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Qualitative analysis of dynamic states of the Larix-permafrost ecosystem under climate warming

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Abstract

Dahurian Larch, Larix gmelinii, grows as a tree in the continuous permafrost region of eastern Siberia. Along with other allied Larch species and/or subspecies (notably L. cajanderi), it can grow on continuous permafrost. The expected warming of the climate in Siberia from global warming will reduce the permanent permafrost area, and will have an effect on the reduction in distribution of the larch. We investigate the possible forest succession effects in the interactive system among larch, dark conifers and climate using a simple conceptual model. The basic variables are the larch biomass, \( B_L \), the dark conifer biomass, \( B_D \), and the water content in the active soil layer, \( W \). External parameters include precipitation, \( P \), and air temperature, \( T_a \). We track three processes: biomass growth as a function of \( T_c \) and \( W \); carbon losses on respiration and decay; competition within a species as well as between species that limit biomass growth. Analysis of evolution the equilibria of the model under current growing-season temperatures has a stable condition of larch forest that can become unstable, so that larch can be replaced by dark conifers. More increased temperatures produce a new non-trivial equilibrium with a coexistence of Larch with “dark conifers” (Pinus sibirica, Picea obovata and Abies sibirica). Further temperature increase leads to a stable state in which the Larch is fully displaced by the dark conifers.

Key words: global warming, Larix gmelinii, continuous permafrost, tree succession.

Introduction

Larch-dominated forests (genus Larix Mill.) cover over 37% of Russian forested territory, and are located primarily in permafrost zone in eastern Siberia. They are a subject of special interest because of ecological importance of continuous permafrost in this region (Osawa et al. 2010). Larix gmelinii can grow under conditions of continuous permafrost as can L. cajanderi in regions east of the Lena River. The taxonomy of L. gmelinii and related taxa is complex (Polezhaeva et al. 2010) and L. cajanderi is considered a subspecies of L. gmelinii by some. Other (dark) conifer species (Pinus sibirica, Picea obovata and Abies sibirica) survive under the conditions in warm river valleys or on hills with a permafrost layer so deep that it does not affect the trees above (Osawa et al., 2010). Expected warming of climate in Siberia (as a result of global warming) will lead to the reduction of permafrost and can be expected to produce change in the L. gmelinii distribution.

Theoretical calculations of stationary state or dynamics of Larix forests have been developed mostly for regional investigations. The models differ in the kind of description of ecological mechanisms involved: semi-phenomenological biogeographical models (Tchebakova et al., 2010); intermediate complexity stationary-biome models (Kaplan and New, 2006); detailed dynamical individual based models or IBMs (Shuman et al., 2011; Zhang et al., 2011). Some of these studies do not include permafrost as an explicit ecological factor.

Of special interest is the phenomenon of bifurcation or “tipping-point” in modern terms, which feature an abrupt reaction to slow changes of system parameters. During the past two decades, examples of expected bifurcation in natural ecosystems have accumulated. Usually, these examples often are the product of examination of two types of models, either detailed mechanical models or low-dimensional dynamical analytical models. Ecosystem examples involve vegetation dynamics that can potentially exhibit tipping-point behavior, including a diversity of examples:

• The existence of two stable climate and vegetation states in northern Africa (Patricola and Cook, 2008 using mechanistic model; Brovkin et al., 1998; Moorcroft, 2003 for low-dimensional model);
• Three distinct modes for tree cover dynamics in the tropics (Nes et al., 2014 from a low-dimensional model), or two modes (Oyama and Nobre, 2003 from a mechanistic model);
• Desert-forest transition with two or more stable states

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(Zeng et al., 2002 - low-dimensional model);
- *Larix* to dark conifer species change (Zhang et al., 2011 – mechanical model).
- Low-dimensional models are used in analysis of possible instabilities in feedbacks with the global or regional climate system induced by global warming. Physical mechanisms of such instability are based on positive feedbacks between variables. Physical systems interactions (e.g., the significant feedback among sea ice, albedo, and climate) allow more precise numerical calculation than systems of interactions that include vegetation cover. However, for the vegetation-involved feedbacks, the problem is usually approached using reasonable estimates of expected responses.

**Model Development**

This paper will explore a simple and familiar model, which is basic in ecological modelling and sufficient to our purposes, namely a version of Lotka-Volterra (Volterra and Berlot, 1931, Lotka 1932) system for competing species rewritten into biomass terms. The model can be analyzed graphically and qualitatively. Despite its conceptual nature, it allows examination of some of the important features of the system, namely: its possible climax states, their stability, variants of stability changes under parameter changes, and whether the loss of stability takes place gradually or abruptly.

Our intention is to explore the expected dynamics of the ecosystem to indicate the classes of dynamics that might proceed from numerical solutions of more specifically parametrized models. This is a standard procedure for theoretical investigations. The reliability of our conclusions principally depends mainly on the degree of mechanistic realism implemented in representing the system-parameter dependence on ecological factors. In our formalization, we intentionally deal with a minimum number of such dependencies represented in a physically realistic form that mimics the observed system features. Our investigation uses equilibrium state(s) analysis, and not the systems dynamics proper. The method involves the graphical analysis of the phase portraits and their change with parameter variation for the system under consideration. In its complete form, this method was proposed by H. Poincaré (see: Oeuvres de Henri Poincaré 1916-1954). It has since been successfully used in numerous works (e.g., Antonovsky et al., 1990; Antonovsky and Korzukhin, 2012). Many introductory ecology textbooks present a simple graphical analysis from this method using the Lotka-Volterra equations as examples.

Adequate description of any system requires knowledge about the principal controlling factors, which in this case is derived from an extensive literature (e.g., Euskirchen et al., 2006; Osawa et al., 2010; Zhang et al., 2011). Factors that are usually mentioned as controlling factors are permafrost, forest fires and soil moisture. Evapotranspiration and soil temperature regime depend on forest and sub canopy cover. All these factors are governed by air temperature and precipitation. The exact mechanisms of interactions and the quantitative interdependencies among these variables are often not clear (see Osawa et al. (2010) for more details).

Field observations indicate that system [*Larix - permafrost*] is self-sustainable. There are indications that after air temperature exceeds a certain threshold, rapid change is probable including altered species composition. This result was obtained numerically in an individual-based model (Shuman et al., 2011; Zhang et al., 2011) with critical temperature increment δΤ around 2-4°C.

In our model, variables are total *Larix* biomass (BL), total dark conifer biomass (BD) and water content in active soil layer (W). External parameters are precipitation, P, and air temperature, Ta. The processes under consideration are biomass growth, carbon losses to respiration and decay, and interspecies competition. As it was mentioned above, the Volterra model (Volterra and Brelot, 1931) is appropriate for our aim, but it has to be extended by equation for W, so the whole system will be

\[
\begin{align*}
\frac{dBL}{dt} &= a_L \times BL - r_{1s} \times BL^2 - c_L \times BL \times BD; \\
\frac{dBD}{dt} &= a_D \times BD - r_{1s} \times BD^2 - c_D \times BL \times BD; \\
\frac{dW}{dt} &= P - fW \times W,
\end{align*}
\]

where: \( a_L, a_D \) are specific rates of biomass growth (net growth that includes all carbon losses), \( r_L, r_D \) describe growth limitation due to interspecies competition, while \( c_L, c_D \) are growth limitations due to responsible for interspecies competition. Function \( fW \) has complex structure and describes the processes of soil-water loss, namely evapotranspiration and percolation, which depend on permafrost depth, soil temperature, and forest biomass. The governing external factor is \( Ta \) (for climate change, precipitation \( P \) is less important than \( Ta \)). The dependencies on \( Ta \) and \( W \) are given below.

**Results and Discussion**

Following sequence of physical relations responsible for stability of [*Larix - permafrost*] system are: increase of \( Ta \) → lowering of permafrost layer → increase of water percolation from root zone → decrease of water available → worsening of mineral supply of trees. Instead of giving functions that describe each of these processes, which is a considerable challenge one can exclude these intermediate steps and postulate \( fW \) as some increasing monotonic function of \( Ta \) that corresponds to direct field observations (e.g., Lopez et al., 2007; Osawa et al., 2010).

Note that permafrost depth and accompanying processes adjust quickly to current temperature value, so that these processes are much faster than forest dynamics proper. This fact allows one to change the last equation in system (1) for its quasistationary analogue that arises from \( dW/dt = 0 \), and to get soil water content as its solution:

\[
W(Ta) = P/fW(Ta).
\]

Specific rates of biomass growth, \( a_L \) and \( a_D \), are...
increasing functions of \( W \) up to very high values when a shortage of oxygen in soil starts. In the system under consideration, the main growth limiting factor is \( W \), so in the first approximation \( a_l \) and \( a_D \) are taken as independent of \( T_a \). Also, \textit{Larix} is more sensitive to \( W \) decrease than dark conifer species because of its shallower root location. After these simplifications, system (1) reduces to:

\[
\begin{align*}
\frac{dL}{dt} &= a_l(W(Ta)) \times BL - r_1 \times BL^2 - c_l \times BL \times BD; \\
\frac{dD}{dt} &= a_D(W(Ta)) \times BD - r_D \times BD^2 - c_D \times BL \times BD;
\end{align*}
\]

This system is completely examined in Lotka (1932) and the results are presented below.

Consider the system \([\text{Larix – evergreen dark conifer species - permafrost}]\) under a temperature increase. Ecological mechanism of the dynamic change consists in soil moisture decrease leading to decrease of growth rates \( a_l(W) \) and \( a_D(W) \), with \( a_l(W) \) (or \( a_l(Ta) \)) falling more rapidly than \( a_D(W) \). For the sake of simplicity, one can suppose that only \( a_l(Ta) \) decreases.

System (3) has two on-axis equilibria: \([BL_0, 0]\) where:

\[
BL_0 = \frac{a_l}{r_1},
\]

and \([0, BD_0]\) where

\[
BD_0 = \frac{a_D}{r_D},
\]

and one nontrivial equilibrium \([BL_{00}, BD_{00}]\), where

\[
BL_{00} = \frac{(a_l r_D - a_D c_D)/(r_1 r_D - c_l c_D)}{a_D r_l - a_l c_l}/(r_1 r_D - c_l c_D); \\
BD_{00} = \frac{(a_r r_l - a_l c_l)/(r_1 r_D - c_l c_D)}{a_D r_l - a_l c_l}/(r_1 r_D - c_l c_D).
\]

Equilibrium \([BL_{00}, BD_{00}]\) do not necessary lay in the positive quadrant.

Stability/instability of these equilibria are governed by signs of corresponding eigenvalues:

\[
[BL_{00}, 0]^T: \lambda L_1 = -a_l; \lambda L_2 = \left(a_0 r_l - a_l c_l\right)/r_1; \\
[0, BD_{00}]^T: \lambda D_1 = -a_D; \lambda D_2 = \left(a_0 r_l - a_l c_l\right)/r_D;
\]

are the roots of quadratic equation

\[
\lambda^2 + \left(r_1 BL_0 + r_D BD_0\right)\lambda + BL_0 BD_0 \left(r_1 r_D - c_l c_D\right) = 0
\]

which roots are always real. Under \((r_1 r_D - c_l c_D) > 0\), \(\lambda D_1, \lambda L_2 < 0\) while under \((r_1 r_D - c_l c_D) < 0\) \(\lambda D_1 > 0\), \(\lambda L_2 < 0\). Consider now an idealized scenario when \(a_l(Ta)\) is a single parameter depending on \(T_a\) while all others are constant, and \(a_l(Ta)\) decreases with \(T_a\).

First, consider the case of weak interspecies competition \((r_1 r_D - c_l c_D) > 0\). Let \(T_{a0}\) be the current value of temperature. When \(a_l(Ta)\) is big enough, \(\lambda L_1, \lambda L_2 < 0\); it is easy to show that \(\lambda D_1 > 0\) so equilibrium \([0, BD_0]\) is unstable and that \([BL_{00}, BD_{00}]\) is out of positive quadrant. So, the system is in the stable equilibrium \([BL_0, 0]\) and the phase plane has the structure depicted in Fig. 1a. This case can be identified with current situation when the \textit{Larix} ecosystem is stable.

The first bifurcation takes place when \(a_l(Ta)\) decreases to the value such that \(\lambda L_2 > 0\); this event coincides with the origin of nontrivial stable equilibrium \([BL_{00}, 0]\). Let \(T_{a1}\) be the current temperature rise. Depending on parameter values, the system can move from originally stable equilibrium \([BL_0, 0]\) \((\circ)\) to \((b)\). Further temperature rise leads to its fusion with stable equilibrium \([0, BD_0]\) \((\circ)\). A second type of evolution goes through the origin of nontrivial unstable equilibrium \([BL_{00}, BD_{00}]\) \((\ast)\) from \([0, BD_0]\) \((\circ)\) to \((d)\); further temperature rise leads to its fusion with stable equilibrium \([BL_0, 0]\) \((\circ)\); the last loses its stability, and the system goes over to the stable equilibrium \([0, BD_0]\).

Figure 1. Phase plane structure shows two conceivable ways of evolution of the \([\text{larix (BL) – evergreen dark conifer (BD) species}]\) system under temperature rise. Depending on parameter values, the system can move from originally stable equilibrium \([BL_0, 0]\) \((\circ)\) which is the nontrivial stable equilibrium \([BL_{00}, BD_{00}]\) \((\ast)\) to \((b)\). Further temperature rise leads to its fusion with stable equilibrium \([0, BD_0]\) \((\circ)\). A second type of evolution goes through the origin of nontrivial unstable equilibrium \([BL_{00}, BD_{00}]\) \((\ast)\) from \([0, BD_0]\) \((\circ)\) \((d)\); further temperature rise leads to its fusion with stable equilibrium \([BL_0, 0]\) \((\circ)\); the last loses its stability, and the system goes over to the stable equilibrium \([0, BD_0]\).\)
Further growth in temperature (decrease of $a_L(Ta)$) leads to the second bifurcation when $\lambda D_2$ becomes negative, so that equilibrium $[0, BD_0]$ becomes stable; that happens when $a_L(Ta_2) = a_D c_D / r_D$ under some $Ta_2 > Ta_1$. This event coincides with the extinction of nontrivial positive equilibrium $[BL_0, BD_0]$ which fuses with $[0, BD_0]$ (which again can be shown from (4)). The phase plane takes the structure depicted on Fig. 1c. This case can be identified with a situation when Larix disappears and only dark conifer species remain.

The case of strong interspecies competition ($r_L r_D - c_L c_D < 0$) is analyzed in the same manner. Briefly, under growing temperature evolution from the original state (Fig. 1a) to the (Fig. 1c) final state goes through the origin of nontrivial unstable positive equilibrium $[BL_0, BD_0]$ (Fig. 1d). The loss of stability of equilibrium $[B_{L0}, 0]$ takes place sharply by means of extinction of its local zone of stability ("tipping-point" effect) when equilibrium $[BL_0, BD_0]$ fuses with $[BL_0, 0]$. If one depicts current and forecasted borders of permafrost, a territory between them can be treated as the potential zone where substitution of Larix by dark conifer species could happen (Fig. 2).

Both of two ways of evolution of forest pattern correspond well to the empirical-model scheme of behavior of $[Larix – evergreen dark conifer species]$ system. In this case, the result was achieved by means of introduction of only one monotonic function of temperature, $a_L(Ta)$, in right parts of basic system (3).

This work examines potential changes in species composition in ecological system of Larch forests, Evergreen dark conifer species, and permafrost situated in eastern Siberia and within the zone of the continuous permafrost with an application of a conceptual, low-dimensional model. One-species models of this kind do exist but their generalization to multi-species case still awaits implementation. For example, the Sheffield Dynamic Global Vegetation Model (Woodward and Lomas, 2004) operates by formalization of one tree species growth in the form of two-variable model (B – stand biomass, and LAI – leaf area index). Inter-species competition is accounted for indirectly (implicitly) by means of comparison of species’ NPP values. This is true for other Dynamic Global Vegetation models (DGVMs and for equilibrium models like BIOME3 (Haxeltine and Prentice, 1996).

![Figure 2. Current range of L. gmelinii (●), and two southern limits of permafrost distribution in Siberia: lower is the currently observed one (Osawa et al., 2010) while the upper is its forecast to the end of this century under global temperature rise $\delta T \sim 4^\circ$C (Romanovsky et al., 2008). Hatched area depicts a territory where L. gmelinii can be displaced by dark conifer species. ■ – location of Yakutsk.](image-url)
References