UNIVERSITA' DEGLI STUDI DELLA TUSCIA

DIPARTIMENTO
PER L'INNOVAZIONE NEI SISTEMI BILOGICI, AGROALIMENTARI E FORESTALI
(DIBAF)

Corso di Dottorato di Ricerca in
ECOLOGIA FORESTALE
XXIV° ciclo
Settore scientifico disciplinare AGR/05

Climate Change Threatens Coexistence within Communities of Mediterranean Forested Wetlands

Coordinatore:	Dottorando:
Prof. Paolo De Angelis	Arianna Di Paola
Tutor:	Cotutor:
Prof. Riccardo Valentini	Dr. Francesco Paparella

A Claudia e Francesco

ABSTRACT

Mediterranean basin supports characteristic Mediterranean forests, woodlands, and scrub vegetation, highly adapted to the mild, rainy winters and hot, dry summers that characterize the Mediterranean climate. Never less the Mediterranean region has been identified as one of the hot spots of climate change. This study aims to understand what are the conditions of coexistence, thus biodiversity, of Mediterranean tree species in humid areas under future scenarios of altered hydrological regimes. The core of the work is a quantitative, dynamic model exploring the coexistence of different mediterranean tree species, typical of the arid or semi-arid wetland where ecological overlaps exist between mesic communities and those dominated by wetland specialists. The original idea of the paper is to address this topic from a deterministic approach using a dynamical model which is validated by existing data on species abundance. The dynamic of the population is broadly-defined according to the distinct adaptive strategies of trees for water stress of summer drought and winter flooding while climate change are explored as external forcing by means of a bifurcation analysis and compared with the major regional climate scenarios.

I argue that at intermediate levels of water supply, which do not benefit either of the two species, the dual role of water (resource and stress) results in the coexistence of two kind of species, namely Hygrophilous and Non-hygrophilous. In order to support the validity of the ideas contained in the present study I applied the model to a Mediterranean coastal forested wetlands of Central Italy located into Castelporziano Estate and Circeo National Park.

The results obtained show that there are distinct rainfall thresholds on the ability of Mediterranean wetlands to maintain species coexistence and hence to sustain biodiversity, calling for an urgent adaptation and mitigation response to prevent human pressure on water resources in proximity of wetland forested areas.

Contents

1. INTRODUCTION

The present thesis deals with dynamic models of wet forest systems. This chapter is devoted to a short introduction about regime shift, resilience and dynamic models in ecological system. In order to justify my choices and my goals I will do an overview of the main issues addressed and the methodology used.

1.1 Aim of the thesis

The aim of this thesis is to develop a competition model that allows for coexistence between trees, or groups of trees, having distinct adaptative strategies for water stress. My purpose is to represent the minimal set of physiological behaviour, by a simple mathematical model, that I believe is central for understanding how coexistence arises and is maintained in transitional forested wetlands.

The main objective is to use the model with an analytic approach as a tool for assessing the resilience to climate changes of states of coexistence of different plants type. In other words, I aim to identify the parameter boundaries within which biodiversity is preserved. For this purpose I have first identified the equilibria of the system and outlined their stability, then I have determined the bifurcation points for changing climatic inputs.

Along an hydric gradient, when water is abundant, hygrophilous species, or drought-sensitive types, have a much higher rate of CO_2 assimilation, thus growing rates, together with higher transpiration rates compared to non-hygrophilous ones (Schulze, 2005; Brian and Hicks, 1982). As soil dries non-hygrophilous types should increase water use efficiency so that under this condition non-hygrophilous types dominate (Schulze, 2005).

I argue that at intermediate levels of water supply, which do not benefit either of the two species, the dual role of water (resource and stress) results in the coexistence of these two kind of species.

These topics are of importance both from a theoretical and practical point of view: understanding the mechanisms that support coexistence into natural system could help to determine the main interactions that have to be considered in more complex predictive models. At the same time, assessing the resilience to climate changes of ecosystems would provide practical information to decision makers to improve management decisions.

In order to support the validity of the ideas contained in the present study I applied the model to a Mediterranean coastal forested wetland of Central Italy (located in the Presidential Park of Castelpoziano Estate and Circeo National Park). This choice has two reasons: (i) this wet forest ecosystem are characterized by high biodiversity and presence of endemism; (ii) despite their strong anthropogenic changes and reduced extension (Presti et al., 1998, Stanisci et al., 1998) they have never been included in Europe's most threatened natural ecosystems and are not listed in Annexe I of the European Habitats Directive as being a *priority forest habitat type*.

However this model is generally applicable to the wet ecotones on arid and semi-arid areas where water is the main limiting factor and where sharp ecological gradients exist between more xeric upland communities and those dominated by wetland specialists.

1.1.1 Model Competitors

In arid and semi-arid wetlands or wherever plants are subjected to alternate periods of summer drought and winter flooding like some sites of the Mediterranean basin, the main resource for which plants compete - namely, water - is also a major stress factor that effects distinct types of plants at distinct times of the year (Rodiriguez Gonzales et al., 2010; Gasith and Resh, 2009). A review of possible adaptive strategies to water stress factors is beyond the scope of this work. Detailed bibliography on the effects of water stress is very rich (Van der Molen et al., 2011, Kozloswsky, 1997).

Here we refer to the *water use efficiency* as the ratio between the plant growth rate and the plant water use, or lost by transpiration. Drought and flooding are generally avoided by several physiological acclimations that, respectively and overall, increase plants water use efficiency or provide a continuous source of water over the growing season and that allows plants to withstand the root asphyxia (Rodiriguez Gonzales et al., 2010; Schulze, 2005; Van Der Molen et al., 2011; Kozlowsky, 1997). Briefly speaking, the two types of water stress with the respective strategies can be summarized as follows:

- Root-anoxia stress during the wet periods. Some hygrophilous plants can survive to water logging by complex interactions of morphological, anatomical, and physiological adaptations (Kozlocvsky, 1997). Important adaptations include production of hypertrophied lenticels, aerenchyma tissue, and adventitious roots. These facilitate the movement of oxygen from leaves and stems to roots, thus permitting them to function in an oxygen-deficient environment (Kozlocvsky, 1997; Van Der Molen et al., 2011). When the flood water drains away, plants may be less drought tolerant because of their low root/shoot ratios (Kozlocvsky, 1997);
- Drought-stress tolerant during the summer. Plants are developmentally and physiologically designed by evolution to reduce water use under drought stress (Schulze, 2005; Blum, 2005). physiological responses of the vegetation to drought include reductions in enzymatic activities as well as stomatal closure to prevent water loss. Mediterranean plants show two contrasting strategies to avoid drought stress: isohydric species, also known as *water savers*, decrease stomatal conductance to prevent leaf water lost (transpiration) while anisohydric species, also known as *water spenders*, are able to exert little or no stomatal control in response to drought they must secure a continuous source of water for example developing a deeper root system of the previous species.

Because of transpiration's control also reduces CO_2 diffusion into the leaf (Van der Molen et al., 2011) isohydric species experience a larger short-term reduction in gross primary production than anisohydric species. Death from drought may result from the starvation that accompanies restricted exchange of CO_2. Tolerance to drought may therefore be achieved by maintaining stomata open in spite of reduced plant water content, thereby avoiding CO_2 starvation (Van Der Molen et al., 2011)

It is worth noticing that the adaptations just described respect to the two different types of stress are not mutually exclusive: For example, plants that are resistant to the submersion of the roots could also be water spenders during drought stress.

For the purpose of my discussion, I single out two broadly defined competitors according to the main adaptation to the above discussed stressor:

- Hygrophilous species, that tolerate the submersion of the roots but are drought sensitive. Hygrophilous species have lower water use efficiency and are able to exert little or no transpiration control in response to drought so that they must endure a continuous source of water (Schulze, 2005; Van Der Molen et al., 2011);

- Non-hygrophilous species, that are drought resistant but cannot tolerate flooding. Non-hygrophilous species have higher water use efficiency, because of their ability in controlling water lost by transpiration in response to drought but may be less productive than hygrophilous ones in case of wet condition.

1.2 Regime shifts, Resilience, and Biodiversity in ecosystem management

Humanity strongly influences biogeochemical, hydrological, and ecological processes, from local to global scales. Humans have, over historical time but with increased intensity after the industrial revolution, reduced the capacity of ecosystems to cope with change through a combination of top-down (e.g., overexploitation of top predators) and bottom-up impacts (e.g., excess nutrient influx), as well as increasing of disturbance regimes such as climatic change. These include changes of land use, climate, nutrient stocks, soil properties, freshwater dynamics, and biomass of long-lived organisms (Gunderson & Pritchard, 2002).

The results of these impacts are depleted, more vulnerable and simplified ecosystems which responses to the disturbances could surprise us with unexpected changes of their quality and services.

Currently human face more the challenge of understanding how ecosystems will respond to disturbances and which hypotheses of management are the most appropriate in perspective of preservation and environmental sustainability.

The will to cope with disturbances and the need to properly manage an ecosystem calls for a change from the existing paradigm of *command-and-control* to one based on managing *resilience* in uncertain environments to secure essential ecosystem services.

The *command and control* paradigm provide us a threshold established *a priori* according to precautionary assumptions that are not based on the specific system to which are assigned. Holling (1973), in his seminal paper, defined *ecosystem resilience* as the magnitude of disturbance that a system can experience before it shifts into a new regime qualitatively different from the first. These changes, also known as *regime shift*, currently represent an area of active research as they provide us qualitative information on opportunities and ways in which an ecosystem could translates from one state to another less desirable.

For example, several studies on shallow lakes have illustrated that the resilience of such natural system can be eroded to reach the point where the system switch with a rapid transition to an ecological status different from the previous (Scheffer, 2001; Scheffer and Carpenter, 2003; Walker et al., 2004). Theory suggests that such shifts, defined catastrophic, can be attributed to alternative stable states (figure 1.1 and phr

1.6 for apprfondition). In other words, chronic disturbances may have little effect until a threshold at which a large shift occurs is reached and that might be difficult to reverse.

Verifying this diagnosis is important because it implies a radically new point of view for management options, especially those involving the global change (Suding *et al*, 2004; Scheffer, 2001; Scheffer and Carpenter, 2003).

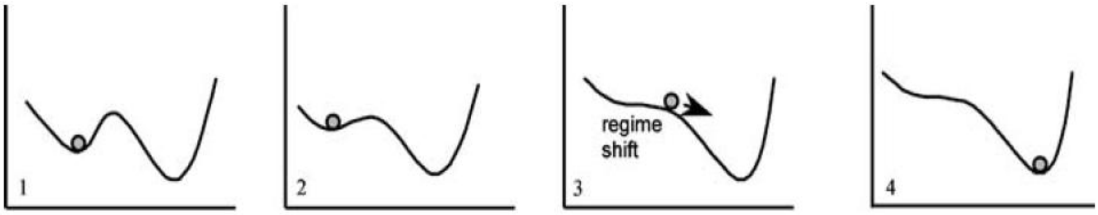


Figure 1.1. An analogy with potential energy of resilience loss and regime shifts dynamics in a natural ecosystems with alternative stable states (modified from Folke et al., 2004)

Strategies to assess whether regime shift may occurs are present are now converging in fields as disparate as desertification, limnology, oceanography and climatology (Walker et al., 2004), suggesting ways in which restoration could be identify, prioritize and addressed.

A growing number of empirical studies demonstrate a positive diversity-stability relationships. The diversity of functional groups, populations and species appear to be critical for resilience and for the generation of ecosystem services (Chapin et al. 1997, Luck et al. 2003). Understanding the relationship between diversity and stability requires a knowledge of how species interact with each other and how they are affected by the environment. However these studies rarely uncover the mechanisms responsible for stability.

Consequently, efforts to reduce the risk of undesired regime shift should address the preservation of resilience, thus diversity, rather than focus all effort into controlling disturbances *a priori*. For this purpose, is essential to identify the specific resilience of an ecosystem affected.

1.2.1 Documented regime shift in natural system

Several studies (Folke et al., 2004; Scheffer and Carpenter, 2003) review the evidence of regime shifts in terrestrial and aquatic environments. Mostly they deal with resilience of complex adaptive ecosystems or with the functional roles of biological diversity in this context. The evidence reveals that the likelihood of regime shifts may increase when humans reduce resilience by such actions as removing response diversity, removing whole functional groups of species, or removing whole trophic levels; impacting on ecosystems via emissions of waste and pollutants and climate change; altering the magnitude, frequency, and duration of disturbance.

Table 1.1 provides an overview of documented regime shifts in natural ecosystems.

On forest system several composition switches have been documented, perhaps due to exogenous driven forces such as the effect of the epidemics diffusion, the passage of ungulates, flooding or change in frequency of fires. Marked fluctuations in grass and woody plant biomass are a common feature of savannas, because of their highly variable rainfall causing primary productivity variety up to tenfold from one year to the next. It is worth noting that such kind of study has never been addressed to the wet forest ecosystems under climate forces. Concerning forest ecosystems, there are few studies on climate change effects on resilience, again only addressed to the arid or semi-arid systems. In contrast, studies concerning wet ecotones, but not forest, do not include the effect of gradual climate change that we are experiencing.

Ecosystem type	**Alternate state 1**	**Alternate state 2**	**References**
Freshwater systems			
Temperate lakes	Clear water	Turbid water	Carpenter 2003
	Game fish abundant	Game fish absent	Post et al. 2002, Walters & Kitchell 2001, Carpenter 2003;
Tropical lakes	Submerged vegetation	Floating plants	Scheffer et al. 2003
Shallow lakes	Benthic vegetation	Blue-green algae	Blindow et al. 1993, Scheffer et al. 1993, Scheffer 1997, Jackson 2003
Wetlands	Sawgrass communities	Cattail communities	Davis 1989, Gunderson 2001
	Salt marsh vegetation	Saline soils	Srivastava & Jefferies 1995
Marine systems			
Coral reefs	Hard coral dominance	Macroalgae dominance	Knowlton 1992, Done 1992, Hughes 1994, McCook 1999

	Hard coral dominance	Sea urchin barren	Glynn 1988, Eakin 1996
Kelp forests	Kelp dominance	Sea urchin dominance	Steneck et al. 2002, Konar & Estes 2003
	Sea urchin dominance	Crab dominance	Steneck et al. 2002
Shallow lagoons	Seagrass beds	Phytoplankton blooms	Gunderson 2001, Newman et al. 1998
Coastal seas	Submerged vegetation	Filamentous algae	Jansson & Jansson 2002, Worm et al. 1999
Benthic foodwebs	Rock lobster predation	Whelk predation	Barkai & McQuaid 1988
Ocean foodwebs	Fish stock abundant	Fish stock depleted	Steele 1998, Walters & Kitchell 2001; de Roos & Persson 2002
Forest systems			
Temperate forests	Spruce-fir dominance	Aspen-birch dominance	Holling 1978
	Pine dominance	Hardwood dominance	Peterson 2002
	Hardwood-hemlock	Aspen-birch	Frelich & Reich 1999
	Birch-spruce succession	Pine dominance	Danell et al. 2003
Tropical forests	Rain forest	Grassland	Trenbath et al. 1989
	Woodland	Grassland	Dublin et al. 1990
	Native crab consumers	Invasive ants	O’Dowd et al. 2003
Savanna and grassland			
Grassland	Perennial grasses	Desert	Wang & Eltahir 2000, Foley et al. 2003; van de Koppel et al. 1997
Savanna	Native vegetation	Invasive species	Vitousek et al. 1987
	Tall shrub, perennial grasses	Low shrub, bare soil	Bisigato & Bertiller 1997
	Grass dominated	Shrub dominated	Anderies et al. 2003, Brown et al. 1997
Arctic, sub-Arctic sysems			
Steppe/tundra	Grass dominated	Moss dominated	Zimov et al. 1995
	Tundra	Boreal forest	Bonan et al. 1992, Higgins et al. 2002

Table 1.1 Documented shifts between states in different kinds of ecosystem (From Folke and Carpenter, 2004)

1.3 Climate Change

1.4.1 Global Climate Change: an overview

Increasing emissions of greenhouse gases are now widely acknowledged by the scientific community as the major cause of recent increases in global mean temperature (about 0.5 °C since 1970, figure 1.2) and changes in the world’s hydrological cycle (IPCC, 2007), including a widening of the Earth’s tropical belt (Seidel et al., 2008; Lu et al., 2009).

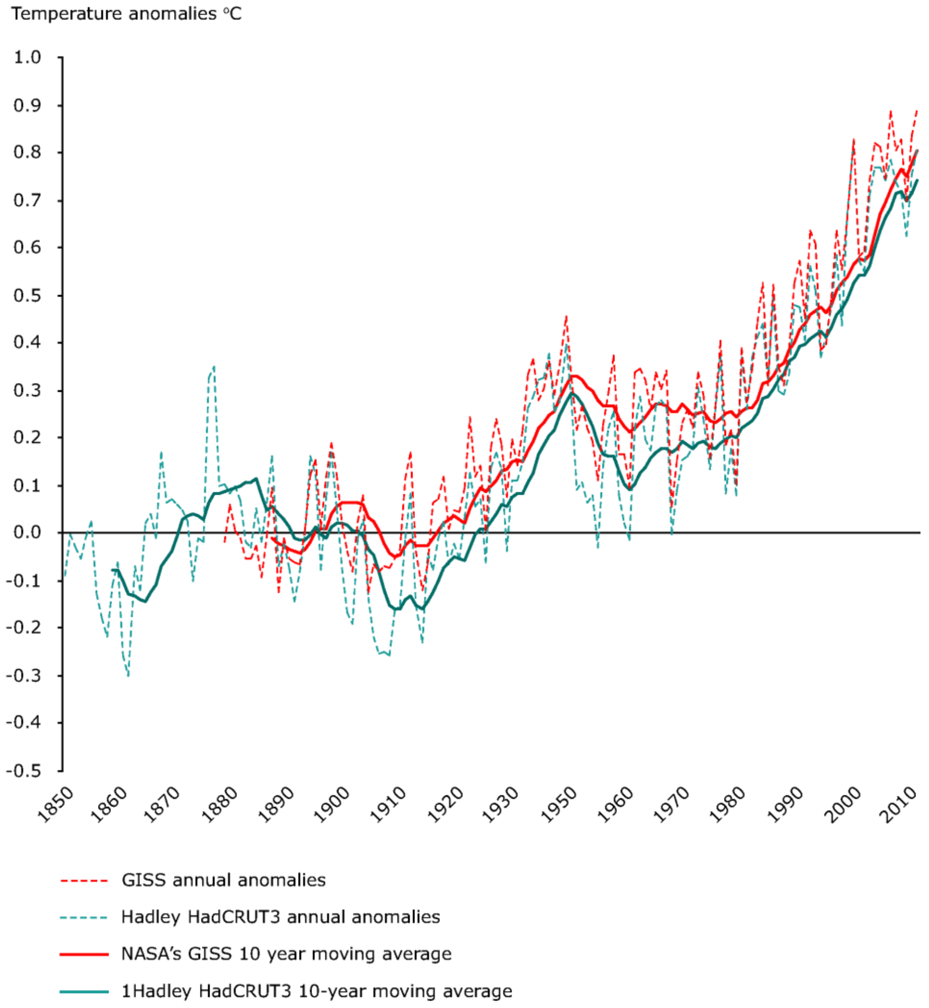


Figure 1.2. Observed global annual average temperature deviations in the period 1850–2010 (in ºC). Different lines refer to different models and databases (available online from http://www.eea.europa.eu/data-and-maps/indicators/global-and-european-temperature/global-and-european-temperature-assessment-4)

Even under conservative scenarios, future climate changes are likely to include further increases in mean temperature (about 2–4 °C globally) with significant drying in some regions (Christensen et al., 2007; Seager et al., 2007), as well as increases in frequency and severity of extreme droughts, hot extremes, and heat waves (IPCC, 2007; Sterl et al., 2008).

As the European Environmental Agency reports, briefly but still concisely,

"*The global average temperature is projected to continue to increase. Globally, the projected increase in this century is between 1.8 and 4.0 0C (best estimate), and is considered likely (66 % probability) to be between 1.1 and 6.4 0C for the six IPCC SRES scenarios and multiple climate models (IPCC, 2007a), comparing the 2080 - 2100 average with the 1961 - 1990 average. These scenarios assume that no additional policies to limit greenhouse gas emissions are implemented (IPCC, 2007). The range results from the uncertainties in future socio-economic development and in climate models. The EU and UNFCCC Copenhagen Accord target of limiting global average warming to not more than 2.0 0C above pre - industrial levels is projected to be exceeded between 2040 and 2060, for all six IPCC scenarios"*

1.3.2 Climate change on Mediterranean basin

The Mediterranean basin is characterized by mild, rainy winters and hot, dry summers. The climate is affected by complex interactions between mid-latitude and tropical processes that, overall, make the Mediterranean a potentially vulnerable region to climatic changes as induced, for example, by increasing concentrations of greenhouse gases (Giorgi and Lionello, 2008; Ulbrich et al., 2006).

Indeed, the Mediterranean region has shown large climate shifts in the past (Luterbacher et al., 2006) and it has been identified as one of the most prominent hot-spots in future climate change projections (Giorgi and Lionello, 2008).

Giorgi and Lionello (2008) have presented a review of climate change projections over the Mediterranean region based on the latest and most advanced sets of global and regional climate model simulations. These simulations have given a collective picture of a substantial drying and warming of the Mediterranean region, especially in the warm season (precipitation decrease exceeding −25–30% and warming exceeding 4–5 °C). These signals are visible in most projections from both Global and Regional Climate Models (RCMs) (CIRCE; Van Der Linden, 2009; Ulbrich et al., 2006), and although there are considerable uncertainties in climate model predictions, they agree that more frequent and intense droughts are expected (figure 1.3).

Looking for more specific climate projections for the Mediterranean , CIRCE project argues that temperature would increase of 2-4°C while a decrease of precipitation of 5-10% is expected in the next 40’s years, projections that overall are consistent with those reported by the European Environmental Agency (figure 1.3)

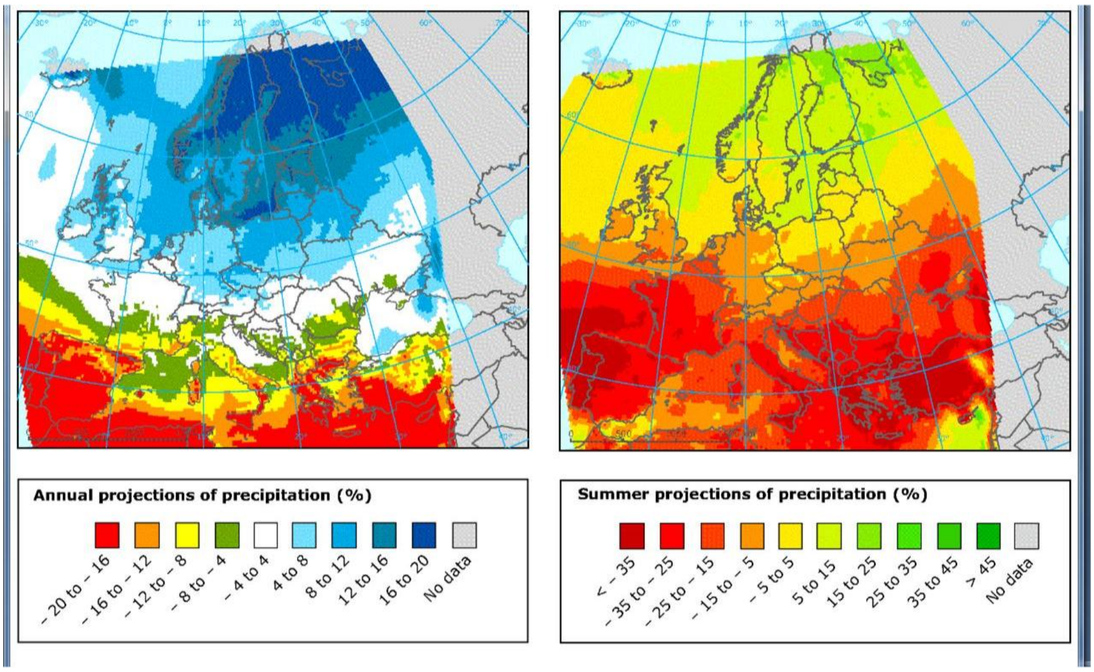


Figure 1.3. Projected changes in % in annual and summer precipitation between 1961–1990 and 2071–2100 as simulated by ENSEMBLES Regional Climate Models for the IPCC SRES A1B emission scenario.

1.3.3 Expected consequences of Climate Change on forest system

Forested ecosystems are being rapidly and directly transformed by the land uses of our expanding human populations and economies. Currently less evident are the impacts of ongoing climate change on the world’s forests. Understanding and predicting the consequences of these climatic changes on ecosystems is emerging as one of the grand challenges for global change scientists, and forecasting the impacts on forests is of particular importance (Boisvenue and Running, 2006; Bonan, 2008). Forests, here broadly defined to include woodlands and savannas, cover 30% of the world’s land surface (FAO, 2006). Around the globe societies rely on forests for essential services such as timber and watershed protection, and less tangible but equally important recreational, aesthetic, and spiritual benefits. The effects of climate change on forests include both positive (e.g. increases in forest vigour and growth from CO_2 fertilization, increased water use efficiency, and longer growing seasons) and negative effects (e.g. reduced growth and increases in stress and mortality due to the combined impacts of climate change and climate-driven changes in the dynamics of forest insects and pathogens) (Ayres and Lombardero, 2000; Bachelet et al., 2003; Lucht et al., 2006; Scholze et al., 2006; Lloyd and Bunn, 2007).

Considerable uncertainty remains in modeling how global climate change will affect the risk of future tree die-off events, referred to hereafter as ‘forest mortality’, under a changing climate (Loehle and LeBlanc, 1996; Hanson and Weltzin, 2000; Bugmann et al., 2001). Although a range of responses can and should be expected, recent cases of increased tree mortality and die-offs triggered by drought and/or high temperatures raise the possibility that amplified forest mortality may already be occurring in some locations in response to global climate change. Examples of recent die-offs are particularly well documented for southern parts of Europe (Penǖelas et al., 2001; Breda et al., 2006; Bigler et al., 2006) and for temperate and boreal forests of western North America, where background mortality rates have increased rapidly in recent decades (Van Mantgem et al., 2009) and widespread death of many tree species in multiple forest types has affected well over 10million ha since 1997 (Raffa et al., 2008). The common implicated causal factor in these examples is elevated temperatures and/or water stress, raising the possibility that the world’s forests are increasingly responding to ongoing warming and drying.

1.4 Wetlands and Water Resource

Water availability is considered the environmental factor that most strongly limits plant growth world-wide (Nemani et al., 2003). Global change is expected to exacerbate alterations in the world's hydrological cycle (IPCC, 2007). An overall decrease in soil moisture is already underway (Jung et al., 2011).

The UN Millennium Ecosystem Assessment (2005) determined that environmental degradation is more prominent for wetland environments than for any other ecosystem on Earth. International conservation efforts and the development of rapid assessment tools are being used in conjunction with each other to inform people about wetland issues (MEA, 2005). Wetlands are among the most species-rich environments known (Ward et al. 1999; Mitsch et., 2007). They may often be described as ecotones providing a transition between water bodies and arid or semi-arid regions. Many of the flora and fauna that are part of wetlands are disappearing. As most species are endemic of wetlands, biologists and other scientists routinely census wetland biota to look for threatened populations. The IUCN's global red list (online available at www.iucn.org) can be accessed on the internet to determine if there is any species within a particular wetland system that has been identified as needing assistance to prevent extinction.

The Mediterranean basin, characterized by mild, rainy winters and hot, dry summers, supports characteristic Mediterranean forests, woodlands, and scrub vegetation. Nevertheless, the Mediterranean has a very large number of wetlands, for a total of over 8 million and a half hectares.

The Mediterranean Wetlands Observatory (2011) presents the results of a three- year project on Mediterranean wetlands studies in which seventeen indicators have been developed and evaluated. The results of these analyzes suggest: contrasting trends for wetlands biodiversity between the Western and the Eastern Mediterranean regions; very strong and growing pressure on water resources and multiple causes of degradation on wetlands; Political and governance issues in addition to the institutional divides between main stakeholders are the main causes of these pressures.

1.4.1 Mediterranean Plain Oak Forests of Central Italy

The vegetation in Mediterranean climates is typically sclerophyllous and ever-green, adapted to water stress during the dry summer period, and able to grow on infertile soils (Gasith andVincent, 1999) . The availability of year-round moisture near streams enables deciduous woody vegetation to occur in the riparian zone as seen in Mediterranean-type streams in the Northern Hemisphere (Holstein, 1994) with equivalent species pairs occurring in different Mediterranean regions (e.g. Israel and California).

Coastal plain forests of the Tyrrhenian, thermophiles and sub-acidophilic, have settled on the morphology of coastal plain with shallow groundwater and alluvial substrates such as the ancient Pleistocene dunes, flattened and pedogenesized.

In the past, hygrophilous and meso-hygrophilous woods behind the dunes and interdunal wet environments, had a wide distribution along the Italian coast. The works of land **reclamation and deforestation** in the sub-coastal plain area of Lazio were made mostly between 1926 and 1936. During the clean most of the interdunal depressions were filled with sediment and channels were built to drain the deepest. Nevertheless, in the woods wrecks left, located above the Pleistocene dune complex, some small depressions, namely *vernal pools* (figure 1.4), have survived and others have been restored. Within these, water accumulates for several months a year. In these pools the water table once emerged on the surface during the rainy periods, but today is a much deeper level.

Figure 1.4 A typical vernal pool in Circeo National Park

The gradual lowering of water table, because of drainage and water collection, has attracted scientific interest on the possible evolution of these environments, particularly in relation to seasonal variations, climatic and succession changes (Stanisci et al, 1998).

Currently, plain forest are scarce and localized, due to strong anthropogenic changes (sewage, drainage, cultivation, construction, tourism). However, in the Tyrrhenian coast of Tuscany and Lazio (Italy) we can still find some rare examples of this type of vegetation, fairly well conserved (Stanisci *et al*, 1998).

The high availability of edaphic water allows the coexistence of sclerophyllous evergreen oak species (*Q. ilex* and *Q. suber*) with deciduous ones (dominated by a typical endemism of *Q. cerris* and *Q. frainetto* and with the significant presence of *Q. robur*) despite the meso-Mediterranean or thermo-Mediterranean climate location (Presti et al., 1998).

Despite the **ecological value of these forests** due to the high biodiversity, micro-heterogeneity and their present reduced extension, few scientific concern has been directed towards these forest complex and their existence is not even mentioned in recent reviews of wetlands. currently they have not ever been included in Europe's most threatened natural ecosystems and are not listed in Annexe I of the European Habitats Directive as being a 'priority forest habitat type'.

Model testing of the present study was carried out at the protected plain forest of Castelporziano Estate (CPE), mainly covered by holm-oak (Figure 1.4). Some information about the plain forest of Circeo National Park (CNP), mainly covered by turkey oak, have been integrated.

1.4.1a Castelporziano Estate (CPE)

The Presidential Estate of Castelporziano, located about 20 km from Rome (41°44′N, 12°25′E), covers an area of 6100 ha (Figure 1.5). This area is fairly flat, ranging from sea level to 85 m a.s.l.

The climate is of Lower Mesomediterranean Thermotype, Upper Arid/Lower Subhumid Ombrotype (Blasi, 1994).

The holm-oak wood of Castelporziano (about 100 ha) is a rare example of holm-oak forest belonging to the Viburno-Quercetum ilicis (Br.-Bl. 1936) Rivas-Martinez (1975) association. This association is the warmest and most thermophilous type of such woods in Italy, formed in a coastal environment on consolidated dunes and on the sea-facing slopes, in a definitely Mediterranean environment (Pignatti, 1998). The soil consists of reddish, quartziferous aeolian sands of the ancient dunes (Manes et al ., 1997c).

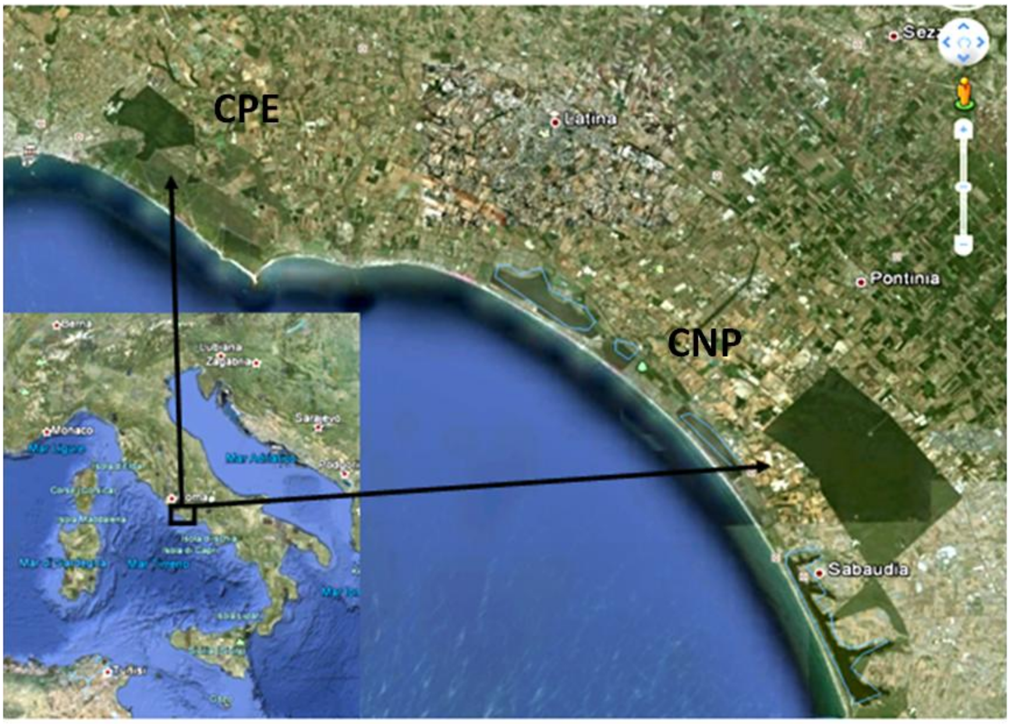
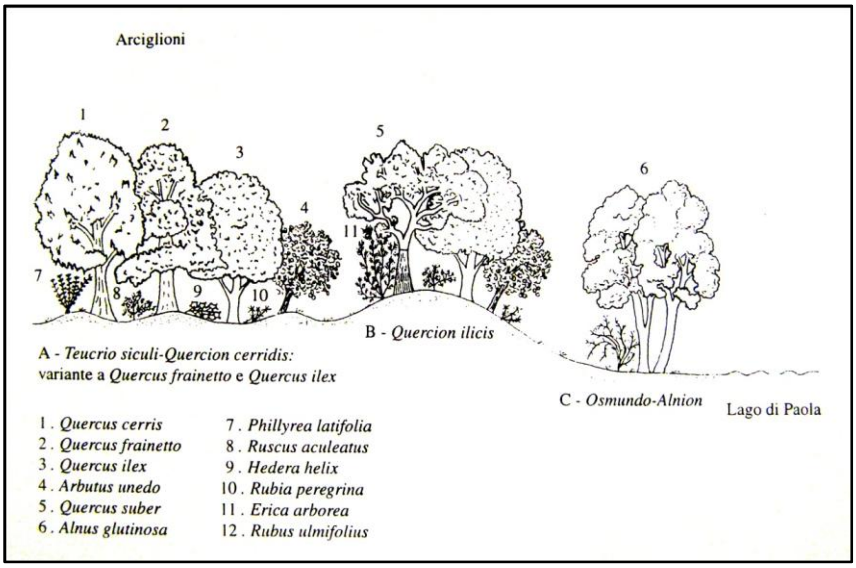


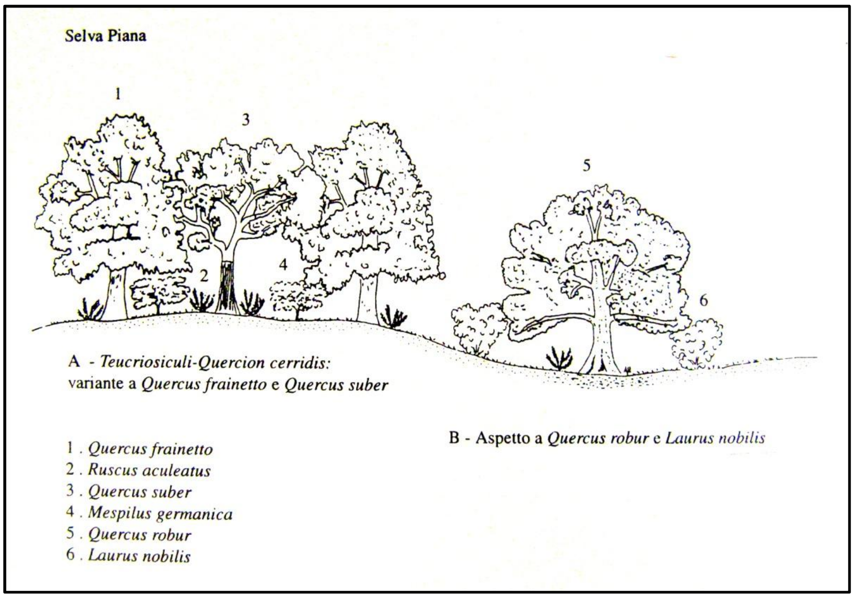
Figura 1.5. Location of the study areas, Circeo National parck (CNP) and Castelporziano Estate (CPE)

1.4.1b Circeo National Park (CNP)

The Circeo National Park, located about 100 km south of Rome, extends from latitude 41°13′N to 41°24′N, and from longitude 12°50′E to 13°07′E (Fig. 1.4). This is a coastal area with a climate of Lower Mesomediterranean Thermotype, Upper Subhumid Ombrotype (Blasi, 1994). In 1977 the Park was included in the network of Biosphere Reserves of UNESCO’s MAB Programme.

Also present are coastal lakes and wetlands, seasonally flooded, which have been declared ‘Wetlands of International Interest’ according to the Ramsar Convention. The Circeo National Park (about 8400 ha) consists of five main environments: the plain forest, four coastal lakes, the coastal dune area, the limestone massif of Mount Circeo, with a maximum height of 541 m a.s.l., and the island of Zannone. The plain forest covers about 3190 hectares and consists mainly of deciduous woods (*Q. cerris* L., *Q. Frainetto* Ten., *Q. Robur* L., *Fraxinus ornus* L. And *Carpinus betulus* L.), with soils that are mainly characterized by Würmian sand with pyroclastic material, referred to as the Vulcano Laziale activity (Manes et al ., 1997a; Dowgiallo & Bottini, 1998). The forest is of relatively mesophytic mixed broad-leaved oaks belonging to the Teucrio siculi-Quercion cerridis (Ubaldi, 1988) Scoppola et Filesi 1993 alliance (figure 1.6), which is well represented in Italy.





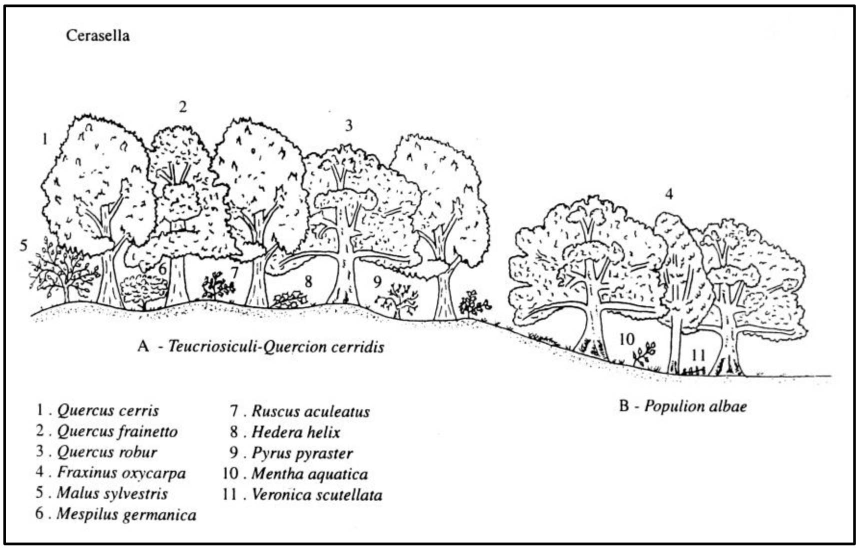


Figure 1.6. Three typical vegetation profile of Circeo National Park plain forest. Arciglioni: contact between the Holm oak and Turkey oak with Hungarian oak (A), the forest of Holm oak and Cork oak (B) and Alders (C); Selvapiana: Hungarian oak wood and Cork in its typical aspect (A) and in the mesophyll with English oak and laurel into bay depressions (B) Cerasella: contact of Turkey oak and Hornbeam with Hungarian oak (A) and the forest with English oak and Ash of the pools (B); (modified by Presti at al., 1998)

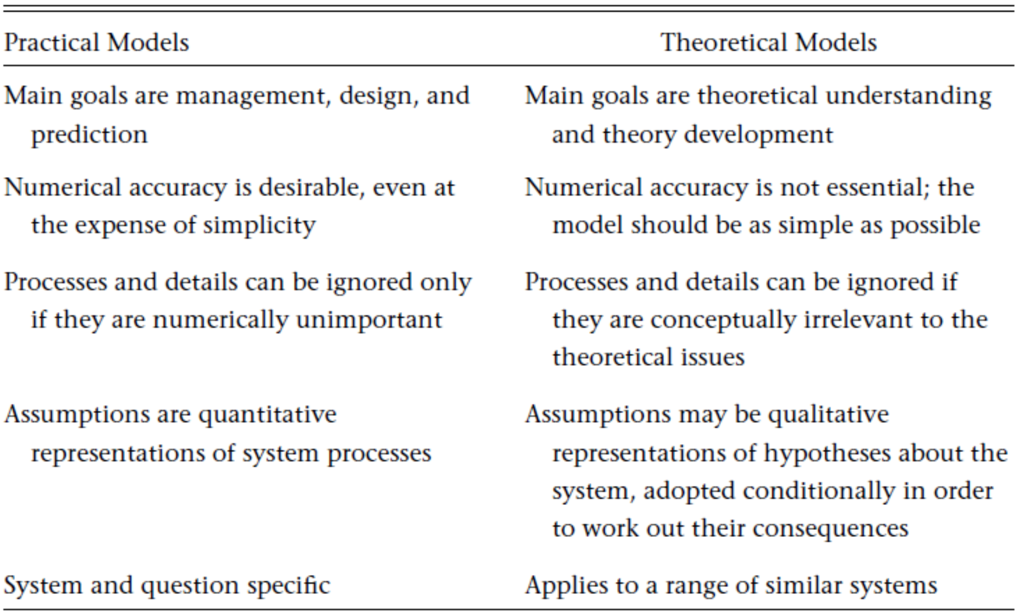
1.5 Theoretical Framework

1.5.1 Why a Dynamical Systems Theory

Models provide a much more powerful tool than qualitative reasoning for showing that certain mechanisms can lead to phenomena of interest such as regime shift (Scheffer and Carpenter, 2003).

Although dynamic models are used for many purpose, we can put them under two broad headings: *theoretical understanding* of how the system operates, and *practical applications* where model predictions will play a role in deciding between different possible courses of action (Table 1.2). It is important to keep in mind this distinction because it affects how we build and evaluate models.

A theoretical model has to be simple enough that we can understand why it is doing what it does. The relationship between hypotheses (model assumptions) and conclusions (properties of model solutions) is what provides understanding of the biological system. Replacing a complex system that we don't understand with a complex model that we also don't understand has not increased our understanding of the system.



Practical Models	Theoretical Models
Main goals are management, design, and prediction	Main goals are theoretical understanding and theory development
Numerical accuracy is desirable, even at the expense of simplicity	Numerical accuracy is not essential; the model should be as simple as possible
Processes and details can be ignored only if they are numerically unimportant	Processes and details can be ignored if they are conceptually irrelevant to the theoretical issues
Assumptions are quantitative representations of system processes	Assumptions may be qualitative representations of hypotheses about the system, adopted conditionally in order to work out their consequences
System and question specific	Applies to a range of similar systems

Table 1.2. Classification of models by objectives

Most models in the literature are so-called *minimal models* because focus on a minimal set of mechanisms needed to produce a certain behaviour. A drawback of simple models is that they necessarily leave out many potentially important aspects. However such models have been useful for exploring mechanisms that are too intricate to grasp from common sense alone (Scheffer and Carpenter, 2003).

Theoretical models are well suited to describe complex ecosystem that are characterized by historical dependency, nonlinear dynamics, threshold effects, multiple basins of attraction, and limited predictability (Levin, 1999). Biological processes are typically characterized by nonlinear relationships and feedback process that often result in unpredictable phenomena.

Many parts dynamical systems theory deal with asymptotic properties of systems behavior, i.e., what happens with the system after a long period of time. Here, the focus is not on finding exact solutions to the equations defining the dynamical system (which is often hopeless), but rather to answer questions like "Will the system settle down to a steady state in the long term, and if so, what are the possible steady states?", or "Does the long-term behaviour of the system depend on its initial condition?". The knowledge of the set of all possible solutions which satisfy the system is not strictly necessary in order to understand the dynamics of a systems. First because it is possible to calculate approximate solutions with a numerical method. Second, because the understanding of the system behaviour is obtained by exploring the structure, or *qualitative proprieties*, of the invariant *phase space*, whose simply represents the curves of the unique solutions (*trajectories*) for different initial conditions. The simplest structure are exhibited by equilibrium points (or *fixed points*) and by *periodic orbits* (Figure 1.7)

The question arises if such characteristic structures are stable and under which conditions the stability is preserved, where the concept of stability means that the trajectories do not change too much under small perturbations of initial conditions.

Various criteria have been developed to prove stability or instability of an structure. Under favourable circumstances, the question may be reduced to a well-studied problem involving eigenvalues of matrices. A more general method involves Lyapunov functions. For a more general survey on dynamical systems theory, see Strogatz (1994) and Kuznetsov (2004).

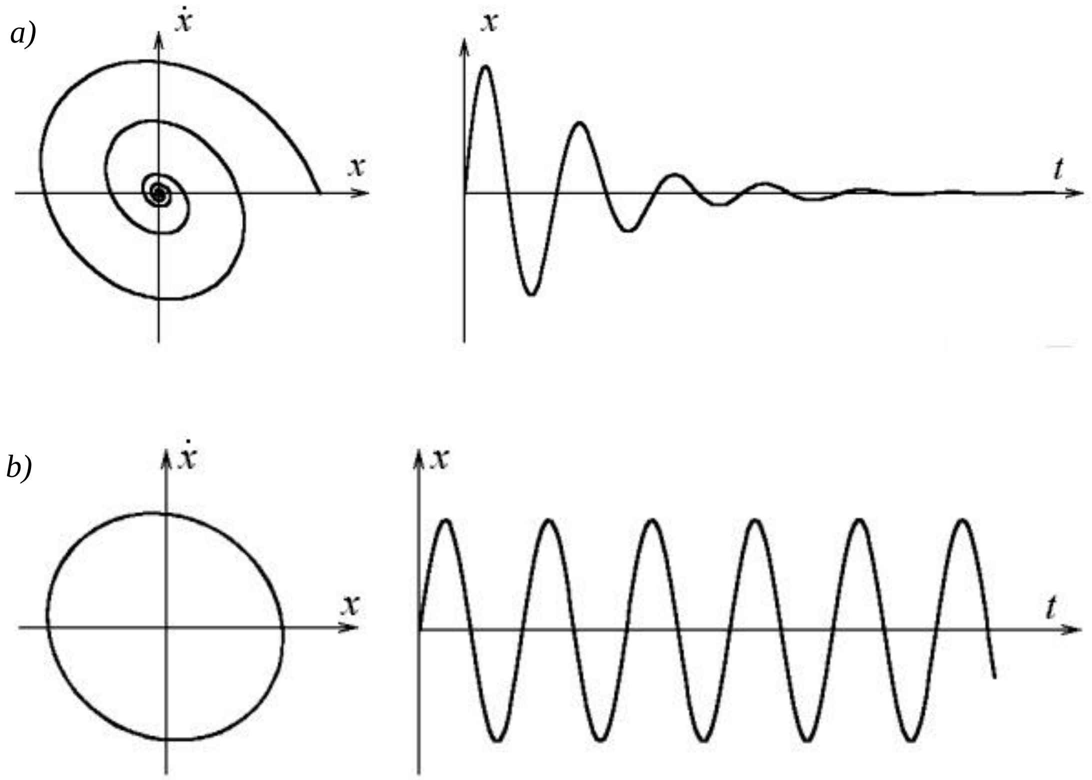


Figure 1.7. Visualisation of simplest dynamical systems structures. *a)* time series of free oscillations for a linear damped model (right side) and the same time series projected into the phase space (left side). We can see a fixed point like an attractor in the phase space. *b)* Time series of linear harmonically loaded system (right side) and the same time series projected into the phase space (left side).

1.5.2 Mathematical formalization

A dynamic model is a mathematical formalization describing the evolution of the state of one or more variables. In deterministic model, the variables must be able to uniquely describe the system. Such as variables are called *State Variables*. A dynamical system consists of three ingredients, namely,

- ✓ Time,
- ✓ State space,
- ✓ Law of evolution.

When the law of evolution does not depend explicitly on the independent variable *t*, the system is called autonomous.

The evolution of the state variables can often be well represented by a system of a few ordinary differential equations (ODEs), e.g., matrix or differential equations. This makes them suitable for any type of study whose different components interact in a nonlinear way.

Generally, such a classic *deterministic scenario* may be written as:

$$\dot{\boldsymbol{x}} = \boldsymbol{f}(x) \tag{1}$$

$$x|_{t=0} = x_0 \tag{2}$$

where $\boldsymbol{x}$ is the vector of state variables, $\boldsymbol{f}(x)$ is the *vector field* defining the law of evolution of the system and $\boldsymbol{x}_0$ is the set of initial conditions from which the system evolves. See Strogatz (1994) for a more detailed description.

The integration of differential equations is possible only for very simple systems. However, an important goal for the *dynamic system theory* is to describe the solutions at the equilibrium states, like *fixed points* and *periodic orbits*, because of they represent the points where the system converges over time. Therefore, I underline what mentioned in the previous paragraph yet: the knowledge of all possible solutions which satisfy the system is not strictly necessary in order to understand the behaviour of a systems.

The solutions at the equilibrium states ($\boldsymbol{x}^*$) can be calculated directly by setting $\dot{\boldsymbol{x}} = \boldsymbol{0}$. At equilibrium points, the system is at rest and equilibrium solutions are constant solutions.

Every equilibrium solutions, together with their proprieties, as being *attractive* or *repellent*, *stable* or *unstable*, could be affected by disturbances, so that, theoretically, the equilibrium point would remain the same forever, but in practice there is rarely such a thing as exactness. Due to perturbation in $\boldsymbol{x}$ of $\boldsymbol{f}$, the location of the equilibrium varies slightly. So the question is how equilibrium solutions $\boldsymbol{x}^*(t)$ of the initial value problem (1-2) behave under the effect of one or more disturbances.

1.5.3 Linear stability analysis

A stationary solution $\boldsymbol{x^*}$ is linearly asymptotically stable if the response to a small perturbation approaches zero as the time approaches infinity. A linearly asymptotically stable equilibrium is also called *sink* and is an example of an *attractor*.

A stationary solution $\boldsymbol{x^*}$ is stable if the response to a small perturbation remains small as the time approaches infinity.

Otherwise the stationary solution is called *unstable* and the deviation grows.

It is crucial to realize that the above definitions of stability are local in nature. An equilibrium may be stable for a small perturbation but unstable for a large perturbation.

The behaviour of the system near an equilibrium state is described by the local *stability analysis* which can be determined by means of a standard mathematical method (Ellner and Guckenheimer, 2006)

Briefly speaking the equations describing the model are first linearly expanded around the equilibrium point by a Taylor series expansion.

$$\dot{x} = f(x) = \frac{df(x^*)}{dx}(x - x^*) + \ temrs\ of\ higher\ order \tag{3}$$

For more than one state variables, this system of equations is easily written down using the notation of the *Jacobian matrix* $\boldsymbol{J}$ of the first-order partial derivatives. Evaluated at the equilibrium, the Jacobian is

$$\boldsymbol{J} = \frac{\partial f}{\partial x}(x^*) = \begin{bmatrix} \frac{\partial f_1}{\partial x_1}(x_1^*, \dots, x_n^*) & \dots & \frac{\partial f_1}{\partial x_n}(x_1^*, \dots, x_n^*) \\ \vdots & \ddots & \vdots \\ \frac{\partial f_n}{\partial x_1}(x_1^*, \dots, x_n^*) & \dots & \frac{\partial f_n}{\partial x_n}(x_1^*, \dots, x_n^*) \end{bmatrix}$$

Now the linearized system in vector notation reads

$$\dot{\boldsymbol{x}} = \boldsymbol{J}x \tag{4}$$

We can ask how the system behaves.

Consider the linear system $\dot{\boldsymbol{x}} = \boldsymbol{J}x$, with equilibrium $x^* = 0$. In the one-variable case $\dot{\boldsymbol{x}} = \boldsymbol{J}x$ we get exponential solutions, $e^{\boldsymbol{J}\boldsymbol{t}}x(0)$. In the multivariable case, we get something similar from the eigenvectors and eigenvalues of the matrix $\boldsymbol{J}$.

Recalling the definition: λ is an *eigenvalue* of $\boldsymbol{J}$, and $\boldsymbol{\omega} \neq 0$ a corresponding *eigenvector*, if $\boldsymbol{J\omega} = \lambda\boldsymbol{\omega}$ **(**Ellner and Guckenheimer, 2006).

It is important to note that eigenvectors are only defined up to constant: if $\boldsymbol{\omega}$ is an eigenvector for $\boldsymbol{J}$ so is $c\boldsymbol{\omega}$ for any constant $c \neq 0$. The requirement that $\boldsymbol{\omega} \neq 0$ is important. Without it any number $\boldsymbol{c}$ would be an "eigenvalue" corresponding to $\omega = 0$, because $\boldsymbol{J}0 = c0 = 0$.

Eigenvalues are important because they may give exponentially growing or decaying solutions if they are real numbers, or oscillatory behaviour if they are complex numbers.

$$x(t) = e^{\lambda t}\boldsymbol{\omega} \tag{5}$$

This can be demonstrated by direct substitution:

$$\dot{\boldsymbol{x}} = \lambda e^{\lambda t}\boldsymbol{\omega}$$

$$\boldsymbol{J}x = e^{\lambda t}\boldsymbol{J\omega} = e^{\lambda t}\lambda\boldsymbol{\omega} = \lambda e^{\lambda t}\boldsymbol{\omega}$$

The typical situation for a matrix $\boldsymbol{J}$, that also admits complex eigenvalues, of size $k \times k$ is that it will have k distinct eigenvalues and corresponding eigenvectors. Then the general solution of $\dot{\boldsymbol{x}} = \boldsymbol{J}x$ is:

$$x(t) = c_1 e^{\lambda_1 t}\omega_1 + c_2 e^{\lambda_2 t}\omega_2 + \cdots + c_k e^{\lambda_k t}\omega_k \tag{6}$$

As said before, because of the eigenvalues may be complex number, this exponential notation may be include pure exponential terms as well as oscillating terms.

For the stability of a fixed point only one term in (6) really matters: local stability of a fixed point for a system of differential equations depends on the eigenvalue of the Jacobian matrix with largest real part (Ellner and Guckenheimer, 2006) They may be evaluated simply by finding the roots of the characteristic equation

$$\det(\boldsymbol{J}_{\boldsymbol{x}} - \lambda\boldsymbol{I})\boldsymbol{\omega} = 0 \tag{7}$$

Where ***I*** is the identity matrix.

The stability of a fixed point may be:

- ✓ Stable if all eigenvalues of the Jacobian have negative real part.
- ✓ Unstable if any eigenvalue of the Jacobian has positive real part.
- ✓ If the real part of any eigenvalue is exactly 0, the equilibrium may either be stable or unstable – local linearization is inconclusive.

A more comprehensive discussion of the topic can be found in Ellner and Guckenheimer (2006) and Kuznetsov (2004).

A stable fixed point may be *attractive*, meaning that if the system starts out in a nearby state, it will converge towards the fixed point. Similarly, one is interested in *periodic points*, states of the system which repeat themselves after several time steps. Even simple nonlinear dynamical systems often exhibit almost random, completely unpredictable behaviour that has been called *chaos*.

Behaviour and fixed point can be observed in a *phase space*, that is a Cartesian representation whose axes are of state variables and whose each possible state of the system corresponding to one unique point in the phase space (see 1.7)

When two different phase portraits represent the same qualitative dynamic behaviour (i.e. a single attractor, limit cycle etc.) the behaviour of different systems are defined as *topological equivalent*. The set of initial conditions that lead to the same final system behaviour define the *attraction basin,* that is the *ecological resilience.*

1.5.4. Bifurcation

The parameter change may causes the stability of an structure to change. In particular, fixed points can be created or destroyed, or their stability can change. This qualitative change in the dynamics are called *Bifurcations*, and the parameters values at which they occur are called *Bifurcation Points*. Bifurcations are important scientifically because of they provide models of transitions and instabilities as some *control parameters* are varied.

In continuous systems, this corresponds to the real part of an eigenvalue of an equilibrium passing through zero. Bifurcations occur in both continuous systems (described by ODEs, DDEs or PDEs), and discrete systems (described by maps). Bifurcation may be:

- Local, which can be analysed entirely through changes in the local stability properties of equilibria, periodic orbits or other invariant sets as parameters cross through critical thresholds;
- Global, which often occur when larger invariant sets of the system 'collide' with each other, or with equilibria of the system. They cannot be detected purely by a stability analysis of the equilibria (fixed points).

Now I introduce the simplex types of bifurcations to which it is possible to link the majority of cases with only one control parameter.

1.6.4a Saddle-node Bifurcation

In the mathematical area of bifurcation theory a *saddle-node* bifurcation, *tangential bifurcation* or *fold bifurcation* is a local bifurcation in which two fixed points (or equilibria) of a dynamical system collide and annihilate each other. The term *saddle-node bifurcation* is most often used in reference to continuous dynamical systems. In discrete dynamical systems, the same bifurcation is often instead called a fold bifurcation. Another name is *blue skies* bifurcation in reference to the sudden creation of two fixed points.

The prototypical example of a saddle-node bifurcation is given by the first-order system

$$\dot{x} = r + x^2 \tag{8}$$

Where *r* is a parameter, which may be positive, negative, or zero. When r is negative, there are two fixed points, one stable and one unstable.

As r approaches 0 from below, the parabola moves up and the two fixed points move toward each other. When $r = 0$, the fixed points coalesce into a half-stable fixed point at $x^* = 0$. This type of fixed point is extremely delicate since it vanishes as soon as $r > 0$ and now there are no fixes points at all. In this example, we say that a bifurcation occurred at $r = 0$, since the vector field for $r < 0$ and $r > 0$ are qualitatively different.

The most common way to depict the bifurcation is to invert the axes of Figure 1.10

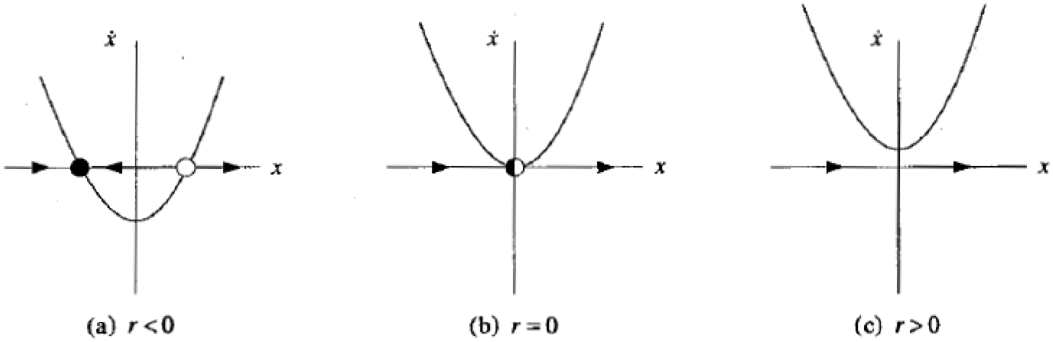


Figure 1.10 Saddle-node bifurcation for eq. (8).

The rationale is that r play the role of an independent variable, and so should be plotted horizontally. The drawback is that now the x-axis has to be plotted vertically, which looks strange at first. Arrows are sometimes included in the picture, but not always. This picture is called *bifurcation diagram*.

In a certain sense, the prototypical form, or *normal forms*, are representative of *all* the same type of bifurcation, like in this case it is representative of the all saddle-node bifurcations. The idea is that, close to a common bifurcation, the dynamics typically look like its normal form.

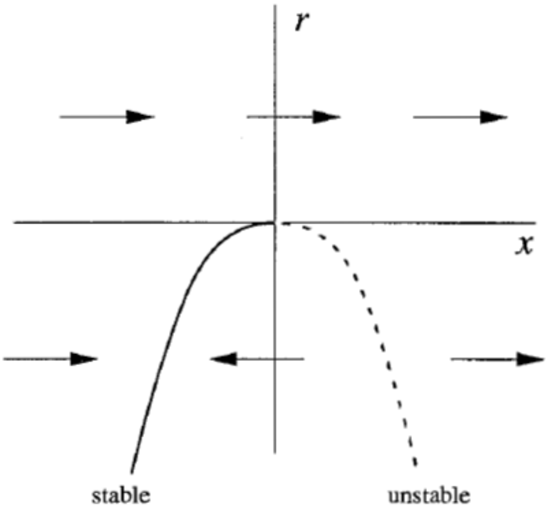


Figure 1.11 Saddle-node diagram bifurcation for eq. (1.10)

1.5.4b Transcritical Bifurcation

Mathematically a transcritical bifurcation is a particular kind of local bifurcation, characterized by an equilibrium having an eigenvalue whose real part passes through zero.

In such type of bifurcation a fixed point exists for all values of a parameter and is never destroyed. However, such a fixed point interchanges its stability with another fixed point as the parameter is varied. In other words, both before and after the bifurcation, there is one unstable and one stable fixed point. However, their stability is exchanged when they collide. So the unstable fixed point becomes stable and vice versa.

The normal form of a transcritical bifurcation is

$$\dot{x} = rx - x^2 \tag{9}$$

This equation is similar to logistic equation but in this case we allow r and x to be positive or negative (while in the logistic equation x and r must be non-negative). The two fixed points are at $x = 0$ and $x = r$. When the parameter r is negative, the fixed point at $x = 0$ is stable and the fixed point $x = r$ is unstable. But for $r > 0$ 0, the point at $x = 0$ is unstable and the point at $x = r$ is stable. So the bifurcation occurs at $r = 0$.

Figure1.12 shows the vector field as r varies. Note that there is a fixed point at $x^* = 0$ for *all* values of *r*.

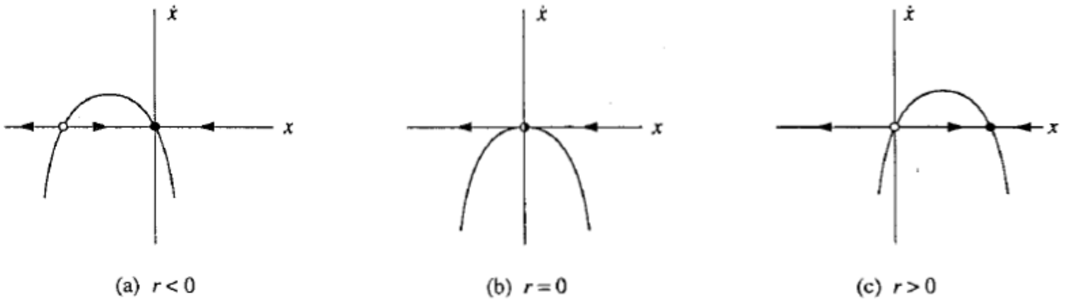


Figure 1.12 Transcritical bifurcation for eq. (9)

Figure 1.13 shows the bifurcation diagram for the transcritical bifurcation. As in figure ppp the parameter r is regarded as the independent variable, and the fixed points $x^* = 0$ and $x^* = r$ are shown as dependent variables.

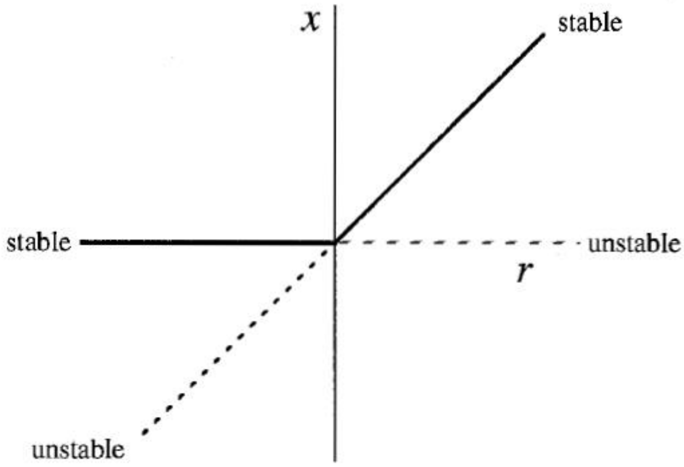


Figure 1.13 Transcritical bifurcation diagram for eq. (9)

1.5.4c Pitchfork Bifurcation

In continuous dynamical systems, pitchfork bifurcations occur generically in systems with symmetry. There are two very different types of pitchfork bifurcation. The simpler type is called *supercritical*, the other one *subcritical*.

The normal form of the **supercritical** pitchfork bifurcation is

$$\dot{x} = rx - x^3 \tag{10}$$

This equation is invariant under the change of variables $x \to -x$. This invariance is the mathematical expression of the left-right symmetry mentioned earlier. Figure 1.14 shows the vector field for different values of r.

When $r < 0,$ the origin is the only fixed point, and it is stable. When $r = 0$, the origin is still stable, but much more weakly so, since the linearization vanishes. Finally, when $r > 0,$ the origin has became unstable. Two new stable fixed points appear on either side of the origin, symmetrically located at $x^* = \pm\sqrt{r}$.

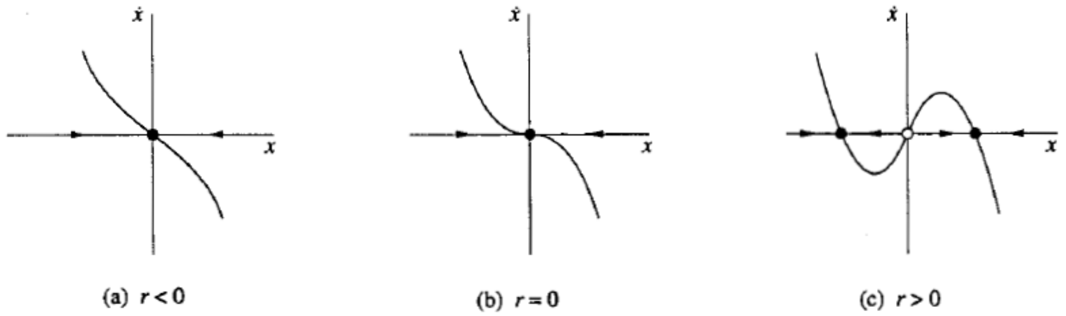


Figure 1.14 supercritical pitchfork bifurcation for eq. (10).

The bifurcation diagram is shown in figure 1.15

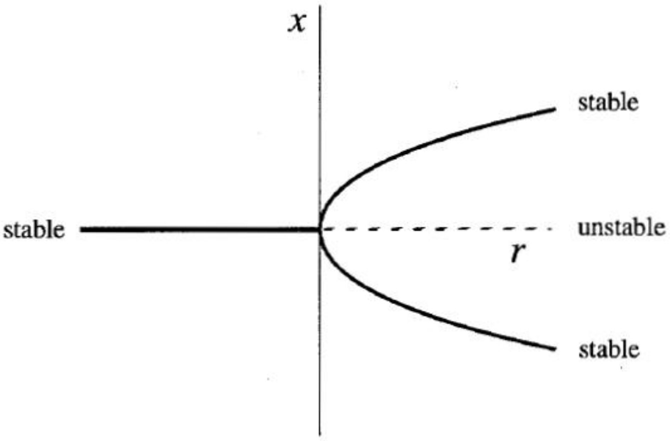


Figure 1.15 Supercritical pitchfork diagram for eq. (10).

In a specular way to the previous one, the normal form for the **subcritical case** is:

$$\dot{x} = rx + x^3 \tag{11}$$

And the pitchfork is inverted: in this case, for $r < 0$ the equilibrium at $x = 0$ is stable, and there are two unstable equilibria at $x^* = \pm\sqrt{-r}$. For $r > 0$ the equilibrium at $x = 0$ is unstable. It is important to note that the origin is stable for $r < 0$ and unstable for $r > 0$, as in the supercritical case, but now the instability for $r > 0$ is not opposed by the cubic term. The cubic term lends an helping hand in driving the trajectories out to infinity.

The subcritical bifurcation diagram is show in figure 1.16

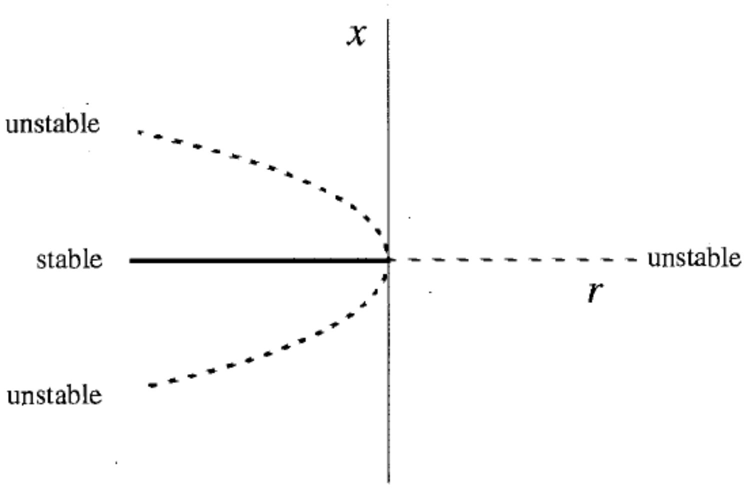


Figure 1.16 Subcritical pitchfork bifurcation for eq. (11).

2. METHODS

In this chapter I will derive a simple competition model to describe wet forests dynamics. The model includes three state variables, the mass density of the hygrophilous species X *(kg* m^{-2}*)*, the mass density of the non-hygrophilous ones Y (*kg* m^{-2}*)* and the soil water content in the rooting zone W *(kg* m^{-2} *or mm).*

The model is spatially implicit this, means that densities are averaged over space, spatial anomalies are not considered and that populations are well-mixed.

2.1 The Model

Growth and functional response of plants to resource availability are generally regarded as the minimum set of factors that should be accounted for in order to explain the observed coexistence of different plant types in forested wetlands (Rodriguez Gonzalez et al., 2010). An abstract dynamic model may therefore take the following form:

$$\dot{X} = F(W)X - k(X+Y)X \tag{12}$$

$$\dot{Y} = H(W)Y - k(X+Y)Y \tag{13}$$

$$\dot{W} = -T_X(W)X - T_Y(W)Y + S(W) \tag{14}$$

where X and Y are the biomass densities (*Kg* m^{-2}*)* of, respectively, the hygrophilous and non-hygrophilous species; W is the soil water concentration (*Kg* m^{-2}*)*; the water-dependent functions F and H are *net growth rates* (yr^{-1}*)* of the hygrophilous and non-hygrophilous species; the term $k(X+Y)$ is the death rate (yr^{-1}*)* due to competition for space, which is proportional to the total biomass, with constant k *(*m^{2} Kg^{-1} yr^{-1}*)*; the water-dependent functions T_X and T_Y (yr^{-1}*)* model the water loss to transpiration per unit biomass; the function S (*Kg* $m^{-2}yr^{-1}$*)* represents the algebraic sum of all biomass-independent sources and sinks of water (e.g. precipitation, percolation, etc.). It is generally reasonable to assume $dS/dW<0$ because some sinks (e.g. percolation) increase their flow rate for increasing soil water content, even if some sources (e.g. precipitation) could be largely independent of it.

This abstract formulation should be thought of as valid within an intermediate range of water concentration. The lower end of this range must be above the permanent wilting point, and the upper end must be below the soil saturation concentration. The model values must also be taken as yearly averages, and are not representative of conditions that may occur for shorter times (such as extreme or anomaly events). Outside the validity range of the model, even if the equations remain mathematically well-posed, other biological and ecological factors, which are neglected here, step into the picture. Therefore the model will not yield believable results in arid or permanently swampy environments.

The hygrophilous species' net growth rate F is assumed to be a growing function of soil water concentration W: it attains its highest value at the upper end of the water concentration interval, and its lowest value at the lower end of the interval. The net growth rate H of the non-hygrophilous species is assumed to be a growing function of W only up to some intermediate value of water concentration. For larger water concentrations it either decreases, or, at least, it doesn't increase as rapidly as *F*.

These assumptions are suggested by the dual role of water as a resource and stress factor. In order to better understand this different water responses it is convenient to express the net growth rates as the sum of two terms, that I shall call *growth rates (f, h)* and *mortalities (m,n)*.

$$F(W) = f(W) + m(W) \tag{15}$$

$$H(W) = h(W) + n(W) \tag{16}$$

The growth rates *f* and *h* model the metabolic growth processes of plants. They are monotonically growing functions of the soil water content, and saturate at high water levels. An explicit expression for *f* and *h* may be given by Michaelis-Menten functions (also known as *Hollings Type I*)

$$f(W) = g_x \frac{W}{W + W_X}; \qquad h(W) = g_Y \frac{W}{W + W_Y}; \tag{17}$$

where g_x *and* g_y are the maximum growth rate, attainable in completely idealized conditions. The coefficient W_X and W_Y are half-saturation constants.

In the introduction we have defined non-hygrophilous species as drought-resistant due to their capability to increase the water use efficiency, i.e. the ratio between plant growth and water lost, as the soil dries. Schulze (2005) reports the metabolic activity of plants in relation with water, his work shows that species which assimilate large quantities of CO_2 are less stress tolerant (figure 2.1). In those plants, CO_2 assimilation decreases with very little soil drying. In contrast species with low rates of CO_2 assimilation usually are able to endure drought stress to a a greater degree. Therefore, although we expect those coefficients to be numerically close to each other, we may generally assume $W_X > W_Y$ to define a different water range for growth optimality, and $g_x \geq g_y$ to single out the different maximum assimilation rates.

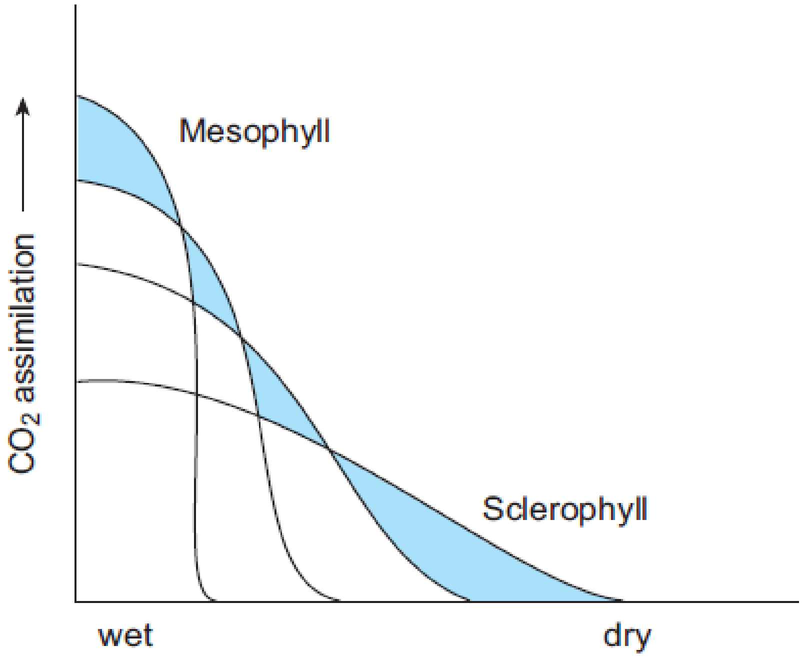


Figure 2.1 The dependence of CO2 assimilation on soil water content for different functional plant types that are sensitive or resistant to drying. Sensitive types have a much higher rate of CO2 assimilation that resistant types when water is abundant (from Schultze, 2005)

The water-dependent mortality functions *m* and *n* have distinct behaviour for the two species. For the hygrophilous species, the scarcity of water is a stress. Therefore we will take *m* as a monotonically decreasing function of *W*. For the non-hygrophilous species is the opposite holds: too much water is a stress factor. Therefore we take *n* as a monotonically growing function of W . Below we shall use simple rational functions to express mathematically m and n.

$$m(W) = \frac{aW_\phi + bW}{W_\phi + W}; \qquad n(W) = \frac{cW_\theta + dW}{W_\theta + W}\ ; \tag{18}$$

Where the coefficients W_ϕ and W_θ are expresses in *Kg m*$^{-2}$; the coefficients a, c, and b, d (formally the water-induced mortalities of the hygrophilous and non-hygrophilous species, respectively, in the limit $W \to 0, W \to \infty$) are in *yr*$^{-1}$;

Figure 2.2. summarizes graphically the water-dependent growth and mortality functions of the model. Note that the curves representing the net water-dependent growth rates F and H may or may not meet within the model validity region, depending on the physiological properties of the species being modelled.

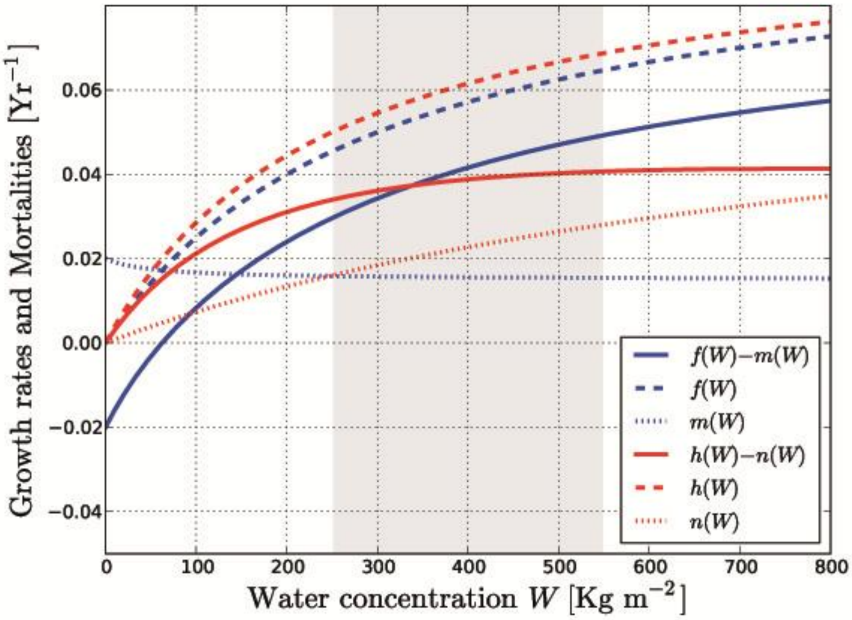


Figure 2.2. Water-dependent growth and mortality rates as in equations (1-7). Blue and red lines refer to the hygrophilous and non-hygrophilous species, respectively. The grey shaded area is the validity range of the model. Dashed lines are the growth rates, assumed to be proportional to transpiration; dotted lines are mortalities; solid lines are the resulting net growth rates $F(W)=f(W)-m(W)$ and $H(W)=h(W)-n(W)$. The parameter values used to draw the figure are: $g=0.1\ Yr^{-1}$, $W_x=250\ Kg\ m^{-2}$, $W_y=300\ Kg\ m^{-2}$, $a=0.02\ Yr^{-1}$, $b=0.075\ Yr^{-1}$, $c=0\ Yr^{-1}$, $d=0.015\ Yr^{-1}$, $W_\theta=90\ Kg\ m^{-2}$, $W_\phi=920\ Kg\ m^{-2}$.

Competition for space is modeled by a water-independent death term, proportional to the total biomass. Of course, the last term in equations (12) and (13) disregards completely a large number of complicated ecologic interactions which may be possible among plants. However, at least as a working hypothesis, it is best to assume that the mere crowding of the forest is the dominant factor affecting the death of trees. Note that, if the water concentration W is externally kept fixed, and one of the two plant species is absent (i.e. $Y=0$ or $X=0$), the equation for the other reduces to a logistic equation with carrying capacity $F(W)/k$ or $H(W)/k$. For simplicity, we keep the same coefficient k for both the hygrophilous and the non-hygrophilous species. This choice appears to be appropriate in the case study that we present in section 2.2. If necessary, distinct coefficients may be used, with minimal adjustments to the mathematical analysis presented below.

There is a strong correlation between the growth of plants and their transpiration (Brian and Hicks, 1982) The exact functional form linking the growth rate and the flux of transpired water is unknown, although there is evidence that it changes among different species, at different life stages of the plants, and that it is affected by the local climate (Law et al., 2001, Donovan et al., 1991). However, experimental data for midlatitude forests show that a simple proportionality should be a reasonable approximation (Law et al., 2001; Yu et al., 2008, Brian and Hicks, 1982). Therefore we have, for suitable coefficients, α, β *(dimensionless)*

$$T_X(W) = \alpha f(W), \qquad T_Y(W) = \beta h(W) \tag{19}$$

The transpiration rates in response to water variations can be thought of as a necessary cost associated with the metabolic growth. Because of the different strategies for water use efficiency, that cost is not the same for the two species: non-hygrophilous (or drought-resistant) species show lower transpiration rates than hygrophilous species both in drought and in wet conditions. In drought conditions, resistant species are able to control stomata better than sensitive ones: this allows them to achieve relatively high photosynthetic rates with transpiration rates lower than their hygrophilous competitors (Schulze, 2005; Van der Molen et al., 2011; Brian and Hicks, 1982). In the presence of abundant water, hygrophilous species reach photosynthetic rates higher than those of resistant species, but at the expense of higher transpiration rates (Rodriguez Gonzalez et al., 2010; Schulze, 2005; Brian and Hicks, 1982). Therefore we shall assume that $\alpha > \beta$.

The only source of water in the model is precipitation, p , assumed to be constant. According to the observational evidence for midlatitude forests (Schulze, 2005; Reichstein et al., 2003), there also exist a non-negligible average evaporation rate e that is independent of plant transpiration. Finally we take the flux of water lost to deep percolation as proportional to the water concentration in the soil, with proportionality constant q. Therefore, the biomass-independent sources and sinks term S assumes the form

$$S(W) = p - e - qW \tag{20}$$

With the modelling choices discussed above (4-9), the model equations become

$$\dot{X} = g\frac{W}{W + W_X}X - \frac{aW_\phi + bW}{W_\phi + W}X - kX(X + Y) \tag{21}$$

$$\dot{Y} = g\frac{W}{W + W_Y}Y - \frac{cW_\theta + dW}{W_\theta + W}Y - kY(X + Y) \tag{22}$$

$$\dot{W} = P - \left(\alpha g\frac{W}{W + W_X}X + \beta g\frac{W}{W + W_Y}Y\right) - e - qW \tag{23}$$

where the parameter's definition and units are listed in table 2.1

Parameter or process	**Description**	**Unit**
g	Relative growth rate	Yr^{-1}
W_X, W_Y	Half saturation constant	Kgm^{-2}
a, c	X and Y's mortality in the limit in which W tends to 0	Yr^{-1}
b, d	X and Y's mortality in the limit in which W tends to ∞	Yr^{-1}
W_ϕ , W_θ	Coefficients that determine the shape of mortalities curve	Kgm^{-2}
k	Death rates due to space competition,	$m^2\ Kg^{-1}\ Yr^{-1}$
p	Precipitation	Kgm^{-2}
α, β	X and Y's max transpiration rates	*(dimensionless)*
e	Soil evaporation	Kgm^{-2}
q	Average Deep Percolation	$Kgm^{-2}Yr^{-1}$

Table 2.1 Model parameters

2.2 Comparison with observations

In order to calibrate the model, I have fitted the parameters with the available experimental data measured at two Mediterranean plain forests of Central Italy (Circeo National Park and Presidential Estate of Castelporziano) assuming, for simplicity, that those ecosystem are at equilibrium state. The goal of this analysis is twofold: on one hand, it shows that the model is able to describe the coexistence of hygrophilous and non-hygrophilous species in a way which is coherent with the observed state of the forest ecosystem; on the other hand, it gives a quantitative tool for assessing the resilience of states of coexistence to climate change.

All parameters have been determined, either directly or indirectly, from available data in literature, referring to year-averaged quantities. Due to the experimental uncertainties, some parameters can only be roughly estimated, while others allow for a precise fit.

However, it should be noted that, generally, the results of a such theoretical model, based on initial qualitatively assumption and with secondary neglected factors, are unlikely to be accuracy comparable with empirical observations. Rather what we expect is a good agreement with the orders of magnitude and the range within which these processes vary for different imposed conditions

2.2.1 Observations on Mediterranean plain forest

Observational data about Mediterranean coastal plain oak forests can be summarized in the following points: (i) deciduous species generally show cavitation at higher soil water content than the evergreen (Tyree and Cochard, 1996) which makes them more vulnerable to drought stress (figure 2.3); (ii) oaks vary their leaf area index, adjust their stomatal openings, and extend their root system to tap groundwater in such a way as to ensure that evaporation is less than the water supply (Baldocchi and Xu, 2007); This will be the reason why climatic change will be introduced in the model by modifying the soil water supply, i.e. changing difference *p-e* rather than the potential transpiration ratios α and β; (iii) forest conenoses distribution is closely related to micro-geomorphological conditions of soil and water. In these areas the water availability has been identified as the major factor shaping vegetation distribution and controlling plant functions (Presti et al., 1998; Rambal, 2011). According to what I have shown in section 1.1.1, I define the deciduous species as the Hygrophilous competitors while the evergreen will represent the non-hygrophilous ones. Now let's have a look at a range in the model parameters that enable model to qualitatively reproduce all the three points of section 2.2.

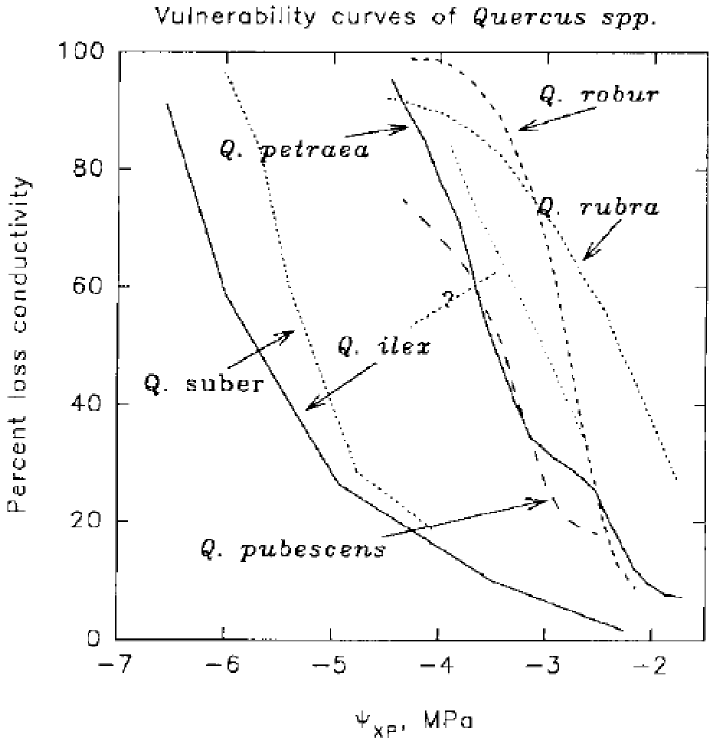


Figure 2.3. Vulnerability curves for six species of oak. X-axis is the xylem pressure potential needed to induce the percent loss hydraulic conductivity on the Y-axis (from Tyree and Cochard, 1996)

2.2.2 Model parameterization

The model has 15 parameters. So it would take at least 15 independent data.

Due to the lack of sufficient data, some parameters were calibrated according to the expected orders of magnitude and according to some assumptions delivered *a priori*.

2.2.2a Independent Constraints

POTENTIAL GROWTH RATES

The potential growth rate, g, was obtained from the national yield table (Castellani, 1970) which data report the relative increase recorded for a large number of forest species. The data supported the choice of setting the value of g_x and g_y equal for all species involved (Q. *Ilex*, Q. *cerris*, Q. *Robur*), i.e. to $0.1\ yr^{-1}$.

For simplicity I will use the simplest notation:

$$g = g_x = g_y$$

TRANSPIRATIO RATIOS (α *and* β)

The maximum transpiration rate is the maximum rate of water loss from plants and can be thought of as a necessary "cost" associated with the opening of the stomata to allow the diffusion of carbon dioxide gas from the air for photosynthesis. The amount of water lost by a plant depends on its size, along with surrounding light intensity (Debbie and Hogan, 2010), temperature, humidity, and wind speed (all of which influence evaporative demand). Soil water supply and soil temperature can influence stomatal opening, and thus transpiration rates (Van Der Molen et al., 2011). In the model α and β represent the transpiration ratio, i.e. the mass of water transpired to the biomass produced, that, for simplicity, I suppose to be constant and homogeneous.

I assign them a value by taking into account the constraint that non-hygrophilous species have about 25-30% higher water use efficiency than hygrophilous ones (see figure 2.4) (Beer et al., 2009, Baldocchi et al., 2010, Tognetti et al., 1998, Kazda et al., 2000), and the work of Vitale et al. (2003) that simulate the effects of temperature increase on net primary production and total canopy transpiration in the Holm oak forests of Castelporziano (annual transpiration of 207 Kg $m^{-2}yr^{-1}$ and 284 Kg $m^{-2}yr^{-1}$ with, respectively, average annual air temperatures of 14.6 °C and 18.0 ◦C)

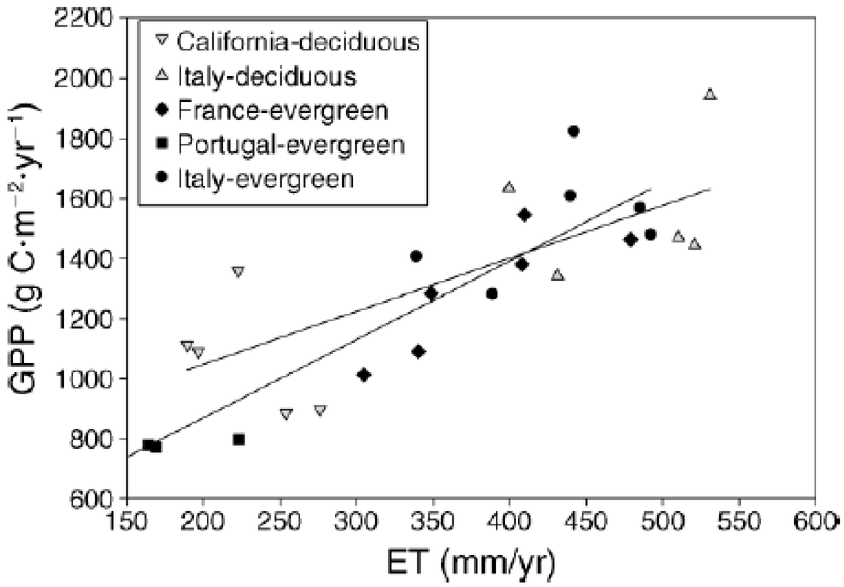


Figure 2.4. The relationship between evaporation and gross primary productivity. The slope is 1.76 ± 0.55 gC m^{-2} mm^{-1} ($r^2 = 0.55$) for the deciduous oaks and 2.61 ± 0.31 gC m^{-2} mm^{-1} ($r^2 = 0.83$) for the evergreen oaks (from Baldocchi et al., 2010)

CLIMATE *(p and e)*

Precipitation and soil evaporation are initially considered as constants. Their values are readily available from literature (Baldocchi et al., 2007; Pezzotta, 1998; Manes et al., 1997). They also represent the exogenous driving forces capable of disrupting the system and eventually shift its equilibria. Because one of our main goals is to identify the climate conditions that preserve the coexistence, these parameters will be made to vary within a range of possibilities according to the future climate scenarios available for the Mediterranean basin (EEA; Giorgi and Lionello, 2008; Ulbrich et al., 2006). However, for the firsts numerical simulation, I set the precipitation equal to 780mm yr^{-1}, that is the average annual rainfall of Castelporziano site (Baldocchi et al., 2010; Manes et al., 1997).

To quantify the magnitude order of expected increase of evaporation, I have fitted the average climate data of the Agropontino region for the last ten years with the *Penman-Montheit* equation. My aim is to outline an evapotranspiration-temperature relationship that is meaningful for the local climate, since a precise relationship would be difficult to estimate, neither serves for the purpose of this study. Data were retrieved from the UCEA database, available online, for the Borgo San Michele Station. The slope of the inferred relationship, depicted in Figure 2.5, is equal to

4.76. The current average annual temperature of Castelporziano is 14,6°C (Manes et al., 1997).

Based on both this information and considering two different climate scenarios provided by CIRCE project for the next 40 years, I esteemed the corresponding increasing of annual evapotranspiration. At the same time, considering an average annual rainfall of 780mm, I calculate the corresponding change in precipitation. Table 2.2 summarizes the expected climate scenarios in the Mediterranean expressed in millimetres per year equivalent.

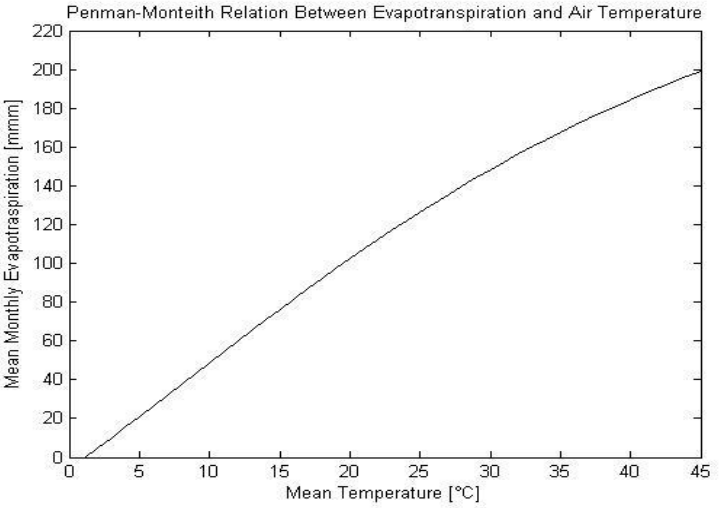


Figure 2.5. Increased potential evapotranspiration with mean air temperature. The correlation has been calculated on ten years of climate data for the Agropontino resort.

Parameter	CIRCE project scenario	Corresponding variation
Temperature	+Δ2°C 40yr^{-1}	+0.24mm/yr
	+Δ4°C 40yr^{-1}	+0.47mm/yr
Precipitation	-5% 40yr^{-1}	-1mm/yr
	-10% 40yr^{-1}	-2mm/yr

Table 2.2. Expected climate scenarios in the Mediterranean expressed in millimetres per year equivalent.

QUADRATIC MORTALITY (k)

The quadratic mortality terms in equations (12-13), which represent the competition for space, set the time scale with which the system reacts to perturbations on total biomass. Based on the data in (Bernetti, 1995) on the recovery time after cuts I estimate $k(X+Y)^{-1} \approx 30yr^{-1}$, which gives a first guess of the value of k . That value is then tuned in such a way that the model reproduces the observed total forest biomass of the study areas (about $6.45\ Kg\ m^{-2}$ according to the National Forest Inventory Database).

OTHER INDIPENDNET CONSTRAINS

From the National Forest Inventory Database I derived also the metabolic growth rate of the whole ecosystem, equal to 2.8-4% (yr^{-1}) The items chosen are *Hygrophilous* and *Oak woods* of Lazio.

In this model the Net Forest Growth Rate, i.e. $F(W)+H(W)$ of eq.(12,13), represents the woody expansion or contraction year by year. A positive Net Forest Growth Rate can be roughly compared to the forest productivity or current yield.

During the parameter assignment, I define the range of increasing biomass keeping into account both the data recorded by the national forest inventory database *(arboreal phytomass* growth rate of $0.18\text{-}0.26\ yr^{-1}$) and the results on productivity estimations obtained for Castelporziano site by Vitale et al (2003) through of an ecophysiological model ($5.09\ tC\ ha^{-1}yr^{-1}$), by Tirone et al. (2000) and Baldocchi et al. (2001) through measurement using eddy covariance technique (*5.72 and 6.6* $tCha^{-1}yr^{-1}$, respectively) and by Tirone et al. (2001) using destructive sampling ($4.95\ tCha^{-1}yr^{-1}$), all approximately equivalent to a growth rate of 0.15-0.18 yr^{-1}.

Finally, from the FLUXNET (Baldocchi et al., 2001) database I obtain the average annual soil water content of Castelporziano site, equal to 37% vol (ie. about 370 Kgm^{-2}), available for the last 10 years. Table 2.3 summarizes the observational constraints that I have used to infer the value of the model parameters.

Independent constraints	Description	Range or Value	Reference
$X+Y$	Total Biomass Density, Kgm^{-2}	6.45	Infc
$f(W)X+h(W)Y$	Total Forest Growth Rate, $Kgm^{-2}Yr^{-1}$	0.15-0.26;	Infc; Baldocchi et al., 2010;
$m(W)X+m(W)Y$	Total Forest Mortality Rate, $Kgm^{-2}Yr^{-1}$	0.12-0.18	[Infc]
$T_X(W)X+T_Y(W)Y$	Total Forest Transpiration, $Kgm^{-2}\ Yr^{-1}$	200-300	[Vitale]
ETa	Mean annual Evapotraspiration $Kgm^{-2}\ Yr^{-1}$	410-450	Baldocchi et al., 2010;
W	Soil Water content $Kgm^{-2}\ Yr^{-1}$	300-400	Fluxnet
p	Precipitation $Kgm^{-2}\ Yr^{-1}$	740-820	Reichstein et al., 2003; Baldocchi et al., 2010; Manes et al., 2007; Vitale et al., 2003
e	Soil evaporation (ET_O-ETa) $Kgm^{-2}\ Yr^{-1}$	250	Baldocchi
g	Max growth rate	0.1	Castellani, 1970

Table 2.3 Indipendent constraints

2.2.2.b Uncertain parameters

In this paragraphs, due the scarcity or the total absence of some basic data needed for model calibration, I use hypothesis and numerical simulations to assign values to the remaining parameters that, overall, best represent the actual features of the oak plain forest of Central Italy.

PLANTS MORTALITY ($m(W)$ and $n(W)$)

Understanding of how droughts or root anoxia kill trees is surprisingly limited (Van Der Molen et al., 2011). The representation in current vegetation models tends to be very crude, with assumed constant mortality rates (Allen et al., 2010), unless climate-induced disturbances are explicitly accounted for. Adams et al., (2009) and Van Der Molen et al., (2011) reviewed a series of studies about the effect of drought on mortality in different forest systems. Overall it appears that the effects of drought on tree mortality rate under warmer conditions increased by as much as 2-5 times, i.e.

ca. *1%* yr^{-1} to *2-5%* yr^{-1}. Some previous studies assume that tree mortality could range in intensity from background (*<5%* yr^{-1}) to catastrophic (*>5%* yr^{-1}) (Lugo e Scatena, 1996). Conversely, observations on the mortality rates due to radical anoxia for woody areas and/or at the regional scale are absent in literature. In our case study plants known as flood-tolerant are *Fraxinus oxicarpae* and *Quercus robur*. These plants can survive periods of submergence of the soil between 3 and 4 months (Gellini and Grossoni, 1997; Glenz et al., 2006). Flood tolerance varies greatly with plant species and genotype, rootstock, age of plants, time and duration of flooding, and condition of the floodwater (Kozlowsky, 1997). Furthermore sensitivity to flooding also varies among closely related woody plants (Kozlowsky, 1997). For simplicity, we consider only the average duration of flooding that is the resident times of vernal pools that characterize the small basins or depressions in the terrain of the studies areas, varying from 2 to 4 months a year during the late winter-early spring.

Because of parameters of mortality functions $m(W)$ and $n(W)$ are the most difficult to calibrate due their complexity, I propose three different calibration for both the mortality function. Each of this calibrations represent a water-dependent mortality hypothesis that I define, respectively, of *low*, *medium* and *high* impact. The aim of this approach is to be able to assign *a priori* a certain incidence of mortality to the species according to their relative sensitivity to water stress.

	Hygrophilous Species		**Non Hygrophilous Species**		**Mortality Hypothesis**
	Parameters	*Values [yr*$^{-1}$*]*	*Parameters*	*Values [yr*$^{-1}$*]*	
Min mortality rate	b	0.015	c	0.0	
Max mortality rates	a	0.02	d	0.05	***Low***
		0.05		0.075	***Medium***
		0.10		0.10	***High***
Shape	W_{ϕ}	50	W_{θ}	920	

Table 2.4. Parameters for different calibrations of mortalities curves.

Therefore, for both functions, I assumed an intrinsic mortality rates of 1% and, at the same time, I assigned three different possible maximal mortality rates, a and b, respectively equal to 2%, 5% and 10% for the Hygrophilous species and 5%, 7,5% and 10% for the Non-Hygrophilous ones. (Table 2.4).

Mathematically, the parameters W_ϕ and W_θ fix the shape of the curves and their values should be thought, respectively, as the effects of the wilting point constant and the soil saturation water content.

Knowledge on the flood-induced mortality is related to the maximum time of plant resistance to soil submergence. Generally wood plants known as flood-tolerant can survive periods of submergence of the soil from 1 to 3 months (Glenz et al., 2006). The submersion of the soil corresponds to a critical situation in which all the soil's pores are filled up by water. Therefore, the soil is considered to be flooded whenever its water content exceeds the saturation value. Generally, soil saturation is considered as a soil propriety constant (Giordano, 1999). It varies into the small range of 40-50% of the total volume, according to the soil texture (Figure 2.6).

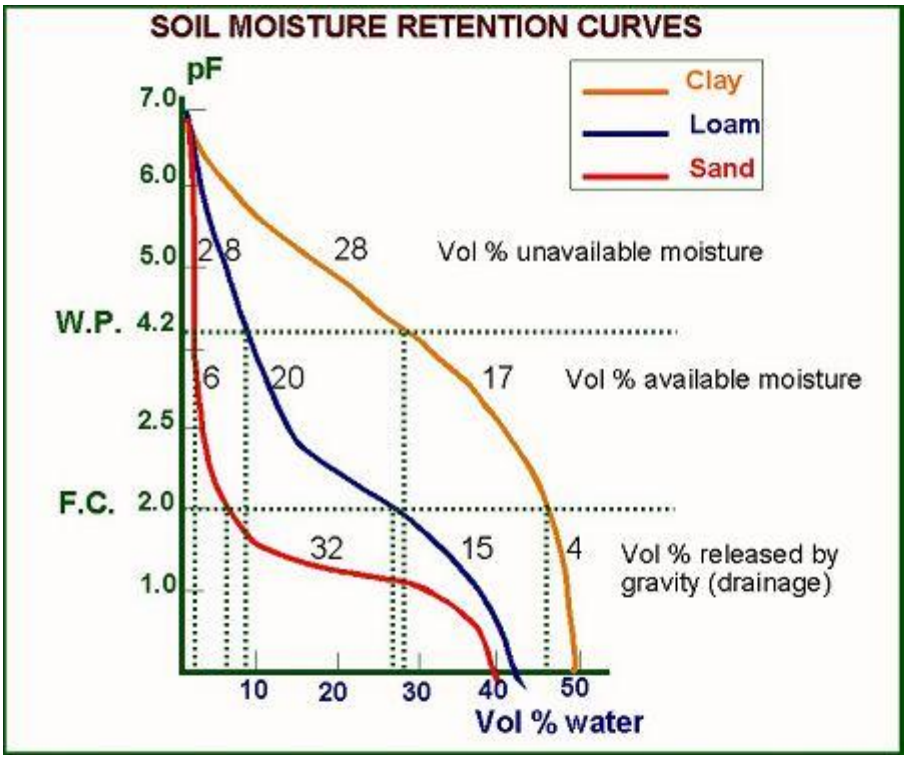


Figure 2.6. Soil Moisture retention curve for three different type of soil texture. W.P.= wilting point; F.C.= filed capacity. (from Giordano, 1999)

Because of the study areas of present work are generally characterized by sandy silt-sandy soils (Manes et al., 1997) I assigned a soil saturation equal to 46% in volume (i.e. about 460 Kg m^{-2}). Similarly, it is reasonable to consider a critical wilting point changing from 5% into silt sandy-loam soils to up 30% into clay soils. Generally, the wilting points corresponds to a soil water tension of about 1500 KPa (Giordano, 1999), that is the critical osmotic pressure for most of the plants of agricultural interest. For the interest of this work I have assigned a value of wilting point equal to 10% of total volume.

It should be noted that the values of soil saturation and wilting point, which determine the shape of the curves, are constants that depend closely to the specific site where the model is applied. These values can therefore be reasonably set by knowing the chemical and physical characteristics of the soil.

Therefore, the whole calibration for each mortality function, shown in Figure 2.7, are calibrated according to for both soil physical properties (that determine the shape of the curves) and different mortality rates hypothesized.

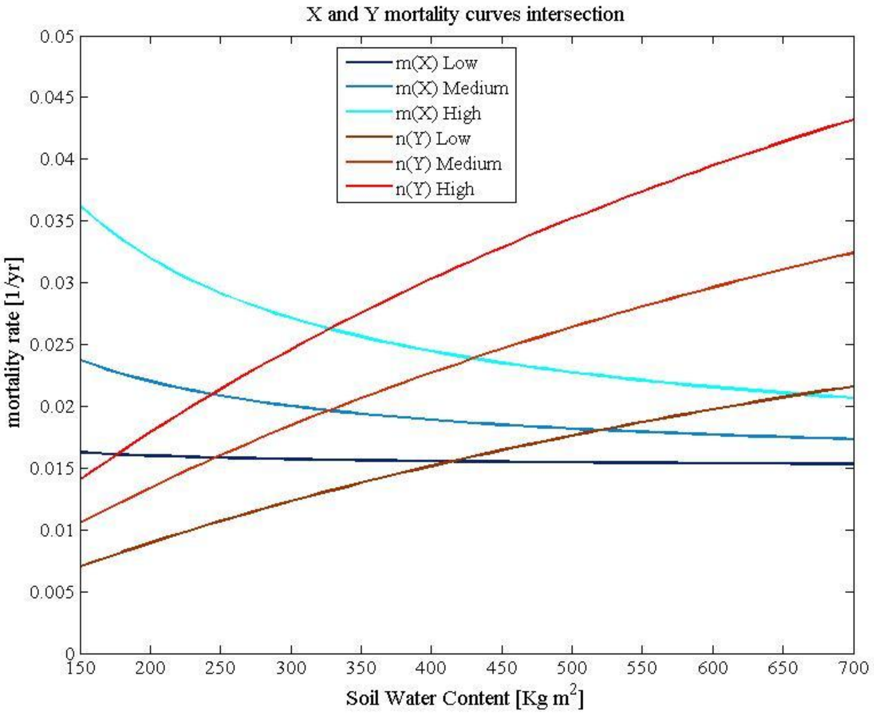


Figure 2.7 Three different calibration for mortality curve for both Hygrophilous (blue lines) and non-hygrophilous (red lines) species. The graph shows the possible intersections of different mortality rates within the investigated water range.

HALF SATURATION CONSTANTS *(W_X and W_Y)*

Holling curves are saturation functions between 0 and 1 that correct the growth rate from potential (*g*) to real as a function of the explicit limiting resources, namely water.

The half-saturation constants W_X and W_Y, mathematically, represent the soil water content for which the growth rates of the two species reached half of their potential.

The valued of W_x and W_y should reasonably ranged between the wilting and saturation point equal to 50-550 Kgm^{-2}.

This kind of information can be found only in plants and organisms to rapid life cycle on which it was possible to conduct laboratory experiments under controlled conditions. In the absence of this information, even necessary, the two constants will be extracted from numerical simulations to obtain the actual forest growth rate, with the only constraint that $Wx > Wy$.

2.2.2c Numerical simulation looking for coexistence

Running the model with three distinct mortality sets for each species, nine possible couplings are obtained. Each of these couplings have been explored by assigning two distinct reasonable half-saturation constants for each species (Figure 2.8)

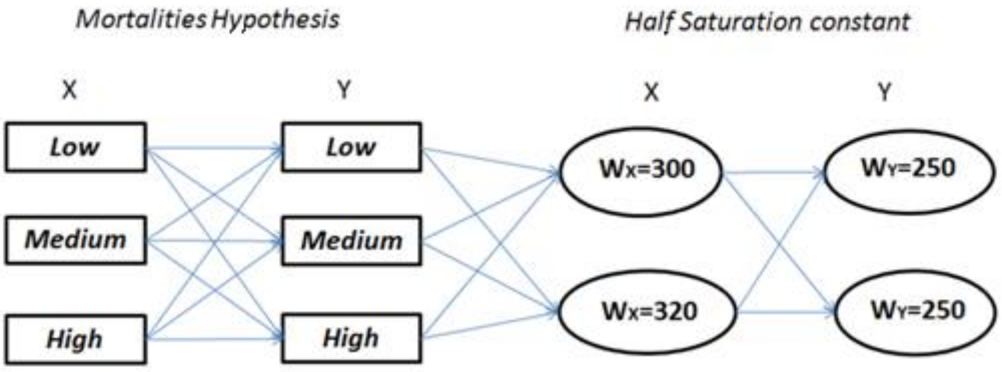


Figure 2.8 Combinations of mortality and competitiveness investigated with numerical simulations.

Among the all possible coupling simulations of figure 2.8, only two different pairs of hypothesis of mortality, even if with different combination of half saturation constants, allow for coexistence: *low* for *X* species and *medium* for *Y* species match;

high for both species match. For simplicity I will call the two mortality combination, respectively, as *low-med* and *high hypothesis.*

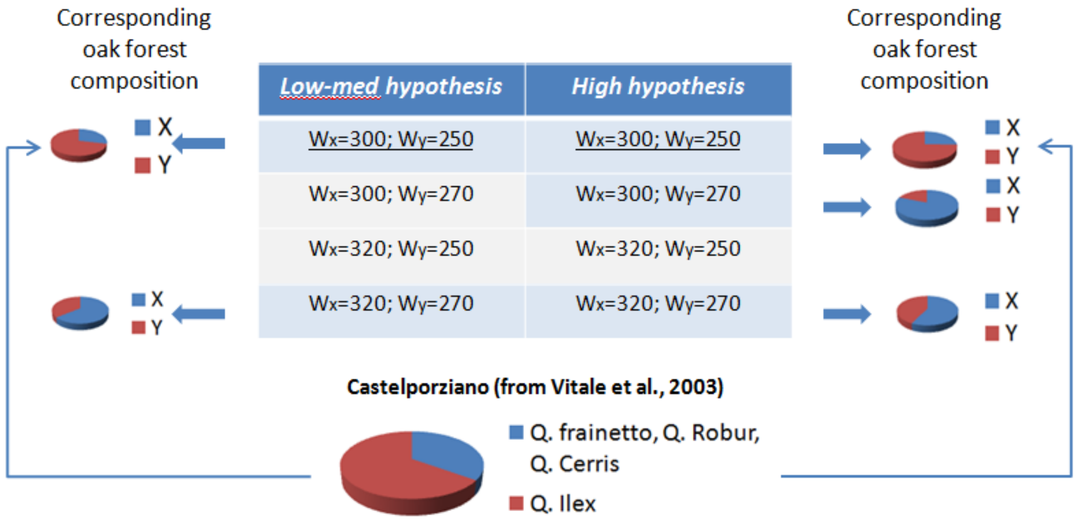
Table 2.6 shows the values obtained at equilibrium by numerical simulations of the three state variables (*X, Y, W*), total biomass (*X+Y)* and the percentage of the non-hygrophilous species respect to the total biomass only for the numerical simulations that return a stable coexistence.

Each simulation reproduces reasonable results for each state variable. In particular, the equilibrium value of the soil water content is always included into a relatively narrow range of 330-380 Kg m^{-2} which is consistent with the actual annual average of 370 Kg m^{-2} measured in the last 10 years near eddy covariance station of Castelporziano.

	Half-saturation constant setting	W [Kg m^{-2}]	X [Kg m^{-2}]	Y [Kg m^{-2}]	X+Y [Kg m^{-2}]	% of Y
Low-Medium mortalities	**Wx=300, Wy=250**	337,87	1,95	4,84	6,78	**71**
	Wx=320, Wx=270	331,98	4,10	2,31	6,41	36
High mortalities	**Wx=300, Wy=250**	381,10	1,43	4,22	5,65	**75**
	Wx=300, Wy=270	358,11	4,28	1,00	5,28	19
	Wx=320, Wy=270	337,83	3,05	2,26	6,31	36

Table 2.6. Fixed point of state variables and corresponding total forest biomass for the different combination that allows for coexistence. Those in bold are consistent with the data of Castelporziano

Looking to Castelporziano site where more data are available, I chose the settings for both the half-saturation constants and mortalities hypothesise that best fit the actual composition of Castalporziano site (figure 2.9). Vitale et al. (2003) argues that the oak forest of Castelporziano is characterized by 60-70% by *Q. Ilex* witch percentage is well represent by setting *Wx=300* and *Wy=250* for both the mortality hypothesis.



Low-med hypothesis	*High hypothesis*
Wx=300; Wy=250	Wx=300; Wy=250
Wx=300; Wy=270	Wx=300; Wy=270
Wx=320; Wy=250	Wx=320; Wy=250
Wx=320; Wy=270	Wx=320; Wy=270

Figure 2.9 Model Simulation biomass output for both different hypothesis of mortality and different half saturation constant sets. The best fit chosen are those who reproduce the actual forest composition of Castelporziano site.

Now all parameters have a corresponding assigned value. Table 2.7 summarized the whole information about model parameters and constraints.

Parameter or process	**Description**	**Assigned Value**	**Reference**
g	relative growth rate, Yr^{-1}	0.1	INFC
W_X, W_Y	half saturation constant, Kgm^{-2}	300; 250	Calibrated according to INFC
b, c	X and Y's mortality in the limit in which W tends to 0, Yr^{-1}	0.015; 0.00	Calibrated according to (Van Der Molen et al., 2011; Adams et al., 2009; Gellini and Grossoni, 1997; ,Glenz et a., 2006).
a, d	X and Y's mortality in the limit in which W tends to ∞, Yr^{-1}	(Low-med) 0.020; 0.075 (high) 0.1; 0.1	Calibrated according to (Van Der Molen et al., 2011; Adams et al., 2009; Gellini and Grossoni, 1997; ,Glenz et a., 2006).
W_ϕ , W_θ	coefficients that determine the shape of mortalities curve, Kgm^{-2}	50; 920	Calibrated according to (Manes et al., 1997; Giordano, 1999)
k	death rates due to space competition, Yr^{-1}	0.0055	Calibrated according to (Bernetti, 1995)
p	Precipitation, Kgm^{-2}	780	(Baldocchi et al., 2010; Manes et al., 1997)
α, β	X and Y's max transpiration rates (dimensionless)	900; 600	(Beer et al., 2009, Baldocchi et al., 2010, Tognetti et al., 1998, Kazda et al., 2000; Vitale at al., 2003)
e	soil evaporation, Kgm^{-2}	250	(Baldocchi and Xu, 2007)
q	percolation factor (dimensionless)	0.8	Calibrated according to (Baldocchi et al., 2001)
$X+Y$	Total Biomass Density, Kgm^{-2}	6.45	INFC
$f(W)X+h(W)Y$	Total Forest Growth Rate, $Kgm^{-2}Yr^{-1}$	0.18-0.26;	INFC; Vitale et al., 2003; Tirone et al., 2000; Tirone et al., 2001; Baldocchi et al., 2001;
$m(W)X+m(W)Y$	Total Forest Mortality Rate, $Kgm^{-2}Yr^{-1}$	0.12-0.18	INFC
$T_X(W)X+T_Y(W)Y$	Total Forest Transpiration, Kgm^{-2} Yr^{-1}	207-284	Vitale et al., 2003

Table 2.7. Assigned values and References of model's parameters.

3. RESULTS AND DISCUSSION

In this section I will identify the equilibria of the system and outline the conditions for their stability, determining the bifurcation points for changing climatic inputs.

Each results is carried out for Castelporziano site and for both *low-med* and *high* mortality hypothesis. The results obtained are discuss and some considerations are carried out.

3.1 Equilibria

The model embodied by equations (12-14) allows for more than one equilibrium, that is, for more than one triplet $(X_0 Y_0 W_0)$ corresponding to zeros of the expressions on the right-hand side. Once an equilibrium has been found, linear stability analysis may be used to determine whether, upon a small external perturbation, the system will return to equilibrium or not.

Local stability analysis can be determined by a standard mathematical method (see section 1.5). Briefly speaking, in the present case study, all the water-dependent highly nonlinear functions that appear in the eqs. (12-14) are first linearly expanded ,by a *Taylor's expansion trounced to the first order,* around the water equilibrium point, *W₀*, to obtain an linearly approximate system, which describes the dynamics in proximity of the equilibrium.

$$\dot{X} = [F_0 + F_0'(W - W_0)]X - k(X + Y)X \tag{24}$$

$$\dot{Y} = [H_0 + H_0'(W - W_0)]Y - k(X + Y)Y \tag{25}$$

$$\dot{W} = -[T_{x0} + T_{x0}'(W - W_0)]X - \left[T_{y0} + T_{y0}'(W - W_0)\right]Y + p - e - qW \tag{26}$$

With, for notational simplification

$$F_0 = F(W_0); \qquad H_0 = H(W_0); \qquad T_{x0} = T_x(W_0); \qquad T_{y0} = T_y(W_0);$$

$$F_0' = \frac{dF}{dW}(W_0); \quad H_0' = \frac{dH}{dW}(W_0); \qquad T_{x0}' = \frac{dT_x}{dW}(W_0); \qquad T_{y0}' = \frac{dT_y}{dW}(W_0);$$

Then, the eigenvalues and eigenvectors of the corresponding Jacobian matrix at W_0 are calculated. The approximate equations (24-26) greatly simplify the study of the stability of equilibria. In the follow subsection, I will show the states allowed by the system.

3.1.1 Instability of the state with no vegetation

For any choice of the parameters, as long as $S(W) = p - e - qW,$ with $q \neq 0$, the model always has the trivial equilibrium

$$(X_0, Y_0, W_0) = (0, 0, (p-e)/q)\ . \tag{27}$$

The Jacobian matrix of equations (24-26) evaluated at the equilibrium (27) is

$$J_0 = \begin{pmatrix} F_0 & 0 & 0 \\ 0 & H_0 & 0 \\ -T_{x0} & -T_{y0} & -S_0' \end{pmatrix}$$

Where I have taken $S'(W_0) = S_0' = -q,$ coherently with (20). In this case the eigenvalues coincide with the entries on the main diagonal.

Generally we expect $S_0' < 0$ which means that the loss of soil water (e.g. through percolation) increases when the soil water concentration increases.

Therefore, recalling that the equilibrium is linearly stable when all the eigenvalues have negative real part, and it is unstable when at least one of them has a positive real part, this fixed point is unstable to infinitesimal perturbations if

$$F_0 > 0 \qquad \text{or} \qquad H_0 > 0 \tag{28}$$

that is, if the water-dependent growth rate of at least one of the two species is positive, the state with no vegetation is unstable.

3.1.2 Single Species

For biologically meaningful choices of the function F, H, T_X, T_Y and S, there are two fixed points, one with Y=0 , the other with X=0. The first, that I will call *Hygrophilous Equilibrium*, occurs setting Y=0 in eq.(12-14). By substitution the system will lead to the following simplest equations:

$$F(W_0)X - kX^2 = 0 \tag{29}$$

$$S(W_0) - T_X(W_0)X = 0 \tag{30}$$

With X_0 roots equal to: $X_{0,1}$=0; $X_{0,2}$=F_0/k. Therefore the *Hygrophilous species* has the following fixed point

$$(X_0, Y_0, W_0) = \left(\frac{F_0}{k}, 0, W_0\right) \tag{31}$$

which is meaningful only if $X_0 > 0$, that is if $F_0 > 0$ and only for some value W_0 of water concentration that admits a solution of the following equation

$$S_0 = \frac{T_{x0}F_0}{k} \tag{32}$$

The Jacobian matrix evaluated at the equilibrium (31) of (24-26) is

$$J_h = \begin{pmatrix} -F_0 & -F_0 & k^{-1}F_0F_0' \\ 0 & H_0 - F_0 & 0 \\ -T_{x0} & -T_{y0} & S_0' - k^{-1}F_0T_{x0}' \end{pmatrix}$$

Recalling the definition of the characteristic polynomial of a square matrix:

$$P(\lambda) = \det\,(J - \lambda I)$$

The cubic characteristic polynomial of J_0 is easily calculated and factored into a first and a second degree polynomial:

$$P(\lambda) = (H_0 - F_0 - \lambda)[\lambda^2 + \lambda(-S_0' + k^{-1}F_0T_{x0}' + F_0) + k^{-1}F_0(-kS_0' + T_{x0}F_0' + T_{xo}'F_0)] \qquad (33)$$

The second degree polynomial has strictly positive coefficients. In fact $F_0 > 0$ is required to have a positive biomass concentration at equilibrium, $T_{xo}', F_0' > 0$ as a result of the assumptions of the assumptions of monotonicity discussed in section 2.1 and $S_0' < 0$ as above. Therefore its two roots have strictly negative real part. The root of the first degree polynomial yields the eigenvalues

$$\lambda_0 = H_0 - F_0$$

Which destabilized the equilibrium if it is positive. Therefore the state with the **hygrophilous species** alone is stable if

$$F_0 > H_0 \qquad (34)$$

i.e. if, at equilibrium, its growth rate is larger than that of the non- hygrophilous species, otherwise it is unstable.

The specular *Non-Hygrophilous Equilibrium*, i.e. the fixed point with *X=0*, occurs if there is a water concentration value W_0 such that

$$S_0 = \frac{T_{y0}H_0}{k} \qquad (35)$$

which yields the equilibrium

$$(X_0, Y_0, W_0) = \left(0, \frac{H_0}{k}, W_0\right) \qquad (36)$$

And which is meaningful only if $Y_0 > 0$, that is if $H(W_0) > 0$.

The analysis is completely specular to the previous one, and the characteristic polynomial is

$$P(\lambda) = (F_0 - H_0 - \lambda)\left[\lambda^2 + \lambda\left(-S_0' + k^{-1}H_0T_{y0}' + H_0\right) + k^{-1}H_0\left(-kS_0' + T_{y0}H_0' + T_{yo}'H_0\right)\right] \quad (37)$$

Similarly to the previous one, this equilibrium is stable if

$$H_0 > F_0 \tag{38}$$

However, looking to the second degree polynomial, the coefficients are not strictly positive because of the sign of H_0' is not known beforehand: *H(W)* could be a decreasing function of W for large values of W. If

$$H_0' < -\frac{H_0 T_{y0}' + kS_0'}{T_{y0}} \tag{39}$$

then the second-degree polynomial has a negative constant term and positive first- and second-degree coefficient. Therefore it has a positive and a negative real root, which implies instability.

A necessary and sufficient criterion for stability in thus obtained for both inequalities (38) and reversing (39).

3.1.3 Coexistence

Equations (12-14), may also have a coexistence equilibrium. It is rather straightforward to observe that if (X_0, Y_0, W_0) is a coexistence equilibrium, then it is

$$F_0 = H_0 \tag{40}$$

In fact, setting $\dot{X} = \dot{Y} = \dot{W} = 0$, eqs (12-14) lead to the following simple case

$$[F_0 - k(X + Y)]X = 0 \tag{41}$$

$$[H_0 - k(X + Y)]Y = 0 \tag{42}$$

from which follows (40).

In other words, the intersection of the net growth rates as in Figure 2.2 is a necessary condition in order to have coexistence. After W_0 has been determined, it is easy to deduct the equilibrium biomass densities of equations (12-14):

$$X_0 = \frac{kS_0 - T_{y0}F_0}{k(T_{x0} - T_{y0})}; \qquad Y_0 = \frac{T_{x0}F_0 - kS_0}{k(T_{x0} - T_{y0})}; \tag{43}$$

Note that this result is trivially extended to the case where the coefficient k is distinct for the two species. In addition, many reasonable choices for mortality term would yield coexistence equilibria. Here we shall not further pursue these generalizations, but we simply observe that the coexistence equilibrium does not appear to be the by-product of an oversimplified modeling of the ecological competition among the two species.

The coexistence equilibrium is biologically meaningful if both X_0 and Y_0 have positive values. This happens if

$$\frac{T_{y0}F_0}{k} > S_0 > \frac{T_{x0}F_0}{k} \qquad if\ T_{y0} > T_{x0} \tag{44}$$

$$\frac{T_{x0}F_0}{k} > S_0 > \frac{T_{y0}F_0}{k} \qquad if\ T_{x0} > T_{y0} \tag{45}$$

Coexistence may hence be possible if the net equilibrium water input S_0 is bracketed between two values which are proportional to the transpiration rates of the X and Y species.

At the coexistence equilibrium, the Jacobian matrix of eqs. (24-26) may be written as

$$J_c = \begin{pmatrix} kX_0 & kX_0 & -X_0F_0' \\ kY_0 & kY_0 & -Y_0H_0' \\ T_{x0} & T_{y0} & Y_0T_{y0}' + X_0T_{x0}' + q \end{pmatrix}$$

The characteristic polynomial of J_c is not easily factored. Although the Cardano-Lagrange formulae would allow to write down explicitly the eigenvalues of J_0 , the resulting expressions are rather unwieldy, and it is not straightforward to determine the sign of the real part of the eigenvalues. Therefore I use an indirect approach. First we observe that the determinant of J_0

$$\Delta_c = -k\left(T_{x0} - T_{y0}\right)(F_0' - H_0')X_0Y_0 \tag{46}$$

Recalling that the determinant is the product of three eigenvalues of J_0, it is clear that a necessary condition for stability is $\Delta < 0$, that is either all eigenvalues negative or one negative and two positive. All the quantities with appearing in the expression above are positive, except for H_c' which may have any sign. However, $(F_0' - H_0') > 0$, because according to the assumptions discussed in section 2.1, we have

$$F(W) < H(W) \qquad for\, W < W_0 \tag{47}$$

$$F(W) > H(W) \qquad for\, W > W_0 \tag{48}$$

Therefore, the necessary condition for stability becomes

$$T_{x0} > T_{y0} \tag{49}$$

that is, the coexistence is unstable (hence unobservable in practice) unless, at equilibrium, the transpiration rate of the hygrophilous species is larger than that of the non-hygrophilous species.

From (19) it follows that the criterion (49) for the complete model equations (21-23) is equivalent to

$$\frac{\alpha}{\beta} > \frac{h(W_0)}{f(W_0)} \tag{50}$$

In order to rule out the case of two eigenvalues both with positive real part, it is necessary to supplement the criterion (13) with an additional inequality. This is accomplished by the use of the Routh-Hurwitz criterion. A review of the criterion is well beyond the scope of this thesis. See Gantmacher (2000) for an exhaustive treatment of the subject, or Otto and Day (2007) for a simple exposition with examples taken from biological problems. In our case, after straightforward but long calculations, it was obtained that the equilibrium is stable if and only if $\Delta<0$ and

$$\begin{aligned} H'_o \quad > \quad & -\left(T_{yo}Y_o^2T'_{yo} + T_{yo}X_oY_oT'_{xo} + kT_{yo}Y_o^2 + kT_{xo}X_oY_o + qT_{yo}Y_o\right)^{-1} \\ & [F'_o\left(T_{xo}X_oY_oT'_{yo} + T_{xo}X_o^2T'_{xo} + kT_{yo}X_oY_o + kT_{xo}X_o^2 + qT_{xo}X_o\right) + \\ & +kY_o^3T'^2_{yo} + kX_oY_o^2T'^2_{yo} + 2kX_oY_o^2T'_{xo}T'_{yo} + 2kX_o^2Y_oT'_{xo}T'_{yo} + \\ & +k^2Y_o^3T'_{yo} + 2k^2X_oY_o^2T'_{yo} + 2kqY_o^2T'_{yo} + k^2X_o^2Y_oT'_{yo} + \\ & +2kqX_oY_oT'_{yo} + kX_o^2Y_oT'^2_{xo} + kX_o^3T'^2_{xo} + k^2X_oY_o^2T'_{xo} + \\ & +2k^2X_o^2Y_oT'_{xo} + 2kqX_oY_oT'_{xo} + k^2X_o^3T'_{xo} + 2kqX_o^2T'_{xo} + \\ & +k^2qY_o^2 + 2k^2qX_oY_o + kq^2Y_o + k^2qX_o^2 + kq^2X_o] \end{aligned}$$

Where I set $-S'_0 = q > 0$. Although this expression is too long to be of any direct practical use, it still carries useful information if one observes that the right-hand side is a negative quantity. Therefore if one finds

$$\Delta<0$$

and a positive value of H'_0, i.e.

$$dH_0/dW > 0 \tag{51}$$

then the coexistence fixed point is stable.

Finally, let me observe that the existence of a stable coexistence equilibrium depends crucially on the net water input *S*, which must lie in the range given by (45). However, in that range, neither the water concentration, not the total biomass density X_0+Y_0 depend on *S*, which is a sharp difference with the single species case, where the stability is independent of abiotic factors. Therefore, our model predicts that a forest in a state of coexistence between hygrophilous and non-hygrophilous species is able to maintain a homeostatic equilibrium of biomass and soil water content.

The necessary conditions for the stability of different possible states are summarized in table 3.1.

State	***Necessary condictions for stability***	***Necessary condiction for biological meaningful***
No vegetation	$F_0 < 0$ or $H_0 < 0$	
Hygrophilous species	$F_0 > H_0$	$X_0 > 0$, that is $F_0 > 0$.
Non Hygrophilous species	$H_0 > F_0$; $\frac{dH_0}{dW} > -\frac{H_0 T'_{y0} + kq}{T_{y0}}$	$Y_0 > 0$, that is $H(W_0) > 0$.
Coexistence	$F_0 = H_0$ $T_{x0} > T_{y0}$ $dH_0/dW > 0$	$\frac{T_{y0}F_0}{k} > S_0 > \frac{T_{x0}F_0}{k} \quad if\ T_{y0} > T_{x0}$ $\frac{T_{x0}F_0}{k} > S_0 > \frac{T_{y0}F_0}{k} \quad if\ T_{x0} > T_{y0}$

Table 3.1 States of the system and necessary condition for stability

3.2 Model robustness

Although the parameters of Table 3.1 have been determined on the basis of reliable observational data, they are affected by much uncertainty, and by a little amount of guesswork. Those determining the shape of the net growth rates, F and H, are important, but not crucial: other functional forms could be chosen for F and H in alternative to those proposed in equations (21-22) and little would change, provided that their graphs still crossed at approximately the same value of W, with approximately the same slopes, as shown by the stability analysis in the appendix.

Eq. (51) a third necessary condition to have coexistence providing us that the partial derivative of the net growth rate of the non-hygrophilous species respect to the soil water content must be positive. Intuitively it is clear that, otherwise, non-hygrophilous species would be in a hydric condition not favourable to their development, thus, to their competitiveness and ability to sustain coexistence.

Other parameters are more important in determining the properties of the model's equilibria. It is therefore important to picture how the equilibria change their stability when these parameters change their value, and discuss the resulting bifurcation diagrams.

3.2.1 Bifurcations for changing transpiration ratios

Condition of eq. (49), provides that the transpiration rate of the hygrophilous species is greater than the non-hygrophilous. In other words it must be valid that

$$\frac{\alpha}{\beta} > \frac{h(W_0)}{f(W_0)} \tag{52}$$

Now, I would like to know what happens if the parameters α and β, which determine the amount of transpired water per on the basis of the metabolic activity of the plants (see eq. 19), would be varied slightly along a gradient of reasonable possibility.

Figure 3.1 shows a bifurcation diagram in a wide interval of values of α and β, including also regions that probably are physiologically meaningless.

Stable coexistence is possible for relatively high ratio α of transpiration of the hygrophilous plants, and relatively low ratio β of transpiration of non-hygrophilous plants. This is the opaque green regions in the four panels of Figure 3.1, which appears to be the most physiologically sound.

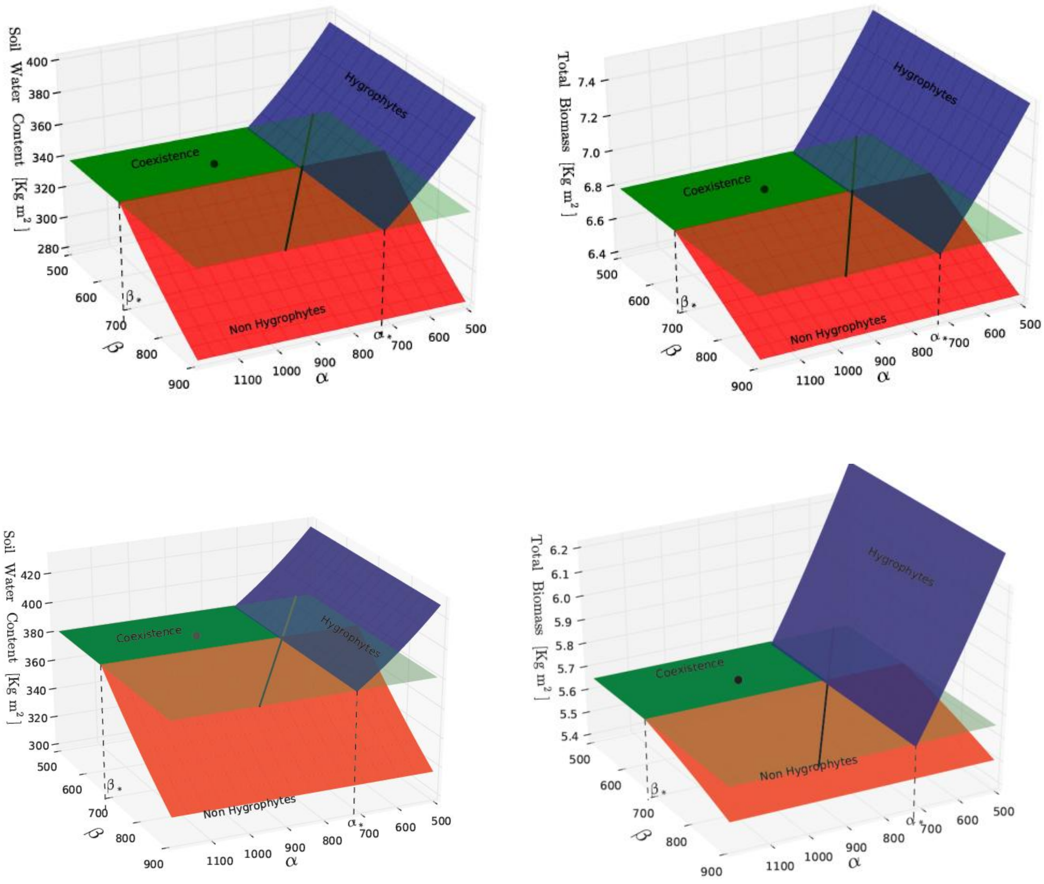


Figure 3.1. Bifurcation diagram of coexistence and single-species equilibria using α and β as the control parameters for the mid-low hypothesis. Left panel: soil water concentration. Right panel: total biomass. The other parameters are those of Table 1. The red and the blue surfaces represent the stable equilibria with, respectively, only the hygrophilous and the non-hygrophilous species. To avoid visual clutter, unstable branches of these equilibria are not show. The green plane represents the coexistence equilibrium. It is opaque where the equilibrium is stable, and it is transparent where the equilibrium either is unstable or one of the two species has a negative biomass value. The black line lying on the coexistence plane shows where Txo=Tyo . The black dot is the equilibrium state corresponding to the parameters of Table 1. The vertical dashed lines show the position of the bifurcation values α^* ,β^*

If β were larger than a threshold value β^* (which is independent of α, and is $\beta^* \sim 700$ for both the *lowmed* and *high* hypothesis of mortality), keeping the other parameters as in Table 2.7) then the coexistence equilibrium looses stability, as the equilibrium biomass X_o in equation (43) assumes a biologically meaningless negative value. For $\beta > \beta^*$ the equilibrium in which only the non-hygrophilus species exists is stable (the red surfaces in Figure 3.1) and it is unstable for $\beta < \beta^*$. At $\beta = \beta^*$ we are in the presence of a transcritical bifurcation where the coexistence and the single-species equilibrium coincide and exchange their stability (e.g. Glendinning, 1994). Analogously, if α were lower than a threshold α^* (independent of β; $\alpha^* \sim 725$ for both the *lowmed* and *high* hypothesis of mortality with the parameters of Table 2.7) then the single-species equilibrium becoming stable through a transcritical bifurcation is that of the hygrophilous species (the blue surface in Figure 3.1)

The coexistence equilibrium exists for any value of α and β , except those that make $T_{xo}=T_{yo}$, corresponding to singularities in the solutions (43). These special values are identified by the solid black line in the panels of Figure 3.1. For $\alpha < \alpha^*$ and $\beta > \beta^*$ the inequalities (44) hold: the coexistence equilibrium has positive biomass solutions, but it is unstable because it is $T_{xo}<T_{yo}$. Both the single-species equilibria, however, are stable. Which of the two will actually appear depends on the past history of the system. Although the presence of *bistability* is mathematically interesting, I will not investigate further this regime as it does not represent correctly the physiology of species found in Mediterranean transitional wetland forests. Finally we note that for $\beta > \beta^*$, as α exceeds α^*, the single-species equilibrium of the hygrophites exchanges its stability with a stable, but biologically irrelevant, coexistence equilibrium characterized by $T_{xo}<T_{yo}$ and $Y_o<0$; an analogous exchange of stability happens for the non-hygrophites for $\alpha < \alpha^*$ as β drops below β^*.

The state corresponding to the parameters of Table 2.7, shown by the black dots in Figure 3.1, is well within the boundaries of stable coexistence. Therefore any conclusion drawn from the model about the coexistence of the two types of species is robust to some level of uncertainty on the numerical values of α and β .

3.3 Bifurcations induced by climate change

Let me define the *water supply* the difference *p-e* between precipitation and evaporation. Then let me note, from equation (23), that only this difference matters in the model, and not the individual values of precipitation and evaporation. The stability results of section 3.1 show that the water supply enters crucially, through the function *S* defined in equation (20), in the expression of the single-species and coexistence equilibria (equations 32,35,43). I use *p-e* as a control parameter in a bifurcation analysis both because the value of *e* is affect by some uncertainties, and, more importantly, because climate models show that the precipitation *p* will be significantly altered in the Mediterranean area under climate change scenarios.

The bifurcation diagram is shown in Figure 3.2. Each coloured line drawn in the graphs represents the equilibrium points of the three possible meaningful states of different ecosystems: blue for the only hygrophilous state, red for the only non-hygrophilous ones and black for coexistence. The solid lines represent the equilibria points that are stable, while the dotted ones the unstable ones.

Reading the graphs from left to right, i.e. for increasing values of supply, we note that the non-hygrophilous state is stable and persists until the first bifurcation point, slightly more than 500 $Kg\ m^{-2}\ yr^{-1}$ for both mortalities hypothesis. After this threshold the stable state becomes that of coexistence, and the single-species equilibrium loses its stability in a *transcritical bifurcation*: in fact, in such type of bifurcation a fixed point exists for all values of the control parameter *p-e* and is never destroyed. Moreover such a fixed point (Non-Hygrophilous equilibrium) interchanges its stability with another fixed point (that of coexistence) as the control parameter *p-e* is varied. This type of bifurcation is typically that of *transcritical bifurcation* as shown in section 1.5.4.b.

Increasing further the water supply, for *p-e* ~600 $Kg\ m^{-2}yr^{-1}$ the system undergoes yet another transcritical bifurcation where the coexistence equilibrium becomes unstable, and the single-species equilibrium corresponding to hygrophilous plants becomes stable.

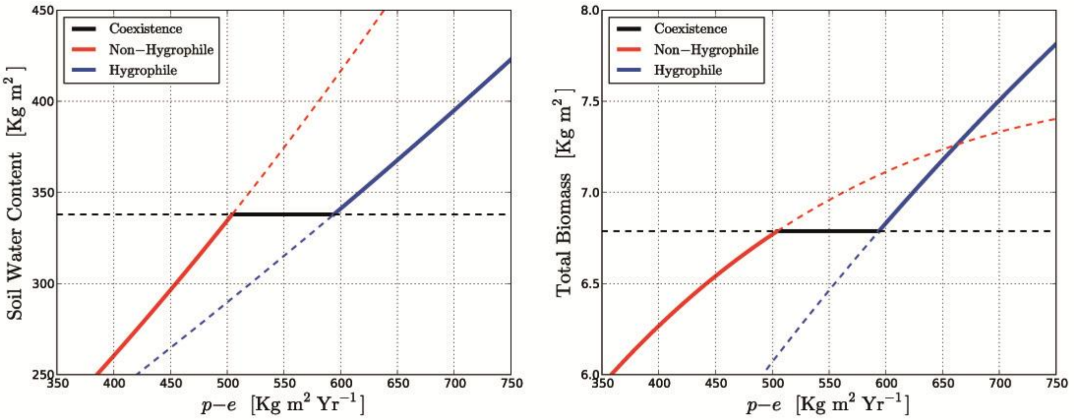


Figure3.2. System Bifurcation diagram for changing water supply (p-e) for low-medium mortality hypothesis. Solid and dot lines represent, respectively, the stable and instable equilibrium for the tree possible equilibria: Coexistence (black lines), Hygrophilous (blue lines) and non-Hgrophilous (red lines).

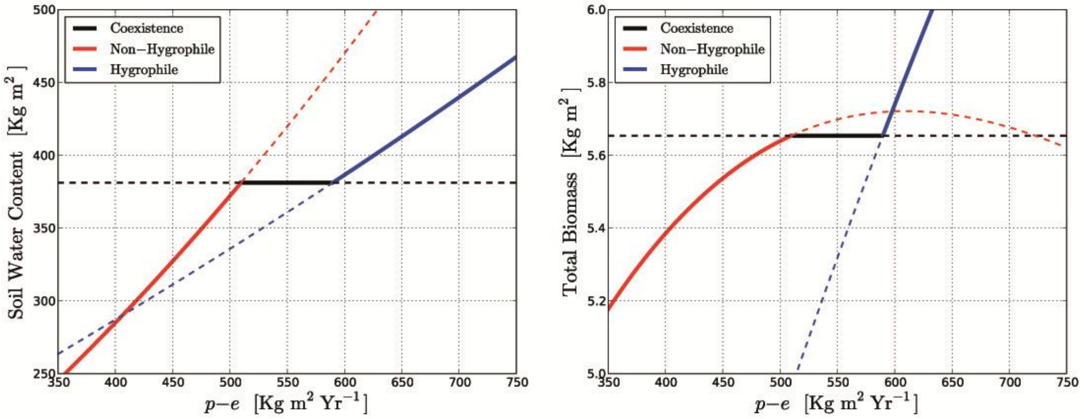


Figure3.3. System Bifurcation diagram for changing water supply (p-e) for high mortality hypothesis. Solid and dot lines represent, respectively, the stable and instable equilibrium for the tree possible equilibria: Coexistence (black lines), Hygrophilous (blue lines) and non-Hgrophilous (red lines).

It is worth noting that the bifurcation diagrams of Figure 3.2 and 3.3 show no significant differences on the thresholds of coexistence between the different hypothesis of mortality: with the high hypothesis the water supply allowing for coexistence is reduced just by 10 $Kg\ m^{-2}\ yr^{-1}$ (i.e 10 $mm\ yr^{-1}$). Rather, the different rates of mortality results in different equilibrium values of biomass density and soil water content as already shown in section 2.2.2c.

Lastly, from a mathematic point of view, as I mentioned at the end of sec 3.1.3, the soil water content and the total biomass density at the coexistence equilibrium are independent of the water supply. What changes for varying water supply is the proportion of the hygrophilous and non-hygrophilous species. Rearranging equations

(43), we may express the fraction of hygrophites and non hygrophites biomass with respect to the total biomass as

$$X_0 = \frac{kS_0 - T_{y0}F_0}{k(T_{x0} - T_{y0})}; \qquad Y_0 = \frac{T_{x0}F_0 - kS_0}{k(T_{x0} - T_{y0})}; \tag{53}$$

$$\frac{X_0}{X_0 + Y_0} = \frac{kS_0 - T_{y0}F_0}{(T_{x0} - T_{y0})F_0}; \qquad \frac{Y_0}{X_0 + Y_0} = \frac{T_{x0}F_0 - kS_0}{(T_{x0} - T_{y0})F_0}; \tag{54}$$

where $S_0=p\text{-}e\text{-}qW_0$. When *p-e* is as low as to make $kS_0=T_{y0}F_0$ (the leftmost bifurcation point in Figure 3.2 and 3.3) then 100% of the biomass is made of non-hygrophites. For rising water supply the fraction of hygrophites rises at the expenses of the non-hygrophites, until, for *p-e* sufficiently high as to make $kS_0=T_{x0}F_0$, 100% of the biomass is composed by hygrophites (this is the rightmost bifurcation point in Figure 3.2 and 3.3)

Figure 3.4 show the ratio between the two species, that I called *Coexistence Index*, characterizing the state of coexistence respect with the water supply. The cusp shape of the graph show an abrupt disappearance of a species for changing water supply suggesting a eligible close water supply for a well-balanced ratio between the two species.

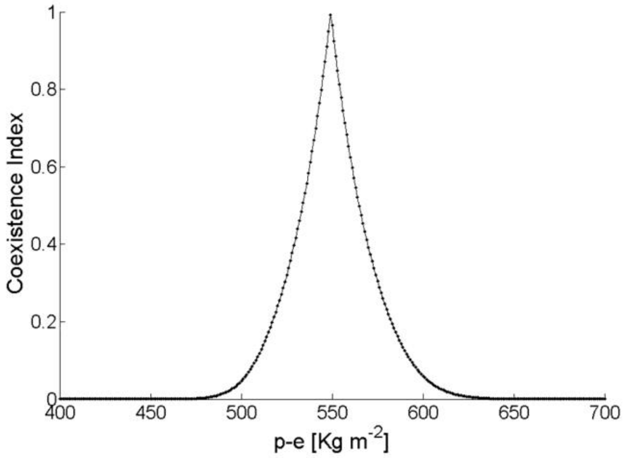


Figure 3.4. Ratio between the Hygrophilous and Non-Hygrophilous species for low-medium mortality hypothesis along the water supply explored.

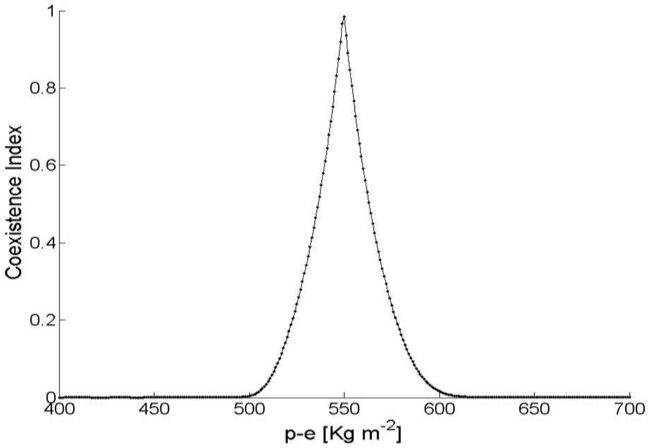


Figure 3.5. Ratio between the Hygrophilous and Non-Hygrophilous species for high mortality hypothesis along the water supply explored.

3.3.1 Bifurcations for changing precipitation

In order to split the different weight of precipitation and air temperature on the stability of the state of coexistence, I analyzed the single effect of both climate parameters (see Table 3.2) according to the expected climate scenarios for the next century. Assuming a constant evaporative rate of 250 $Kgm^{-2}yr^{-1}$ (i.e. as calibrated in section 2.2.2a), the range of precipitation that allows for coexistence is $750 < p < 850$ $Kgm^{-2}yr^{-1}$ and $760 < p < 840$ $Kg\ m^{-2}\ yr^{-1}$ for the mortality hypothesis, respectively, of *low-med* and *high* ones. Considering an actual average annual precipitation of 780 $Kgm^{-2}yr^{-1}$ together with the two scenarios described in Table 2.2 expected state of coexistence loses its stability because of decreasing rainfall in just 15-30 years. For the next 40 years, the same results would be obtained if the precipitation was reduced between 2.5% to 4%. Table shows the breakdown for each scenarios separately for the two hypothesis of mortality.

3.3.2 Bifurcations for changing temperature

Now let's me do a specular reasoning assuming a constant annual average precipitation of 780 $Kgm^{-2}yr^{-1}$. By a simple algebraic subtraction I obtain that the range of evaporative rate that allows for coexistence, at present, is $180 < e < 280$ $Kgm^{-2}yr^{-1}$ [1] and $200 < e < 270$ $Kgm^{-2}yr^{-1}$ for the mortality hypothesis, respectively, of *low-med* and *high* ones (Table 3.4). Considering an actual average annual evaporative rate of 250 $Kgm^{-2}yr^{-1}$ together with the two scenarios of described in paragraph 1.3.2 expected state of coexistence could lose its stability because of increasing temperature in 42-125 years. Considering the same time period investigated by the CIRCE project, the same results would be obtained if the temperature was increased to 5.6-8°C (Table 3.2).

3.3.3 The coupled effect of climate parameters

Now that the climate parameters have been split some conclusions may be drawn.

The variation in precipitation, as provided by the major climate scenarios, has a more immediate effect on the stability of coexistence. In fact the expected time for exceeding the precipitation point of bifurcation is much shorter respect to the temperature ones. Furthermore, the present scenario of precipitation (decreasing of 5-10% for the next 40 yr) is already out of bounds for coexistence survival.

If the scenario of temperature occurs without exceeding the expected gains (i.e. assuming a temperature increase up to a maximum of 4 °C) the state of coexistence would probably eroded but still stable. However, although already alarming, this predictions will be underestimating as long as their coupled effects will be not considered.

Ccoupling both the climate factors, the perspective becomes even more critical because of the water supply necessary for the survival of the state of coexistence is likely to fail in just a decade (see Table 3.3).

Overall, the results obtained are highly related to the study area. The model, as calibrated, allows for coexistence of species hygrophilous and non-hygrophilous in the plain forests of central Italy by setting a relatively simple water balance in which the only input of water is rainfall, a choice supported by bibliography (Macella et al., 1997). This implies that other inputs like runoff and aquifer outcrop are neglected. Although the choice is justified and the results are worrying, consider the precipitation as the only water input could be a risky assumption that over-estimates the results just shown.

Mortality Hypothesis	**Range of *p* for coexistence** [Kg m^{-2} yr^{-1}]	**Current *p*** [Kg m^{-2} yr^{-1}]	***p* shift to reach the bifurcation** [Kg m^{-2} yr^{-1}]	***p* Scenario for the next 40yr**	**Expected Time** [yr]	**Equivalent scenario**
Low-med	$750<p<850$	*840*	*30*	*-5%*	*30*	*-4%*
				-10%	*15*	
High	$760<p<840$		*20*	*-5%*	*20*	*-2%*
				-10%	*10*	

Table 3.2. Expected regime shift of state of coexistence induced by changing precipitation.

Mortality Hypothesis	**Range of *e* for coexistence** [Kg m^{-2} yr^{-1}]	**Current *e*** [Kg m^{-2} yr^{-1}]	***e* shift to reach the bifurcation** [Kg m^{-2} yr^{-1}]	***e* Scenario for the next 40yr**	**Expected Time** [yr]	**Equivalent scenario**
Low-med	$180<e<280$	*250*	*30*	+Δ2°C	*125*	*+8°C*
				+Δ4°C	*64*	
High	$200<e<270$		*20*	+Δ2°C	*83*	*+5,6°C*
				+Δ4°C	*42*	

Table 3.3. Expected regime shift of state of coexistence induced by changing temperature

Scenario of Temperature	**Scenario of Precipitation**	***Δs*** **[mm yr^{-1}]**	**Expected years to the bifurcation**	
			Mortality hypothesis	
			Low-med	*High*
+2°C	-5%	-1,24	23,2	16,1
	-10%	-2,24	13,4	8,9
+4°C	-5%	-1,47	20,4	13,6
	-10%	-2,24	12.1	8,1

Table 3.3 Climate scenarios and expected time to react the bifurcation points of figure 3.2 and 3.3

3.4 Robustness of the regime-shift scenarios induced by climate change

The bifurcation analysis carried out implies the possibility of a regime shift accompanied by a dramatic loss of biodiversity if the climate control parameter *p-e* moves beyond the threshold shown in Figure 3, thus destabilizing the coexistence equilibrium. It is therefore important to assess whether such a scenario is robust with respect to uncertainties in the values of the parameters. As we have argued above, the most important ones in this respect are the transpiration coefficients α and β.

As shown by equations (53), the destabilization of a coexistence equilibrium for varying *p-e* happens by pushing to zero the biomass density of one of the two types of trees. The inequalities (45) mark the boundaries of his stability region, and involve *p-e* (contained in So), and α and β (contained in T_{xo} and T_{yo}, respectively).

Figure 3.6 is a graphical depiction of the boundaries given by (45). For any fixed value of β, the stability region of coexistence is represented by a wedge in the *p-e* vs α plane. The position of the left side of this wedge, corresponding to the bifurcation where coexistence is replaced by the non-hygrophites alone, is independent of α. The right side, corresponding to coexistence replaced by just the hygrophites, is a sloping straight line (the same for all values of β) that opens-up the wedge as α increases. Figure 3.6 shows with different colors the stability wedges for seven distinct values of β, piling-up on top of each other.

It is evident that the possibility of a regime-shift as *p-e* changes is always present. Uncertainties in the value of the transpiration rates are reflected as uncertainties in the exact position of the bifurcation threshold. Nevertheless, the boundaries of the *p-e* stability intervals in Figure 3.6 are always attained at values reasonable for a Mediterranean forest.

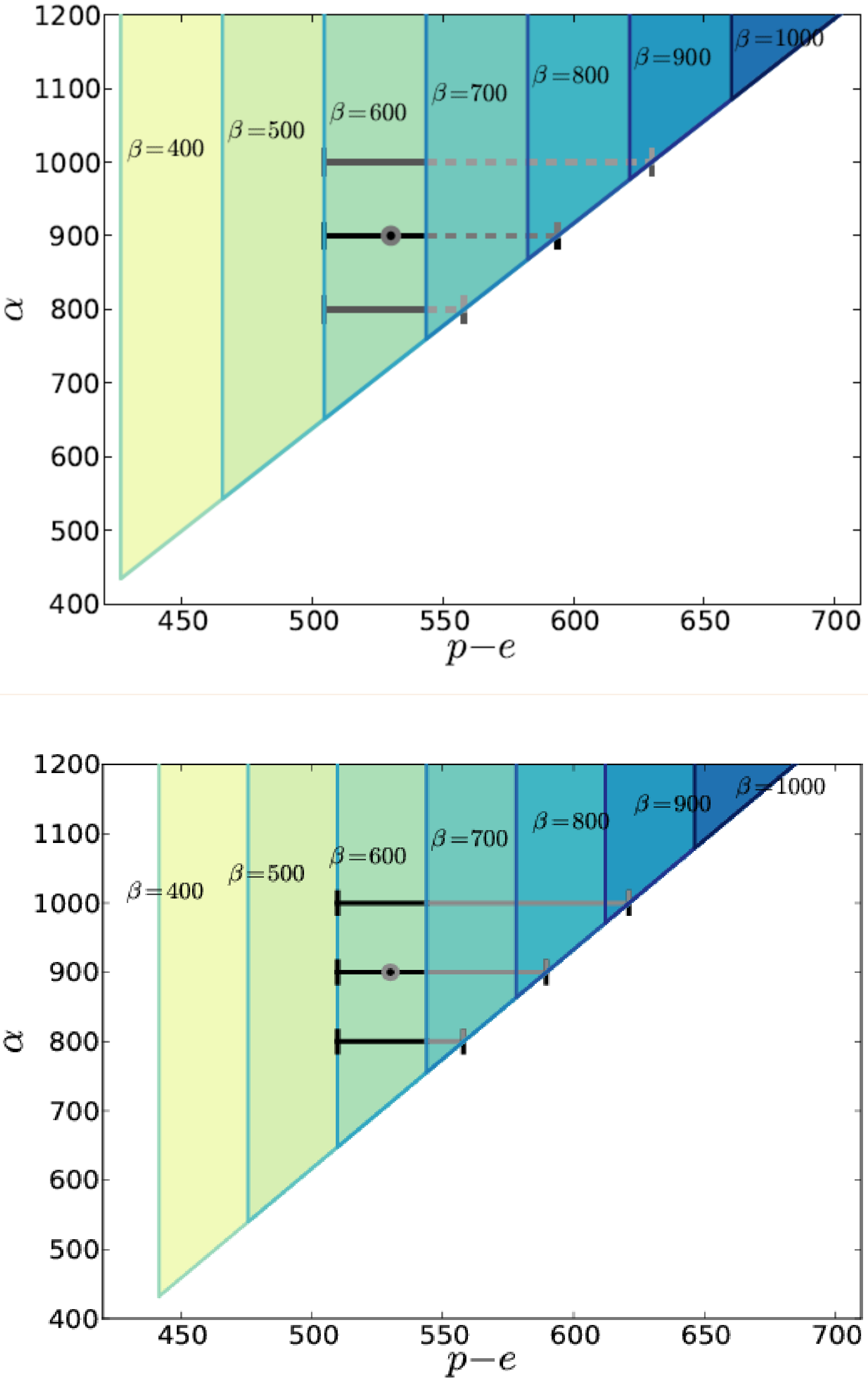


Figure 3.6. Wedges of stable coexistence for varying *p-e* , α at seven distinct values of β . The black dot corresponds to the parameters of Table 1. The horizontal segment containing the dot is the same coexistence interval appearing in Figure 3. The other two horizontal segments show the stable coexistence *p-e* intervals for α=800 and α=1000 within the β=600 wedge.

4. CONCLUDING REMARKS

I consider that scientific knowledge on the physiological processes underlying trees adaptative strategies to water stress has reached the point where we can, with reasonable confidence, make simplifications that have allowed us to develop a model which should be of value as a research tool for ecological analysis in forested wetlands coexistence. I propose one such model that allows for coexistence of distinct plant types in forested wetlands as a research tool for assessing the resilience to climate changes of states of coexistence, thus diversity. The model, through a mathematical representation of a set of physiologic mechanisms, should reproduce the overall ecologic behaviour at ecotones where water can be both a limiting resource and a chronic stressor.

The study of the resilience of coexistence has been carried out using a dynamic model developed and analyzed with an analytical approach. However, unlike the classical analytical models, this one is highly contextualized to the study area in which it is applied to. Moreover the processes and the interference between species and the resource and between the species themselves are not described in phenomenological form since the model parameters are clearly linked to measurable attributes such as forest growth and transpiration.

From an ecological point of view, the strong contextualization with the site and the application of experimental knowledge to define the model's structure makes this tool investigation highly innovative and powerful.

Like all theoretical models, the present study provide us a *theoretical understanding* of how the system operates. At the same time the model predictions give rise to *practical applications* since it may help decision makers to choose between different possible courses of action.

Potentially, the practical implications are both the quantification of some variables still scarce in bibliography (as the case of semi-saturation constant) and the identification of critical thresholds beyond which the system changes its qualitative characteristics (regime shift). In other words, the classical predictive models are able to provide us trends and scenarios with some degree of certainty. This type of deterministic model application, however, can provide us the extent to which the ecosystem can withstand and absorb these trends and scenarios. These approaches, of course, are complementary.

It must be pointed out that the main characteristic of such an approach is the simplicity with which the model is defined that in turn allows an understanding of mechanisms behind forested wetlands dynamics.

This simplicity was possible because I assumed that populations are well mixed. Thus, I neglected possible effects associated with explicit spatial patterns. Spatial patterns can be unequivocally important (e.g., Gilad et al., 2007), also they can be studied with analytical techniques (e.g., Bolker and Pacala, 1997, 1999). However, some interesting features are predicted even in this simple case and I believe that is worth showing these results before using more sophisticated techniques.

4.1 Resilience

Although the mechanism of coexistence appears to be robust, and I find coexistence in large regions of the parameter space, the bifurcation analysis shows that coexistence is possible only within a somewhat narrow interval of water supply values (here I identify the supply of water with the difference *p-e* between precipitation and evaporation). Using the model with the best fit of the parameters (Table 2.7), I find that the extinction of the hygrophilous species happens at $p - e \approx 500\, Kg\, m^{-2} yr^{-1}$. According to the expected climate scenarios for the Mediterranean basin (EEA; CIRCE; Giorgi and Lionello, 2008), such a minimum threshold of water supply due climate change (decrease of 2-4% of mean annual rainfall or increasing mean air temperature up to 5,6-8°C for the next 40's years) could be reached in the second half of the current century. Thus our model forecasts a dramatic loss of biodiversity in the coastal plain woodlands of central Italy, exacerbated by the strong local endemism found in those sites.

In other words, the state of coexistence may withstand *disturbances* for a some extent, but despite this, its resilience will be eroded, as shown by the decreasing ratio between the two species, until the complete extinction of one of them will be reached.

However, although the boundaries of the water supply (*p-e*) stability intervals in Figure 3.6 are always attained at values reasonable for a Mediterranean forest, and although the best fit of the transpiration ratios α and β are calibrated according to the actual forest transpiration of Castelporziano site, due to the absence of direct measurement on some parameters, it still remains an uncertainty on the calibration that cannot be ignored and that is reflected as high uncertainty in the exact position of the bifurcation threshold.

Moreover, although alarming, the situation provided does not take into account certain factors, deliberately omitted, which could be decisive in the perseverance of diversity in the meso-hygrophilous plain forests of central Italy: the first is that the model has some limitations that inevitably limit the accuracy of its predictions, that will be discussed in section 4.4; the second is that the bifurcation analysis has carried out regime shifts that are *reversible*: if the control parameter of water supply is turned into the range that supports coexistence, the state of coexistence will be reached again.

4.2 Model structure

Now let me make few comments on the model structure and mechanisms involved in the stability of coexistence.

From an analytical point of view the coexistence is possible when three conditions are met simultaneously: i) the net balance between competitive and survival abilities of the two species are the same; ii) the transpiration rate of the hygrophilous species is higher than the non-hygrophilous one; iii) the net growth rate of non-hygrophilous species increases with increasing soil water content.

Let me drawn some consideration about them. According to the assumption that the non-hygrophilous species have an optimal water range for growth greater than the hygrophilous ones (Figure 2.1), their half-saturation value is set lower than the one of the hygrophilous (*i.e* $W_Y < W_X$). By imposing the same potential growth rate *g*, this results that the non-hygrophilous species has a competitive ability (i.e. *to grow*) than the hygrophilous ones. Consequently, the coexistence is possible only for water regime where the ability to survive of the less competitive species (the hygrophilous) was enough higher than the most competitive (the non-hygrophilous) to match the first condition. From an ecological point of view, this skills balance represents a trade-off between the ability to compete (growth) and to survival (mortality) of both species for the same resource-stressor (water) that enables stable coexistence of different plants. Trade-off between different abilities allowing for coexistence was already observed by other previous studies (Cammarano 2011; Silvertown, 2004; Silvertown et al 1999).

The ability to survival of both species represents the key novelty of the model since it is an explicit modeling of mortality. The mortality is different for the two species and is modeled as a water-dependent process, which may either favor the hygrophilous species and hamper the non-hygrophilous ones, or the other way around, depending on the soil water content. Compared with the ecological bibliography, this feature was never before explicitly discussed neither in the context of coexistence nor in other forest succession models.

The other ingredients that allow for a stable coexistence is the higher water use efficiency of the non-hygrophilous species, and the higher transpiration rates of the hygrophilous ones. This condition has motivated the analysis of model uncertainties for changing transpiration ratios α and β. Now I will explain the ecological significance: Let's me assume that some external cause abruptly increases from the equilibrium values the density of, say, the hygrophilous species, while leaving the other untouched. The immediate consequence of this perturbation is a rapid drop of the water concentration in the soil, caused by the increased total transpiration.

Because of the larger transpiration of the hygrophilous, water concentration is held from returning to its equilibrium value, and remains slightly below it. In this situation the non-hygrophilous species have the larger growth rate, and they may overgrow the hygrophilous one until the full equilibrium is slowly re-established. If, instead, the perturbation had increased the non-hygrophilous species, after the initially strong water loss, there would be an overall smaller water consumption than at equilibrium, and the water concentration would rise slightly above its equilibrium value. This situation would now favour the depleted hygrophilous species, which could slowly overgrow the others. Of course, the case of an initial loss of biomass is specular, and leads again back to equilibrium (figure 4.1).

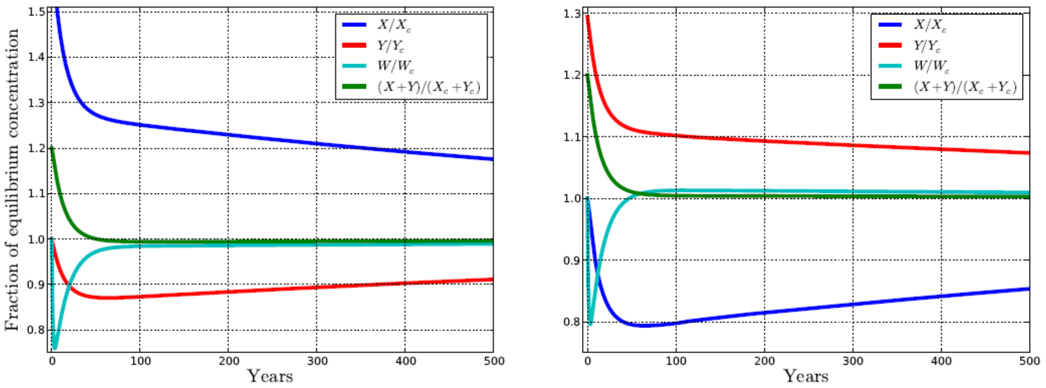


Figure 4.1. Transient dynamics toward the coexistence equilibrium after a perturbation. The blue, red, cyan and green lines are the ratio with their values at the coexistence equilibrium of, respectively, the density of the hygrophilous species, the density of the non-hygrophilous species, the soil water concentration and the total biomass density. Left panel: the density of the hygrophilous species initially is set at the equilibrium value plus an amount equivalent to 20% of the total equilibrium biomass density. Right panel: the 20% increment is applied to the density of the non-hygrophilous species, instead. Note that in the left panel the concentration of water approaches the equilibrium from below; in the right panel the concentration of water, after the initial depletion, raises above the equilibrium value and then approaches the equilibrium from above.

While this argument is not a substitute for the rigorous stability analysis discussed in the paragraph 3.13 , such a negative feedback seems catching the basic ecological mechanism supporting the observed stable coexistence equilibrium, similarly to the results of other previous works such as Vance (1984), Cammarano (2011), Chyper and Boucher (1982).

In his work, Vance (1984) showed that if two species interfere with each other for the resource acquisition, coexistence is possible but such interference have to be species-specific i.e. the growth of a species has to have stronger negative effects on themselves rather than on other species. This is also what happens in this model since the hygrophilous species have greater negative interference on themselves rather than on the non-hygrophilous ones and vice versa (figure 4.2).

Lastly the third condition is intuitively easy to understand because of it requires that at water regime of coexistence where the hygrophilous species have a better ability to survive, the net growth rate of the non-Hygrophilous species continues having a positive trend, thus continues to compete.

Finally, the appearance of a stable, steady equilibrium for two species in a model that only explicitly contains a single resource (namely, water) may raise objections on the basis of the well-known principle of competitive exclusion.

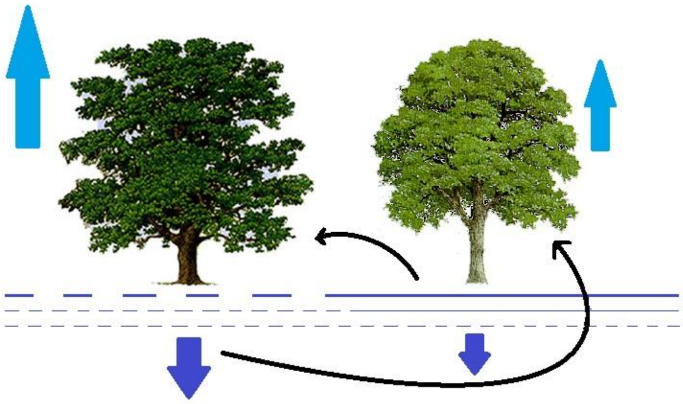


Figure 4.2. Schematic representation of the negative feedback that allows the establishment of a homeostatic balance of biomass and soil water content for the state of coexistence

Doubts about coexistence have been raised by the competitive exclusion principle. Roughly, it states that if two species are too similar (e.g., they feed on the same resource), they cannot coexist (Hardin, 1960). There has been considerable discussion of the assumptions and general validity of the competitive exclusion principle (Silvertown 2004). However, the general conclusion still seems valid when the limiting assumptions of the principle are met (competition occurs in a stable uniform environment for the same limiting resource and equilibrium is achieved): competitive exclusion must occur and one species will eliminate the other. Complete exclusion has been obtained in the laboratory (Tilman and Wedin, 1991; Crombie 1947*)*, nevertheless ecologists are confronted with many examples of different species living together and apparently sharing the same resources. (Silvertown, 2004).) propting them to found new hypothesis to explain coexistence

However, most of the mathematical arguments underlying the principle require linear mortality terms, as, for example, in the analysis of Armstrong and McGehee (1980) and MacArthur and Levins (1964). In the model we use quadratic mortality terms, where the death rate is proportional to the total biomass. The comparison with a logistic growth law (to which our model reduces in the presence of a single species and for a constant soil water content) should make clear that those terms amount to an implicit modeling of an additional resource, namely space. In effect, it can be shown analytically that our model lacks the coexistence equilibrium if one substitutes the quadratic mortality terms with linear ones. Therefore it appears that competition for space, modeled by mortality rates that increase with the total biomass, is also a non-negligible ecologic factor.

4.3 Forest Mortality

The calibration of mortality curves of both species allowing for coexistence have the constraint to balance the respective, well known, growth rates. Among the 9 possible coupling of different calibrations of species mortality that I performed in section 3, two different pairs of hypothesis of mortality enable stable coexistence that I call, respectively, *low-med* and *high hypothesis.* The results of all bifurcations are carried out for both of these hypotheses.

*A*s argued in this section the explicit modeling of mortality represent a key novelty of the model. As suggested by the results of the stability analysis, the calibration of the mortality curves has a great importance in determining the equilibrium state of coexistence but not for its stability. It should not surprise, thus, that results for the two different hypothesis of mortality are slow to take some effect on whole dynamics of the model. However, the comparison of the two different set of calibration, reflecting two different hypothesis of mortality, can provide us a starting point for forest ecology studies and for more complex predictive models who want to consider more carefully the processes of mortality.

The first calibration supposes that the maximum mortality rates of Hygrophilous and non-hygrophilous species are respectively of 2% and 5% per year while the second one of 10% for both species. The bifurcation analysis, performed with both mortality hypothesis, evaluates the equilibrium points of total forest biomass and soil water content at stable coexistence, respectively, equal to $6.8\ Kg\ m^{-2}$ and $340\ Kg\ m^{-2}$ for the *low-med hypothesis*, and equal to $5.7\ Kg\ m^{-2}$ and $380\ Kg\ m^{-2}$ for the *high* one.

Therefore, different mortality rates reflect different equilibrium points. The comparison with the observations of total biomass and soil water content can provide us the mortality rates that presumably reflect the actual ones. For the present case study the first hypothesis that suppose an maximum mortality rates of the hygrophilous and non-hygrophilous species, respectively, equal to 2% and 5% per year seems to better fit the available data. These rates may be considered likely as long as the coexistence is stable.

4.4 Model Limitations

The presented model has some assumptions and simplifications that limit the reliability of its predictions. The first of these is certainly the exception of extreme events as a form of external perturbation. Several studies show in fact that regime shifts can occur not only due to small chronic perturbations but also because of individual extreme events. Also as part of studies aimed at global climate change, extreme events seem to take on greater importance because of their observed and expected increase in frequency (IPCC, Jung et al., 2010, Giorgi and Lionello 2008). Another important aspect is the simplification that sets all the parameters as a constant. Analytical models with bifurcation analysis of time-dependent variables are still absent in ecology. Therefore, looking to the major global and regional climate scenarios, it would be desirable to further develop these analytical models, improve their performance and their representativeness of reality to make them more practical for eco-management purposes.

However, I believe that the greater simplifications of this work are *i)* that all parameters have been kept as annual average, so that both the seasonal and interannual variations have been neglected; *ii)* the whole analysis of stability and bifurcation presuppose that the ecosystem state is at equilibrium, even if for such complex biological systems as forest dynamics this assumption may be true only theoretically.

4.5 Management Recommendations

The wrecks of lowland forest are among most exposed areas to human pressure and despite many of these areas have become parks or sites of Community importance, their conservation still requires an effective system of protection.

However, As I mentioned in section 1.3, such ecosystem like plain forest have never been included in Europe's most threatened natural ecosystems and are not listed in Annexe I of the European Habitats Directive as being a *priority forest habitat type*.

With the present case study I focus my attention on the enormous value of the natural lowland forests and remember the urgent need for their protection at national and European level in the light of future concern. The present study, in fact, emphasizes that forested wetland ecosystems are particularly sensitive and subject to climate change. This is due to the strong human impact who scored the composition of these forests, as well as to the very low rates of growth and survival capabilities of many species living in forest ecosystems. These factors can be expected to result in delayed adaptation of these ecosystems compared to the speed with which adverse climate changes occur.

Because of changes in water regimes can affect the survival of the same forest area some management strategies are recommended: i) create surface channels and maintain the existing ones able to recreate the *vernal pools* ii) manage the groundwater uptake in the surrounding region in order to preserve the normal piezometric level, often outcropping. Both of these suggestions assume having to maintain an average annual water supply that protects the presence of hygrophilous species that ultimately are those currently threatened by climate change.

References

Anselmi S, Chiesi M, Giannini M, Manes F, Maselli F. (2004) Estimation of Mediterranean forest transpiration and photosynthesis through the use of an ecosystem simulation model driven by remotely sensed data. Global Ecology and Biogeography. 13(4):371-380.

Adler PB, HilleRisLambers J, Levine JM. (2007) A niche for neutrality. Ecology Letters. 10(2):95–104.

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, et al. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management. 259(4):660–684.

Anderies JM, Janssen MA, Walker BH. 2002. Grazing management, resilience, and the dynamics of a fire-driven rangeland system. *Ecosystems* 5:23–44

Ayres, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Science of the Total Environment 262 (3), 263–286.

Bachelet, D., Neilson, R.P., Hickler, T., Drapek, R.J., Lenihan, et al., 2003. Simulating past and future dynamics of natural ecosystems in the United States. Global Biogeochemistry Cycles 17, 1045 doi:10.1029/2001GB001508.

Baldocchi DD, Ma S, Rambal S, Misson L, Ourcival JM et al (2010). On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. Ecological Applications, 20(6) pp. 1583–1597

Baldocchi DD, Xu L. (2007) What limits evaporation from Mediterranean oak woodlands-The supply of moisture in the soil, physiological control by plants or the demand by the atmosphere? Advances in Water Resources. 30(10):2113–2122.

Baldocchi D, Falge E, Gu LH, Olson R, Hollinger D, et al, (2001) FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor, and energy flux densities. Bulletin of the American Meteorological Society. 82:2415-2434.

Barkai A, McQuaid C. 1988. Predator-prey role reversal in a marine benthic ecosystem. *Science* 242:62–64

Beer C, Ciais P, Reichstein M, Baldocchi D, Law BE, et al. (2009) Temporal and among-site variability of inherent water use efficiency at the ecosystem level. Global Biogeochemical Cycles. 23(2):GB2018.

Beisner, B., Haydon, D., Cuddington, K., 2003. Alternative stable states in ecology. Frontiers Ecology and the Environment 1, 376_382.

Bigler, C., Braker, O.U., Bugmann, H., Dobbertin, M., Rigling, A., 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. Ecosystems 9, 330–343.

Bisigato AJ, Bertiller MB. 1997. Grazing effects on patchy dryland vegetation in Northern Northern Patagonia. *J. Arid Environ.* 36:639– 53

Blasi, C. (1994) Fitoclimatologia del Lazio. *Fitosociologia*, **27**, 151–175.

Blindow I, Anderson G, Hargeby A, Johansson S. 1993. Long-term pattern of alternative stable states in two shallow eutrophic lakes. *Freshw. Biol.* 30:159–67

Blum A (2005) Drought resistance, water-use efficiency, and yield potential—are they compatible, dissonant, or mutually exclusive? Australian Journal of Agricultural Research,56:1159–1168

Boisvenue, C. & Running, S.W. (2006). Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. Glob. Change Biol., 12, 1–21.

Bonan, G.B., 2008. Forests and climate change: forcing, feedbacks, and the climate benefit of forests. Science 320, 1444–1449.

Bonan GB, Pollard D, Thompson SL. 1992. Effects of boreal forest vegetation on global climate. *Nature* 359:716–18

Breda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Annals of Forest Science 63, 625–644.

Brian FC and Hicks JD (1982). The ecology of leaf life spans. Annual Review ofEcology and Systematics, 13:229-259

Bugmann, H.K.M., Wullschleger, S.D., Price, D.T., Ogle, K., Clark, D.F., Solomon, A.M., 2001. Comparing the performance of forest gap models in North America. Climatic Change 51, 349–388.

Brown JH, Valone TJ, Curtin CG. 1997. Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Acad. Sci. USA* 94:9729–33

Cammararo M. (2011). Co-dominance and succession in forest dynamics: The role of interspecific differences in crown transmissivity. Journal of Theoretical Biology Volume 285, Issue 1, 21 September 2011, Pages 46–57

Canham, C. D. (1989). Different responces to gaps among shade-tollerant tree species. Ecology, 70:548–550.

Canham, C. D. (1990). Suppression and release during canopy recruitment of Acer saccharum and Fagus grandifolia. Bulletin of the Torrey Botanical Club, 117:1–7.

Carpenter SR. 2003. *Regime Shifts in Lake Ecosystems: Pattern and Variation.* Excellence in Ecology Series 15. Oldendorf/Luhe, Germany: Ecol. Inst.

Carpenter, S. R., Ludwig, D. & Brock, W. A. 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9, 751±771.

Castellani C, (1970) Tavole stereometriche ed alsometriche costruite per i boschi italiani. Annali dell'Istituto Sperimentale per l'Assestamento forestale e l'Alpicoltura, Vol. I, N. 3 (speciale), Trento.

Chesson, P. (2000). Mechanisms of manteinance of species diversity. Annual Review of Ecology and Systematics, 31:343–366.

Christensen, J. , Hewitson, B. , Busuioc, A. , Chen, A. , Gao, X. , Held, R. , Jones, R. Et al., . (2007): Regional climate projections , Climate Change, 2007: The Physical Science Basis. Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, University Press, Cambridge, Chapter 11, ISBN: 978-0-521-88009-1 .

Chyper, J. and Boucher, D. H. (1982). Beech-maple coexistence and seedling growth rates at Mont-Saint-Hilaire, Quebec. Canadian Journal of Botany, 60:1279–1281.

Crombie, A. C. 1947. Interspecific competition. J. Anim. Ecol. 16:44-73.

Danell K, Bergstr¨om R, Edenius L, Ericsson G. 2003. Ungulates as drivers of tree population dynamics at module and genet levels. *Forest Ecol. Manag.* 181:67–76

Davis SM. 1989. Sawgrass and cattail production in relation to nutrient supply in the Everglades. In *Fresh Water Wetlands & Wildlife, 9th Annual Symposium, Savannah River Ecology Laboratory*, 24–27 March 1986, ed. RR Sharitz, JW Gibbons, pp. 325– 42. Charleston, SC: US Dep. Energy

DeAngelis,D. L. and Waterhouse, J. C. (1987). Equilibrium and nonequilibrium concepts in ecological models. Ecological Monographs, 57:1–21.

de Roos A, Persson L. 2002. Size-dependent life history traits promote catastrophic collapses of top predators. *Proc. Natl. Acad. Sci. USA* 99:12907–12

Debbie S. and Hogan C.M. (2010) Stomata. Encyclopedia of Earth. National Council for Science and the Environment, Washington DC

Done TJ. 1992. Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121–32

Donovan LA, Ehleringer JR. (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. Oecologia. 86(4):594–597

Dowgiallo, G. & Bottini, D. (1998) Pedological aspects of the Circeo National Park. *Flora e vegetazione del parco nazionale del circeo* (ed. by A. Stanisci and S. Zerunian), pp. 33–46. Ministero per le Politiche Agricole, gestione ex A.S.F.D., Sabaudia.

Dublin HT, Sinclair ARE, McGlade J. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *J. Anim. Ecol.* 59:1147–64

Dynamic Models in Biology **Stephen P. Ellner & John Guckenheimer 2006**

Eakin CM. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982– 1983 El Nino at Uva Island in the eastern Pacific. *Coral Reefs* 15:109–19

Eakin CM. 1996. Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific. *Coral Reefs* 15:109–19

Ellner S.P. & Guckenheimer J. (2006) Dynamic Models in Biology ISBN: 9780691125893 352 pp.

FAO, 2006. Global forest resources assessment 2005. Progress towards sustainable forest management. FAO Forestry Paper No. 147. Rome.

Foley JA, Coe MT, Scheffer M,Wang G. 2003. Regime shifts in the Sahara and Sahel: interactions between ecological and climatic systems in Northern Africa. *Ecosystems* 6:524– 39

Forcier, L. K. (1975). Reproductive strategies and the co-occurence of climax tree species. Science, 189:808–810.

Frelich LE, Reich PB. 1999. Neighborhood effects, disturbance severity and community stability in forests. *Ecosystems* 2:151–66

Fussmann F.G., Ellner S.P., Shertzer K.W. Nelson G. Hairston Jr (2000) Crossing the Hopf Bifurcation in a Live Predator-Prey System. Science VOL 290: 1358-1360.

Gasith A. and Vincent H.R (1999) Streams in mediterranean climate regions: Abiotic Influences and Biotic Responses to Predictable Seasonal Events. Annual Review ofEcology and Systematics.30:51-81.

Gantmacher, F. R. (2000). The Theory of Matrices vol. 2. American Mathematical Society, Providence, Rhode Island, USA.

Gellini R. And Grossoni P. (1997) Fagaceae; Oleaceae. In: Botanica Forestale II, Angiosperme. Padova: CEDAM p.

Giorgi F, Lionello P. (2008) Climate change projections for the Mediterranean region. Global and Planetary Change.63(2-3):90-104.

Glenz C, Schlaepfer R, Iorgulescu I, Kienast F. (2006) Flooding tolerance of Central European tree and shrub species. Forest Ecology and Management: 235(1-3):1-13.

Glynn PW. 1988. El Nino warming, coral mortality and reef framework destruction by echinoid bioerosion in the eastern Pacific. *Galaxea* 7:129–60

Gravel, D., Beaudet, M., and Messier, C. (2008). Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. Ecology, 89:2879–2888.

Gunderson LH. 2001. Managing surprising ecosystems in southern Florida. *Ecol. Econ.* 37:371–78

Gunderson LH, Pritchard L, eds. 2002. Resilience and the Behavior of Large-Scale Ecosystems. Washington, DC: Island Press.

Gurney,W. S. C. and Nisbet, R. M. 1998. *Ecological Dynamics.* Oxford University Press, New York.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Science of the Total Environment 262, 205–220.

Hardin G (1960) The Competitive Exclusion Principle. Science 131: 1292-1297.

Higgins PAT, Mastrandrea MD, Schneider SH. 2002. Dynamics of climate and ecosystem coupling: abrupt changes and multiple equilibria. *Philos. Trans. R. Soc. London Ser. B* 357:647–55

Holling CS. 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4:1–23

Holling CS. 1978. The spruce-budworm/forest management problem. In *Adaptive Environmental Assessment and Management.* International International Series on Applied Systems Analysis, ed. CS Holling, 3:143–82. New York: John Wiley & Sons

Holstein G (1984) California riparian forests: deciduous islands in an evergreen sea. In California Riparian Systems, ed. RE Warner, KM Hendrix, pp. 2-22. Berkeley: Univ. Calif. Press. 1035 pp.

Huisman, J. and Weissing, F. J. (2001). Biological conditions for oscillations and chaos generated by multispecies competition. Ecology, 82:2682–2695.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–51

Huston MA, Huston MA. (1994) Biological diversity: the coexistence of species on changing landscapes. Cambridge Univ Pr.

Huston MA. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449-60

INFC, Inventario Nazionale delle Foreste e de Serbatoi Forestali di Carbonio. Ministero delle politiche agricole alimentari e forestali - Corpo Forestale dello Stato. Available: http://www.sian.it/inventarioforestale/jsp/dati_carquant_tab.jsp. Accessed 2008 Dic 10.

IPCC, 2007: Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 pp.

Jackson LJ. 2003. Macrophyte-dominated and turbid states of shallow lakes: evidence from Alberta lakes. *Ecosystems* 6:213–23

Jansson B-O, Jansson AM. 2002. The Baltic Sea: Reversibly unstable or irreversibly stable? See Gunderson & Pritchard 2002, pp. 71–109

Jung M, Reichstein M, Ciais P, Seneviratne SI, Sheffield J, et al. (2010) Recent decline in the global land evapotranspiration trend due to limited moisture supply. Nature. 467(7318):951–954.

Kazda M, Salzer J, Reiter I. (2000) Photosynthetic capacity in relation to nitrogen in the canopy of a Quercus robur, Fraxinus angustifolia and Tilia cordata flood plain forest. Tree physiology. 20(15):1029

Konar B, Estes JA. 2003. The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84:174–85

Kozlowski TT. (1997) Responses of woody plants to flooding and salinity. Tree physiology monograph. 1(1).

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* 32:674–82

Kuznetsov, Yuri A. 2004. Elements of Applied Bifurcation Theory. New York: Springer-Verlag. ISBN 0-387-21906-4.

Law BE, Falge E, Gu L, Baldocchi DD, Bakwin P, et al. (2002) Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. Agricultural and Forest Meteorology. 113(1-4):97–120.

Levin SA. (2006) Fragile dominion: complexity and the commons. MA: Perseus Book.

Lloyd, A.H., Bunn, A.G., 2007. Responses of the circumpolar boreal forest to 20^{TH} century climate variability. Environmental Research Letters 2, 045013, doi:10:1088/1748-9326/2/4/045013.

Loehle, C., LeBlanc, D., 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling 90, 1–31.

Lu J. Deser C. Reichler T. (2009). Cause of the widening of the tropical belt since 1958. Geophysical research letters VOL. 36, doi:10.1029/2008GL036076.

Lucht, W., Schaphoff, S., Erbrecht, T., Heyder, U., Cramer, W., 2006. Terrestrial vegetation redistribution and carbon balance under climate change. Carbon Balance and Management 1, 6 doi:10.1186/1750-0680- 1-6.

Ludwig D, Walker B, Holling CS. 1997. Sustainability, stability, and resilience. Conserv Ecol. Vol. 1. Issue 1. art.7:1-7.

Lugo A.E. and Scatena F.N. (1996) Background and Catastrophic Tree Mortality in Tropical Moist, Wet, and Rain Forests. Biotropica Vol. 28, No. 4, Part A. Special Issue: Long Term Responses of Caribbean Ecosystems to Disturbances (Dec., 1996), pp. 585-599

Macella G., Scandella P., Fricano F., Di Blasi N. (1997) Monitoraggio delle piscine. In: a cura di Morselli L. Progetto di Monitoraggio Ambientale della Tenuta presidenziale di Castelporziano. Creazione di un Sistema Informativo Territoriale Ambientale Castelporziano (SITAC). Tenuta Presidenziale di Castelporziano - Rapporto 1997.

Manes, F., Anselmi, S., Canfora, E. & Giannini, M. (1997a) Remote sensing analysis of Mediterranean ecosystem canopies and upscaling studies. Earth Surface Remote Sensing. London 22–25 September 1997. *EUROPTO Series, Proceedings of SPIE*, **3222**, 246–252.

Manes, F., Grignetti, A., Tinelli, A., Lenz, R. & Ciccioli, P. (1997b) General features of the Castelporziano test site. *Atmospheric Environment*, **31**, 19SI–25SI.

McCook LJ. 1999. Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the reat Barrier Reef. *Coral Reefs* 18:357–67

Millennium Ecosystem Assessment (2005). Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Mitsch WJ, Gosselink JG (2007). Wetlands (4th ed.). New York: John Wiley & Sons. ISBN 978-0471699675.

Nemani RR, Keeling CD, Hashimoto H, Jollye WM, Piper SC, et al. (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science. 300(5625):1560.

Newman S, Schuette J, Grace JB, Rutchey K, Fontaine T, et al. 1998. Factors influencing cattail abundance in the northern Everglades. *Aquat. Bot.* 60:265–80

O'Dowd DJ, Green PT, Lake PS. 2003. Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* 6:812–17

Otto, S. P., Day, T. (2007). A biologist's guide to mathematical modeling in ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

Peñuelas, J., Lloret, F., Montoya, R., 2001. Severe drought effects on mediterranean woody flora in Spain. Forest Science 47, 214–218

Peterson GD. 2002. Forest dynamics in the South-Eastern United States: managing multiple stable states. See Gunderson & Pritchard 2002, pp. 227–46

Pignatti, S. (1998) I boschi d'Italia. Sinecologia e biodiversità. UTET, Torino.

Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, et al. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27:6–17

Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, et al. 2002. Canada's recreational fisheries: the invisible collapse? *Fisheries* 27:6–17

Poulson, T. L. and Platt, W. J. (1996). Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology, 77:1234–1253.

Presti G., Stanisci A., Blasi C. (1998) I boschi umidi relittuari del Parco Nazionale del Circeo. In: Stanisci A., Zerunian S. (eds.), Flora e Vegetazione del Parco Nazionale del Circeo: 223-235. Ministero per le politiche Agricole, Gestione ex A.S.F.D. (Sabaudia). Latina. HD,

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., Romme, W.H., 2008. Crossscale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517.

Rambal S (2001) Hierarchy and productivity of Mediterraneantype ecosystems. In: Terrestrial Global Productivity, Roy J, Saugier B, Mooney HA, eds. Academic Press, San Diego 573 p.

Reichstein M, Tenhunen J, Roupsard O, et al. (2003) Inverse modeling of seasonal drought effects on canopy CO2/H2O exchange in three Mediterranean ecosystems. J. Geophys. Res.108(4726):4716

Rivas-Martinez, S. (1975) La vegetación de la Clase *Quercetea ilicis* de España y Portugal. *Anal. Inst. Bot. Cavanilles*, **3**, 205–259

Rodríguez-González PM,Stella JC, Campelo F, Ferreira MT and Albuquerquea A (2010) Subsidy or stress? Tree structure and growth in wetland forests along a hydrological gradient in Southern Europe. Forest Ecology and Management 259:2015–2025.

Scheffer M, Carpenter SR, Foley J, Folke C, Walker BH. 2001. Catastrophic shifts in ecosystems. Nature 413:591–96

Scheffer M, Carpenter SR. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18:648–56

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* 8:275– 79

Scheffer M, Szabo S, Gragnani A, van Nes EH, Rinaldi S, et al. 2003. Floating plant dominance as a stable state. *Proc. Natl. Acad. Sci. USA* 100:4040–45

Scheffer M. 1997. *The Ecology of Shallow Lakes*. London: Chapman and Hall

Scholze, M., Knorr, W., Arnell, N.W., Prentice, I., 2006. A climate-change risk analysis for world ecosystems. Proceedings of the National Academy of Sciences of the United States of America 103, 13116– 13120.

Schulze ED, Beck E, Muller-Hohenstein K. (2002) Water relations of plants. In: Plant Ecology. Springer-Verlag Berlin Heidelberg New York. ISBN 3-540-20833-X.

Seager, et al. (2007). Model Projections of an Imminent Transition to a More Arid Climate in Southwestern North America. Science 25 May 2007: 1181-1184.DOI:10.1126/science.1139601

Seidel, DJ and Fu, Q. and Randel, WJ and Reichler, TJ (2008) Widening of the tropical belt in a changing climate, Nature Geoscience Nature Geoscience 1 Vol.1 pp:21-24.

Shen, S. S. P. 1993. *A Course on Nonlinear Waves*. Kluwer Academic Publishers, Boston, MA.

Silvertown, J.(2004). Plant coexistence and the niche. Trends in Ecology and Evolution, 19:605–611.

Srivastava DS, Jefferies RL. 1995. Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh. *Can. J. Bot.* 73:75–83

Stanisci A, Acosta A, Di Marzio P, Dowgiallo G, Blasi C. (1998) Variazioni floristico-cenologiche e pedologiche nelle piscine del Parco Nazionale del Circeo. In: Stanisci A., Zerunian S. (eds.), Flora e Vegetazione del Parco Nazionale del Circeo:

223-235. Ministero per le politiche Agricole, Gestione ex A.S.F.D. (Sabaudia). Latina

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, et al. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ. Conserv.* 29:436–59

Suding K.N., Katherine L. G. Houseman G.R. 2004. Alternative states and positive feedbacks in restoration ecology. TRENDS in Ecology and Evolution Vol.19 No.1 January.

Knowlton N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *Am. Zool.* 32:674–82

Steele JH. 1998. Regime shifts in marine ecosystems. *Ecol. Appl.* 8:S33–S36

Sterl A. Severijns C., Dijkstra H., Hazeleger W., Van Oldenborgh G.J. et al., 2008. When can we expect extremely high surface temperatures? Geophysical research letters VOL. 35, L14703, doi:10.1029/2008GL034071

Strogatz, Steven H. 1994. Nonlinear Dynamics and Chaos. Addison Wesley publishing company.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. (1994) Competition and Biodiversity in Spatially Structured Habitats. Ecology 75: 2-16.

Tilman, D. et al. 2001. Forecasting agriculturally driven global environmental change. *Science* 292, 281±284.

Trenbath BR, Conway GR, Craig IA. 1989. Threats to sustainability in intensified agricultural systems: analysis and implications for management. In *Agroecology: Researching the Ecological Basis for Sustainable Agriculture*, ed. SR Gliessman, pp. 337–65. Berlin: Springer-Verlag

Tognetti R, Longobucco A, Miglietta F, Raschi A. (1998) Transpiration and stomatal behaviour of Quercus ilex plants during the summer in a Mediterranean carbon dioxide spring. Plant, Cell & Environment. 21(6):613-622.

Tyree M, Cochard H. (1996) Summer and winter embolism in oak: impact on water relations. In: Annales des sciences forestières.Vol 53.; 173–180.

Ubaldi, D. (1988) La vegetazione boschiva della provincia di Pesaro e Urbino. *Esercitazioni dell' Accademia Agraria in Pesaro*, **3**, 20.

Ulbrich U, May W, Li L, Lionello P, Pinto JG et al. (2006) Chapter 8: The Mediterranean climate change under global warming. In: Mediterranean.Vol Volume 4. Elsevier; 399-415.

Vance, R. R. (1984). Interference competition and the coexistence of two competitors on a single limiting resource. Ecology, 65:1349–1357.

Van de Koppel J, Rietkerk M, Weissing FJ. 1997. Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends Ecol. Evol.* 12:352–56

Van der Linden P., and Mitchell J.F.B. (eds.): ENSEMBLES: Climate Change and its Impacts: Summary of research and results from the ENSEMBLES project. Met Office Hadley Centre, FitzRoy Road, Exeter EX1 3PB, UK. 160pp (2009).

Van der Molen MK, Dolman AJ, Ciais P, Eglin T, Gobron N, et al. (2011) Drought and ecosystem carbon cycling. Agricultural and Forest Meteorology

Van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., et al., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521–524.

Vitale M, Scimone M, Feoli E, Manes F. (2003) Modelling leaf gas exchanges to predict functional trends in Mediterranean Quercus Ilex forest under climatic changes in temperature. Ecological Modelling. 166(1-2):123-134.

Vitousek PM, Walker LR, Whiteaker LD, Muellerdombois D, Matson PA. 1987. Biological invasion by *Myrica-Faya* alters ecosystem development in Hawaii. *Science* 238:802–4

Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. Human. 1997. Domination of Earth's ecosystems. *Science* 277, 494±499 .

Walker B, Holling C.S., Carpenter S.R., Kinzig A., (2004) Resilience , Adaptability and Transformability in Social – ecological Systems. Ecology And Society. Vol 9, Issue: 2,

Walters CJ, Kitchell JF. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58:1–12

Walters CJ, Kitchell JF. 2001. Cultivation/depensation effects on juvenile survival and recruitment: implications for the theory of fishing. *Can. J. Fish. Aquat. Sci.* 58:1–12

Ward J, Tockner K, Schiemer F. (1999) Biodiversity of floodplain river ecosystems: ecotones and connectivity1. Regulated Rivers: Research & Management. 15(1-3):125–139.

Wang GL, Eltahir EAB. 2000. Role of vegetation dynamics in enhancing the low frequency variability of the Sahel rainfall. *Water Resour. Res.* 36:1013–21

Worm B, Lotze H, Bostr¨om C, Engkvist R, Labanauskas V, Sommer U. 1999. Marine diversity shift linked to interactions among grazers, nutrients and propagule banks. *Mar. Ecol. Prog. Ser.* 185:309–14

Yu G, Song X, Wang Q, Liu Y, Guan D, et al. (2008) Water-use efficiency of forest ecosystems in eastern China and its relations to climatic variables. New Phytologist. 177(4):927–937.

Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC. 1995. Steppetundra transition: a herbivore-driven biome shift at the end of the Pleistocene. *Am. Nat.* 146:765–94

A Claudia e Francesco

Acknowledgments