the zone of influence  $ZOI_i$  of the focal tree (i.e., the competitive power of the target tree) to the sum of the overlap areas  $O_{ij}$  of the focal tree  $i$  and all the remaining  $j$  trees (i.e., the total competitive power exerted over the zone of influence of the target tree):

$$c_i = \frac{ZOI_i}{ZOI_i + \sum_{i,i \neq j} O_{ij}}. \quad (C2)$$

If the  $ZOI_i$  of the target tree  $i$  is not overlapped, then the index yields  $c_i = 1$  (i.e., no competition), and if the

competitive power exerted over the ZOI<sub>*i*</sub> of the target tree *i* is much larger than its own competitive power, then the competition index yielded values  $c_i \ll 1$  (with an asymptotic value  $c_i = 0$ ). Wiegand et al. (2006) estimated a value of the unknown parameter  $r = 0.2$  (see their appendix, fig. A1); thus the ZOI of an adult tree was approximately 20% of its height.

Note that the competition index yields asymmetric competition. For example, if the ZOI<sub>*i*</sub> of a smaller tree *i* is totally overlapped by that of a larger tree *j*, then the relative effect of the larger tree on the smaller one ( $c_i = 0.5$ ) is much stronger than the relative effect of the smaller tree on the larger one ( $c_j = \text{ZOI}_j / (\text{ZOI}_i + \text{ZOI}_j) \approx 1$  if  $\text{ZOI}_i \ll \text{ZOI}_j$ ).

*Rule 3: combining the gradients and competition.* In our model, competition reduced tree growth and increased the mortality rate of trees. We hypothesized an impact of the two gradients  $g_g(y)$  and  $g_m(y)$  on tree growth and mortality, respectively, depending on the position *y* on the gradient. We combined competition in the simplest way with the gradients, assuming a multiplicative effect. The resulting growth inhibition factor  $f_g$  and mortality enhancement factor  $f_m$  were calculated as

$$\begin{aligned} f_g(y) &= c^{0.5} g_g(y), \\ f_m(y) &= c^{0.5} g_m(y), \end{aligned} \quad (\text{C3})$$

where  $c$  is the competition index (eq. [C2]). Note that values of  $f_g = 1$  and  $f_m = 1$  indicate that growth is not inhibited (eq. [C8]) and that survival not reduced (eq. [C9]), respectively. In turn, values less than 1 indicate growth inhibition and enhanced mortality.

*Rule 4: safe site.* Seedling establishment was allowed only in safe sites, defined as  $(1\text{-m}^2)$  grid cells that were not within the zone of influence,  $r_{\text{zoi}}$ , of adult trees (for  $r_{\text{zoi}}$ , see “rule 2”) and where space was not preempted by dead trees or by more than one krummholz individual. Note that space was homogeneous in the model; that is, we did not consider differences between substrates, as do Camarero et al. (2000).

*Rule 5: facilitation.* On the basis of the spatial-point-pattern analyses by Camarero et al. (2000) and field experiments by Batllori et al. (2009), a facilitative effect of krummholz on seedling performance was implemented. Grid cells within a radius of 1.5–2.5 m of a krummholz-occupied cell experienced enhanced probabilities of seedling establishment and survival, depending on krummholz height (i.e.,  $p_{\text{establish}} \propto 2f_{\text{facil}} h_{\text{krummholz}}$ , where  $f_{\text{facil}} = 1$  indicates the maximum facilitative effect and  $f_{\text{facil}} = 0$  indicates that facilitation is not important at all). At Capifonts and Portell, the range of the parameter defining the strength of facilitation was constrained ( $f_{\text{facil}} = 0\text{--}0.3$ ). This was necessary to prevent an unrealistic positive effect exerted by the old ( $a > 10$  years) but small-canopied individuals present at these sites (old-seedlings class; see “Study Sites and Characterization of Tree-Line Ecotones”).

*Rule 6: establishment.* We modeled the number of seedlings emerging at a given cell explicitly on the basis of tree fecundity and a dispersal kernel representing seed dispersal and spatial variations in seedling emergence (Ribbens et al. 1994). Seedling establishment was allowed only in safe sites (see “Rule 4” above), and krummholz-mediated facilitation ( $f_{\text{facil}}$ ) increased the establishment probability locally (“Rule 5”). Thus, the probability of seedling establishment at each cell was a function of the distribution of distances to adults, of tree fecundity (expressed as an allometric function of tree size), and of the form of the dispersal kernel:

$$s(x, y) = \sum_{i=1}^{n_{\text{trees}}} F_i K(x - x_i, y - y_i), \quad (\text{C4})$$

$$p_{\text{estab}}(x, y) = \begin{cases} 0 & \text{if no safe site,} \\ p_{\text{rep}}(0.1 + 0.9f_{\text{facil}})s(x, y) & \text{if safe site,} \end{cases} \quad (\text{C5})$$

where  $p_{\text{rep}}$  and  $f_{\text{facil}}$  are parameters that scale overall establishment success and facilitation strength, respectively,  $s(x, y)$  is seedling density at the location with coordinates  $(x, y)$ ,  $F_i$  is the fecundity of tree *i*, and  $K(x_i, y_i)$  is the dispersal kernel. Note that we assumed that the process is isotropic (i.e., seedling input does not vary as a function of the direction from the source trees). With this specification, we could test whether the inclusion of dispersal limitation, included by allowing spatial variation in the probability of seedling emergence, improved the model’s ability to reproduce observed tree-line patterns with respect to previous specifications assuming an infinite, spatially homogeneous seed bank. For those model structures without dispersal limitation, we assumed an infinite seed bank and a homogeneous distribution of seeds.

We examined the lognormal function as a dispersal kernel (i.e., a lognormal is a convex, zero-at-zero

leptokurtic kernel), given that its high performance for wind-dispersed species is well documented (Stoyan and Wagner 2001; Greene and Calogeropoulos 2002; Greene et al. 2004),

$$K(x_i, y_i) = \frac{1}{(2\pi)^{1.5} d(x_i, y_i) S} \exp\left(-\frac{(\ln(d(x_i, y_i)/L))^2}{2S^2}\right), \quad (C6)$$

where  $S$  and  $L$  are kernel parameters to be fitted and  $d(x_i, y_i)$  is the distance between the location  $(x_i, y_i)$  of the reproductive adult tree  $i$  and the target cell location  $(x, y)$ . Other dispersal kernels (exponential and 2Dt) did not provide a better fit (results not shown).

*Rule 7: height growth.* The Gompertz function is a commonly used equation for describing cumulative growth of trees (Frontier and Pichod-Viale 1993). Wiegand et al. (2006) fitted the Gompertz function to data on maximum height of *Pinus uncinata* trees grouped in 10-year age classes (see their fig. A2) and calculated the maximum annual longitudinal growth  $\Delta h_{\max}(\text{age})$  (i.e., potential growth) of a tree according to its age, using the derivative of the fitted Gompertz function,

$$\Delta h_{\max}(\text{age}) = 0.52 \exp\left(-\frac{\text{age} - 47.7}{30.5}\right) - \exp\left(-\frac{\text{age} - 47.7}{30.5}\right), \quad (C7)$$

$$\Delta h(\text{age}, y) = (c^{0.5} g_g(y)) \Delta h_{\max}(\text{age}), \quad (C8)$$

where the first factor in equation (C8) represents equation (C3),  $c$  is the competition factor (eq. [C2]) and  $g_g(y)$  describes the decrease in growth with altitude (eq. [C1]). Note that 47.7 was the age (in years) at which trees reached the maximum height-growth rate. The actual growth  $\Delta h(\text{age}, y)$  at position  $y$  on the gradient was proportional to potential growth but modified by growth inhibition  $f_g(y)$ , which combined the effects of the environmental gradient and competition (eq. [C3]).

*Rule 8: mortality.* Age-dependent survival was further determined by the position on the gradient, as modeled by the following equation:

$$s(\text{age}, y) = \begin{cases} (c^{0.5} g_m(y)) [1 - (m_0 + m_a)(1 - f_{\text{facil}})] & \text{seedling,} \\ (c^{0.5} g_m(y)) [1 - (m_0 \text{age}^{-e} + m_a)] & \text{else,} \end{cases} \quad (C9)$$

where the first factor represents equation (C3),  $c$  is the competition factor (eq. [C2]), and  $g_m(y)$  describes the decrease in survival with altitude (eq. [C1]). For interpretation of equation (C9), we considered first the position  $y = 0$  (i.e., the lowermost position on the gradient) and situations without competition (i.e.,  $c = 1$ ), where  $g_m(y) = 1$  (eq. [C3]). In this case, the mortality rate of trees declined exponentially with age (Monserud and Sterba 1999) and reached an asymptotic value  $m_a$  for older trees. Parameter  $e$  determined how quickly the mortality of young trees decreased to eventually meet that of older trees, and parameter  $m_0$  was the difference between mortality of seedlings and that of old trees. Mortality of seedlings can be reduced by facilitation ( $f_{\text{facil}}$  is the facilitation factor). Competition and/or the gradient reduced survival of all trees by the factor  $f_m(y)$ . Note that equation (C9) describes the mortality of established seedlings in safe sites, which cannot be compared with the mortality of all seedlings (mortality of seedlings 0–10 years old is 90%–95% per year; Camarero and Gutiérrez 1999) because there are only few safe sites and because seedlings that do not germinate in safe sites die (see also “Rule 6”).

*Rule 9: transition between growth forms.* Transitions between growth forms and size classes depend only on age and height (table C1). For example, seedlings that do not reach a height of 0.5 m within the first 10 years of life are counted as krummholz, but they can be considered saplings if they afterward grow taller than 0.5 m.

**Table C1.** Variables and parameters of the tree line model

Variable or parameter	Symbol	Range	Units
Age	age	0–300	years
Height	$h$	0–16	m
Growth form:			
Seedlings		$h < .5$ and age $\leq 10$	
Krummholz		$h < .5$ and age $> 10$	
Sapling		$.5 \leq h < 1$	
Pole		$1 \leq h < 4$	
Adult		$h \geq 4$	
Facilitation	$f_{\text{facil}}^a$	0–1	...
Reproduction probability (eq. [C5])	$p_{\text{rep}}$	0–1	Seedlings $\times$ seeds
Mortality (eq. [C9]):			
Asymptotic mortality rate for older trees	$m_a$	.00005–.00155	year <sup>-1</sup>
Factor of age-dependent term	$m_0$	0–.5	year <sup>-1</sup>
Exponent of age-dependent term	$e$	.7–1.5	...
Gradient of environmental harshness (eq. [C1]):			
No gradient	...	...	
Logistic:			
Growth, mortality	$a_g, a_m$	0–.5	1/m
	$b_g, b_m$	0–180	m
Fecundity	$\beta$	50–1,050	seeds year <sup>-1</sup> m <sup>-<math>\alpha</math></sup>
	$\alpha$	.1–2.1	...
Dispersal kernel (eq. [C6]):			
Lognormal	$L$	10–210	m <sup>2</sup>
	$S$	.5–10.5	...

Note: The range of observed ages in the field at the studied plots was 0–300 years, but in most simulations age did not exceed 100 years. However, *Pinus uncinata* may be as old as 800 years in low-density subalpine forest.

<sup>a</sup> $f_{\text{facil}}$  ranges between 0 and 0.3 in Capifonts and Portell (see rule 5).