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# Stochastic resonance and coherence resonance in groundwater-dependent plant ecosystems

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## ABSTRACT

Several studies have shown that non-linear deterministic dynamical systems forced by external random components can give rise to unexpectedly regular temporal behaviors. Stochastic resonance and coherence resonance, the two best known processes of this type, have been studied in a number of physical and chemical systems. Here, we explore their possible occurrence in the dynamics of groundwater-dependent plant ecosystems. To this end, we develop two eco-hydrological models, which allow us to demonstrate that stochastic and coherence resonance may emerge in the dynamics of phreatophyte vegetation, depending on their deterministic properties and the intensity of external stochastic drivers.

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## 1. Introduction

Environmental dynamics are often affected by random fluctuations, which can play a fundamental role on the composition and structure of ecosystems (e.g., Holling, 1973; Lai and Liu, 2005; Hughes et al., 2007; D'Odorico et al., 2008). Remarkable examples of environmental stochastic drivers include precipitation (e.g., Noy-Meir, 1973; Laio et al., 2001; D'Odorico and Porporato, 2006), fire or pest occurrence (Holling, 1973; D'Odorico et al., 2007), and temperature fluctuations (e.g., Polyak, 1996). Therefore, explaining the response of ecosystems to natural random fluctuations is crucial to the understanding of many environmental dynamics. In fact, the introduction of noise in the temporal dynamics of a deterministic system can lead to unexpected behaviors. Usually, noise is associated with disorder: systems affected by external random forcings or by intrinsic fluctuations of some parameters are expected to give noisy responses whose irregularity depends on the intensity of disturbances. The output signal can exhibit small fluctuations about the deterministic state of the system until the signal becomes totally random for high noise levels. This is the typical “destructive effect” of noise on dynamical systems. However, a number of studies has demonstrated that noise can also play a “constructive” role in the temporal dynamics of

non-linear systems. In that case random fluctuations can induce new dynamical behaviors that do not exist in the deterministic counterpart of the dynamics. Remarkable examples include noise-induced transitions (D'Odorico et al., 2005; Horsthemke and Lefever, 2007; Ridolfi et al., 2011), noise-induced net transport (Reimann, 2002), synchronization by external noise (Pikovsky, 1984), stochastic resonance (Gammaitoni et al., 1998), and coherence resonance (e.g., Pikovsky and Kurths, 1997; Lindner et al., 2004). The constructive role of noise does not occur only in time, but also in space. In fact, it has been shown that stochastic spatiotemporal systems may exhibit the formation of highly organized noise-induced spatial structures (e.g., Garcia-Ojalvo and Sancho, 1999; Borgogno et al., 2007; Sagues et al., 2007). Here, we concentrate on the constructive role of noise in the time domain. In particular, we deal with stochastic resonance (SR) and coherence resonance (CR).

The fundamental ingredients of stochastic resonance are three (e.g., Wellens et al., 2004): (i) a bistable or an excitable dynamical system, (ii) an external and additive random forcing, and (iii) a weak deterministic periodic forcing. This latter is not able to induce any crossing of the potential barrier or any excitation, while the external random forcing can drive the state of the (bistable) system from a deterministic stable state to the other one, or can produce an impulse in the excitable system. When the periodic modulation is absent, the noise-induced transitions between states or the excitation pulses are random, with a typical average timescale,  $\langle t_c \rangle$ , depending on the noise strength and the characteristics of the dynamical system. In contrast, in the

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presence of the periodic driver, a suitable synchronization between the random component and the weak periodic forcing can activate a sort of resonance. In fact, when the semi-period of the periodic modulation,  $t_p = \pi/\omega_p$  (where  $\omega_p$  is the angular frequency), is comparable to the average transition time,  $\langle t_c \rangle$ , periodic and random forcings cooperate to induce regular transitions across the threshold. Stochastic resonance was first introduced by Benzi et al. (1981); since then, SR has drawn the attention of the scientific community, with numerous theoretical and experimental studies in physics and chemistry (e.g., see the reviews by Gammaitoni et al., 1998 and Wellens et al., 2004).

In the case of coherence resonance, the stochastic driver cooperates with an internal deterministic timescale to induce regular firings in an excitable system. Thus, the ingredients of coherence resonance are two: (i) an excitable system close to a transition to a limit cycle (i.e., a Hopf bifurcation) and (ii) a suitable amount of additive or multiplicative noise. When the external noise is able to drive the system sufficiently far from its rest state, the return trajectory to the fixed-point attractor can exhibit (due to closeness to the limit cycle) a non-monotonic transient characterized by typical internal timescale,  $t_e$ . On the other hand, the additive noise may induce excursions from the rest state with another typical timescale,  $t_n$ , depending on the noise intensity and the properties of the dynamical system. When noise has an intermediate intensity, regular (i.e., almost periodic) excursions may occur in time (Pikovsky and Kurths, 1997) (for a recent review see Lindner et al., 2004). The basic mechanism of coherence resonance is therefore similar to the process of SR. In both cases an external noise cooperates with a deterministic periodicity: when the periodicity is externally imposed, the emergence of regular fluctuations is known as stochastic resonance. Conversely, if the periodicity is internal to the dynamical system, the process is known as coherence resonance.

Stochastic resonance and coherence resonance have been rarely invoked as a mechanism capable of explaining ordered fluctuations in ecosystems. For some recent studies see Aparicio and Solari (2001), Kuske et al. (2007), and Sieber et al. (2007). This fact is quite surprising if we consider the pervasive presence of random forcings in ecosystem dynamics (e.g., Azaele et al., 2006; Ridolfi et al., 2011). Moreover, several studies have shown that some environmental systems may exhibit bistable dynamics (e.g., Brovkin et al., 1998; Zeng et al., 1999, 2004) or the attributes of excitable systems close to a transition to a limit cycle (e.g., Ridolfi et al., 2007). In this work we show the possible emergence of SR and CR in groundwater-dependent plant ecosystems. Such environments have a high ecological value due to their high biodiversity and productivity levels (Mitsch and Gosselink, 2000) and complex bio-morphological and ecological dynamics (Malanson, 1993; Hughes, 1997). Moreover, they provide a habitat for several animal populations (LeMaitre et al., 1999) and resources for logging and livestock grazing (Dubé et al., 1995; Roy et al., 2000; Wright and Chambers, 2002).

Several field studies elucidated the strong and complex interplay between phreatic aquifers and vegetation dynamics (Naumburg et al., 2005). For example, decline or rising of water table have been invoked to explain species composition (Moreno-Casasola and Vazquez, 1999; Elmore et al., 2006), invasion of exotic species, and spatial patterning (Munoz-Reinoso and de Castro, 2005; Kong et al., 2009). Our work aims at demonstrating that some recurrent processes in groundwater-dependent environments (logistic growth, vegetation-dependent water depth, periodic oscillations of water table and environmental noise) can cooperate to trigger non-trivial vegetation dynamics characterized by quite regular transitions. In the first part of this paper we will recall two models of ecosystem dynamics in areas with relatively shallow water tables (Ridolfi et al., 2006, 2007). The

first model explains the possible existence of two preferential states in the dynamics of phreatophyte vegetation, while the second model shows the excitable character of the dynamics of two wetland species that interact with a relatively shallow water table. In the second part of the paper we introduce suitable stochastic and periodic drivers, and demonstrate the possible emergence of stochastic resonance and coherence resonance in ecosystems affected by vegetation–water table interactions.

## 2. Two eco-hydrological models for groundwater-dependent vegetation

Recently, we proposed two eco-hydrological models for the study of the interactions between phreatophyte vegetation and shallow water tables (Ridolfi et al., 2006, 2007). The two models follow a minimalistic approach to simplify the complex ecohydrological mechanisms driving these ecosystem, while capturing some key aspects of the interplay between phreatic aquifer and vegetation dynamics. This framework demonstrated the possible occurrence of bistability in the one-species model and the emergence of a Hopf bifurcation in the two-species model. These two dynamic behaviors may be crucial to the occurrence of stochastic resonance and coherence resonance in phreatophyte ecosystem dynamics. In the following sections we recall the main points of these two models.

### 2.1. Occurrence of bistability in vegetation biomass dynamics

We first consider the dynamics of total plant biomass, neglecting interspecies interactions (Ridolfi et al., 2006). Changes in the biomass of phreatophyte vegetation are modeled as a logistic growth (e.g., Noy-Meir, 1975; Tsoularis and Wallace, 2002)

$$\frac{dV}{d\tau} = V(V_{cc} - V), \quad (1)$$

where  $V$  is the dimensionless plant biomass referred to a fixed reference value,  $\tau = \alpha t$  is the dimensionless time— $\alpha$  determines the temporal response (inertia) of the system and  $t$  is time—and  $V_{cc}$  is the ecosystem carrying capacity, i.e., the maximum amount of vegetation sustainable with the available resources. Notice that the structure of the model (1) resembles the one used to investigate the Allee effect (Stephens et al., 1999). Since the interaction between phreatophytes and groundwater is one of the key mechanisms affecting the dynamics of wetland plant ecosystems (Borg et al., 1988; Riekerk, 1989; Roy et al., 2000; Chang, 2003; Ridolfi et al., 2006), Eq. (1) needs to account for the effect of water table depth. There is a broad experimental evidence that this type of vegetation affects the average depth of the local water table (Peck and Williamson, 1987; Borg et al., 1988; Dubé et al., 1995; Chang, 2003). In particular, phreatophytes are able to lower the water table through the action of taproots extracting water directly from the (unconfined) aquifer (Dubé et al., 1995; LeMaitre et al., 1999). Thus, the depth,  $d$ , of the water table can be expressed as a linear function of  $V$

$$d = d_0 + \beta V, \quad (2)$$

where  $d_0$  is the water depth in the absence of vegetation ( $V=0$ ) and  $\beta$  is the sensitivity of the water table to the vegetation biomass. Water table depth,  $d$ , has, in turn, different impacts on wetland vegetation dynamics, depending on the type of vegetation. In particular, phreatophytes suffer stress conditions when the water table is too shallow (waterlogging), due to an increased mortality rate by anoxia and a decreased rate of seedling establishment (e.g., Phipps, 1979; Roy et al., 2000). Moreover, stress conditions appear in phreatophytes when the water table is too

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