Plant-soil feedback effects can have important consequences for interactions between plants. However, quantification of these effects is difficult due to the vast belowground diversity and technical problems inherent to measuring and manipulating soil communities. Therefore, there is a need for mathematical models to improve our understanding of plant-soil interactions. Pioneering mathematical models on plant-soil feedback effects have been developed by Bever and colleagues (Bever et al., 1997; Bever, 1999, 2003). In their most recent version of the model (“Bever model”) a few particular cases where plant-soil feedback affected plant coexistence and dynamics were described, but an exploration of all possible plant-soil feedback effects was not presented. The aim of our paper is to provide a full analysis of the Bever model, which contributes to our general understanding of plant-soil interactions and the consequences for plant community dynamics and diversity. We analyzed the model by means of a new type of graphical analysis, which provides a rather complete analysis of equilibria and their stability, and is still relatively easy to perform and understand. We found that plant coexistence could be explained by an interaction between net soil feedback effect and competition strength between the plants. Net positive feedback generally leads to species exclusion, but when competition coefficients are small enough plant species can coexist. Net negative feedback enhanced the range of plant coexistence by means of competitive oscillations. This result highlights that plant-soil feedbacks may enhance plant community diversity.

Keywords: Graphical analysis, plant-soil feedback, coexistence, oscillations, diversity
Ecologists have long recognized that interactions between plants are mediated by many abiotic (e.g., soil texture, nutrient availability, topography) and biotic factors (e.g., grazing, plant competition and facilitation) (e.g., [Harper, 1977; Tilman, 1988]). More recent research has stressed the influence of below-ground biota (the soil community) on interactions between plants (Klironomos, 2003; Callaway et al., 2004), by exerting positive or negative effects on the growth of specific plants (van der Putten et al., 1993; van der Putten and Van der Stoel, 1998; van der Heijden et al., 1998; Olff et al., 2003; De Deyn et al., 2003; Klironomos, 2003; van der Heijden et al., 2003). These effects have been shown to influence species at higher trophic levels (e.g., plant herbivores and their predators) as well (Soler et al., 2005). Therefore, interactions between soil communities and plants can potentially have a significant influence on species composition and diversity in many different parts of an ecosystem (van der Putten et al., 2001; Wardle et al., 2004).

The interaction between plant growth and soil communities, referred to as plant-soil feedback, is a two-step process: the presence of a specific plant changes the composition of the soil community, which in turn alters the growth rate of that specific plant (Bever, 2003; Reynolds et al., 2003). Quantifying the effect of soil organisms on plant growth, however, is difficult due to the vast below-ground diversity, and the technical problems inherent to measuring and manipulating soil communities (Bever, 2003; van der Putten et al., 2009). Therefore, a coupling of empirical results to mathematical models may improve our understanding of the role of plant-soil interactions in community assembly and diversity (van der Putten et al., 2009).

Pioneering work on coupling empirical soil feedback results to mathematical models has been performed by Bever and colleagues (Bever et al., 1997; Bever, 1999, 2003). These models are appealing to many empirical plant-soil ecologists because they do not require specific knowledge on the diversity of soil communities, or the effects of individual soil-borne species on plant growth. As a result, model predictions can be tested with relatively straightforward experiments (Bever, 1994; Bever et al., 1997). Bever (2003) proposed a framework that introduces plant-soil feedback into the classical Lotka-Volterra competition model, which has motivated several subsequent model studies on similar topics (Bonanomi et al., 2005; Umbanhowar and McCann, 2005; Eppinga et al., 2006; Eppstein et al., 2006; Eppstein and Molofsky, 2007).

Using the model framework, Bever (2003) highlighted two particular cases where plant-soil feedback affected coexistence of 2 competitive plant species: 1) negative plant-soil feedback facilitating coexistence between plants and 2) negative plant-soil feedback driving oscillations in plant abundances (Bever, 2003). However, there may be more ways in which plant-soil feedbacks can affect coexistence and dynamics of plant competitors which can be revealed by a full analysis of the model, i.e., an exploration of all possible parameter combinations. Such an analysis contributes to our general understanding of plant-soil feedback effects (van der Putten et al., 2009). The aim of our study is provide a complete analysis of the model by Bever (2003), referred here as the ‘Bever model’. In section 2 we will introduce the Bever model. In section 3 we will analyze the Bever model using a new graphical technique, which provides a rather complete analysis of equilibria and their stability, and is still
6.2 The Bever model

The "Bever model" (Bever 2003, Fig 6.1) studies the effects of two soil communities $S_A$ and $S_B$ on two plant species A and B. Each soil community in the model is specifically associated with one of the plant species (Yeates 1999; Wardle et al. 2004) that positively affects the growth rate of that specific soil community. On their turn, specific soil communities can have both positive and negative effects on growth of the plant they are associated with, and on the competing plant species (e.g. van der Putten and Van der Stoel 1998; De Deyn et al. 2003; Klironomos 2003), referred to as feedback effects. The dynamics of the plant populations A and B and the soil communities $S_A$ and $S_B$ are described by the following equations:

![Figure 6.1: Schematic representation of potential interactions between two plants A and B and their associated soil communities $S_A$ and $S_B$ in the Bever model.](image-url)
Here $N_i$ is the density of plant species $i$, $r_i$ is the intrinsic per capita growth rate of species $i$, $K_i$ is the carrying capacity of species $i$ when growing in isolation, and $c_i$ is the per capita effect of species $i$ on the growth rate of the competitor species, relative to the per capita effect of $i$ on the growth rate of its own population. In the presence of soil effects, each soil community is associated with one of the two plant species, where $S_i$ is the density of the biota associated with plant species $i$.

$N_A$ and $N_B$ are the densities of the two plant populations, $r_A$ and $r_B$ are the intrinsic per capita growth rates of the plant species, $K_A$ and $K_B$ are the carrying capacities of the plant species when growing in isolation, and $c_A$ and $c_B$ are the competition coefficients which are expressed as the per capita effects of each species on the growth rate of the competitor species (interspecific competition), relative to the per capita effect on the growth rate of its own population (intraspecific competition). $S_A$ and $S_B$ are the densities of the two soil communities, where $S_A$ is specifically associated with plant species A and $S_B$ with plant species B. In the absence of soil effects, the dynamics of the two competing plants species are described by the Lotka-Volterra competition dynamics (6.1a, 6.1b, 6.1c, 6.1d) for $S_A = S_B = 0$.

The specific effects of the soil communities on their plants, $\alpha_A$ and $\beta_B$, for plant A and B respectively, will be called “within” association effects, and the non-specific effects, $\alpha_B$ and $\beta_A$, will be called “cross” association effects. The net feedback effect of soil community composition on plant community dynamics will depend on both within and cross association feedback effects. These feedback effects can take any sign, in correspondence with mutualistic or pathogenic relationships. In mutualistic relationships plant growth may be favored by the presence of their symbionts, e.g. arbuscular mychorrhizal fungi (AMF), which enhance plant access to limiting resources. On the other hand, soil pathogens and root herbivores, e.g. root feeding nematodes, can negatively affect plant growth by direct removal of nutrients from root tissue and by reduction of soil nutrient uptake (Bever et al., 1997).

The effect of the plants on their respective soil communities is measured in relative terms, where $\nu$ is the ratio of the effect of plant B on its soil community against the effect of A on its soil community.

The model of Bever has been based on the dynamics of old-field communities (Bever, 1994). For these communities, it is reasonable to assume that both plant and soil communities have reached a relatively constant biomass density, but that the abundance of plant species still varies between years (Bever, 1994). Hence, it is assumed that $dS_A/dt + dS_B/dt = 0$ implying that the sum $S_A + S_B$ is constant. Bever models the soil
communities as fractions of the total soil community. Hence, \( S_A + S_B = 1 \) and equations (6.1c-6.1d) can be substituted by

\[
\frac{dS_A}{dt} = S_A(1 - S_A) \left( \frac{N_A - \nu N_B}{N_A + N_B} \right)
\]  

(6.2)

6.3 GRAPHICAL ANALYSIS

Our analysis will focus on equilibria and their stability. In order to do this it will be useful to split the analysis in several components. First, we discuss the effects of the soil dynamics on plants growing in isolation, which lead us to the concept of soil stability. Second, we consider the effects of a fixed soil composition on plant competition, which help us define the concept of competitive stability. Third, we take into account the net effects of the plant-soil feedbacks, and how to distinguish when they are positive or negative. Fourth, we integrate our criteria for soil stability, competitive stability, and feedbacks in a graphical methodology for the analysis of the complete system of equations (6.1a-6.1b) and (6.2).

6.3.1 Plant monocultures

Let us start by considering the absence of plant B, i.e. \( N_B = 0 \). This means that plant A is a monoculture, and its dynamical equation (6.1a) becomes

\[
\frac{dN_A}{dt} = \tau_A N_A \left\{ 1 + \alpha_A S_A + \beta_A S_B - \frac{N_A}{K_A} \right\}
\]

which has the structure of a logistic equation and where (after rearrangement) the carrying capacity takes the form of

\[
\kappa_A = K_A (1 + \alpha_A S_A + \beta_A S_B)
\]  

(6.3a)

In the absence of plant B the soil dynamics (6.2) follows \( dS_A/dt = S_A(1 - S_A) \), which is positive for \( 0 < S_A < 1 \). Because of the constraint \( S_A + S_B = 1 \), in a monoculture of A the soil community associated with plant A completely eliminates the soil community associated with plant B. As a consequence, in the long term plant A attains a stable monoculture equilibrium \( A_A : K_A (1 + \alpha_A) \) corresponding to the state where its soil biota is dominant \( (S_A = 1) \). There is another monoculture equilibrium \( A_B : K_B (1 + \beta_A) \), corresponding to dominance by B’s soil biota \( (S_A = 0) \) which is unstable.

If we reverse the roles and consider plant B the monoculture, i.e. \( N_A = 0 \), the soil dependent carrying capacity of plant B will be

\[
\kappa_B = K_B (1 + \alpha_B S_A + \beta_B S_B)
\]  

(6.3b)

Mutatis mutandis, in the monoculture of B the soil community associated with plant B completely replaces the soil community associated with plant A. Thus the monoculture of B has two equilibria, \( B_A : N_B = K_B (1 + \alpha_B) \) corresponding to dominance of A’s soil community \( (S_A = 1) \) which is unstable; and \( B_B : N_B = K_B (1 + \beta_B) \) corresponding to dominance of B’s soil community \( (S_A = 0) \) which is stable.
Recapitulating, we have that $A_B$ is unstable regarding fluctuations in soil composition (to increases above $S_A = 0$), whereas $A_A$ is stable (to decreases below $S_A = 1$) in this respect. For this reason, we say that $A_B$ is soil-unstable and $A_A$ is soil-stable. On the other hand $B_B$ is soil-stable (to increases above $S_A = 0$) and $B_A$ is soil-unstable (to decreases below $S_A = 1$).

The concept of soil stability is important not only for judging the stability of monoculture equilibria but also for community equilibria that happen to be characterized by $S_A$ being 0 or 1.

It is important to remind that the monoculture equilibria $A_A, A_B, B_A, B_B$ can only exist if $\alpha_A, \beta_A, \alpha_B, \beta_B > -1$ respectively. This is an assumption that we will maintain for the rest of this article.

### 6.3.2 Effect of a static soil community on plant competition

Consider a static soil composition, i.e. $dS_A/dt = dS_B/dt = 0$. In that case the Lotka-Volterra equations alone (6.1a, 6.1b) suffice to describe the plant competition. The conditions for coexistence or exclusion can be found by means of the graphical analysis of the system nullclines (Case, 2000), which are

$$\kappa_A = N_A + c_B N_B$$  \hspace{1cm} (6.4a)  
$$\kappa_B = N_B + c_A N_A$$  \hspace{1cm} (6.4b)  

for plants species A and B respectively, at a given fixed composition of the soil community. It is a standard result from Lotka-Volterra competition theory that a community equilibrium where both A and B coexist does exist when one of the following two conditions are met:

- $c_A < \kappa_B / \kappa_A$ and $c_B < \kappa_A / \kappa_B$. In this case both monocultures can be invaded by the other species, and the coexistence equilibrium is globally stable.
- $c_A > \kappa_B / \kappa_A$ and $c_B > \kappa_A / \kappa_B$. In this case both monocultures are stable, and the community equilibrium is unstable. The outcome of competition depends on the initial conditions.

Hence a community or “interior” equilibrium does exist whenever

$$\left( \frac{\kappa_B}{\kappa_A} - c_A \right) \left( \frac{\kappa_A}{\kappa_B} - c_B \right) > 0$$  \hspace{1cm} (6.5)  

and such equilibrium is stable whenever $c_A c_B < 1$ (i.e. interspecific competition is on average weaker than intraspecific competition).

It is useful to illustrate the conditions for equilibrium and stability using a plot like in Figure 6.2. Let define the ratios of (soil dependent) carrying capacities $x \equiv \kappa_B / \kappa_A$ and $y \equiv \kappa_A / \kappa_B$, thus the relation between $x$ and $c_A$ determines whether B can invade the monoculture of A, while the relation between $y$ and $c_B$ determines whether A can invade the monoculture of B. For given $c_A$ and $c_B$ all feasible plant competitive systems belong to the hyperbola $xy = 1$ in the $xy$ plane. If $c_A c_B < 1$ (Fig. 6.2a), this hyperbola intersects the coexistence region (doubly hatched area), which means that stable coexistence is possible.
Figure 6.2: Outcomes of the Lotka-Volterra system (6.1a, 6.1b). The plane is divided into four invasibility zones I, II, III, IV, such that B invades if \( x > c_A \) and A invades if \( x > c_B \), where \( x \equiv \kappa_B / \kappa_A, y \equiv \kappa_A / \kappa_B \) are the carrying capacity ratios in (6.5). (a) If \( c_A c_B < 1 \) stable equilibria exist at the intersection of the hyperbola \( xy = 1 \) with zone III, in which A and B invade. (b) If \( c_A c_B > 1 \) unstable equilibria exist at the intersection of \( xy = 1 \) with zone IV, where neither A or B can invade, and depending on the initial conditions A or B wins the competition. Intersection at I or II do not result in equilibrium, instead A or B always wins, respectively.

for certain ratios \( \kappa_B / \kappa_A \). But in case of \( c_A c_B > 1 \) (Fig. 6.2b), the hyperbola intersects the mutual exclusion region and stable coexistence is not possible at all.

Summarizing, for a given soil composition, monocultures and community equilibria (if they exist) are classified as stable or unstable regarding fluctuations in population densities. As we did before with respect to soil fluctuations, it is proper to define competitive stability: a monoculture is competitively stable if it cannot be invaded, or competitively unstable if it is invadable; a community equilibrium is competitively stable if \( c_A c_B < 1 \), or competitively unstable if \( c_A c_B > 1 \).

### 6.3.3 Positive versus negative feedbacks

According to (6.3), in the total absence soil feedback effects (\( \alpha_A = \alpha_B = \beta_A = \beta_B = 0 \)) \( \kappa_A = K_A \) and \( \kappa_B = K_B \) for any value of \( S_A \). As a consequence \( x = K_B / K_A \) and \( y = K_A / K_B \), i.e. all feasible competitive systems are represented by a single point of the hyperbola \( xy = 1 \) in Figure 6.2 no matter the soil composition. In the presence of soil feedbacks we have instead that \( x \) and \( y \) vary with \( S_A \), which can take any value between 0 and 1. This means that all feasible competitive systems belong to a continuous portion of the \( xy = 1 \) hyperbola, which we will refer to as the feasibility arc or simply the “arc”. Figure 6.3 indicates that the coordinates of the end points of this arc are
Figure 6.3: Effects of soil feedbacks on the feasibility of equilibria. Since soil composition $S_A$ is bounded by $[0,1]$ the set of feasible Lotka-Volterra systems belong to a feasibility arc of the unit hyperbola $xy = 1$, the end points of which are determined by the feedback ratios $\gamma_A, \gamma_B$. (a) If $\gamma_A \gamma_B > 1$ the net feedback is positive, plants attain maximum relative densities when their associate soil biotas are dominant, i.e. $\kappa_A / \kappa_B$ is maximum at $S_A = 1$, and $\kappa_B / \kappa_A$ is maximum at $S_A = 0$. (b) If $\gamma_A \gamma_B < 1$ the net feedback is negative, and plants attain minimum relative densities when their associated soil biotas are dominant.

\[
\begin{align*}
\text{at } S_A = 0 : & \quad x = \gamma_B, \quad y = \gamma_B^{-1} \\
\text{at } S_A = 1 : & \quad x = \gamma_A^{-1}, \quad y = \gamma_A
\end{align*}
\]

where the quantities $\gamma_A$ and $\gamma_B$ are

\[
\gamma_A = \frac{K_A(1 + \alpha_A)}{K_B(1 + \alpha_B)}, \quad \gamma_B = \frac{K_B(1 + \beta_B)}{K_A(1 + \beta_A)}
\] (6.6)

According to the model’s description (equations 6.1 and Fig. 6.1) we can interpret $\gamma_A$ and $\gamma_B$ in the following way. If we consider plant species A, the numerator of $\gamma_A$ turns out to be the maximum monoculture density that A attains with its associated soil community, i.e. due to “within” association feedback; on the other hand the denominator of $\gamma_A$ is the maximum monoculture density that B attains due to “cross” feedbacks. Thus $\gamma_A$ measures the net contribution of the feedback for plant A after accounting the non-specific effects of its soil community, i.e. losses, towards plant B. For this reason we call $\gamma_A$ the feedback ratio for plant A, and similarly $\gamma_B$ will be the feedback ratio for plant B. The product $\gamma_A \gamma_B$ of the feedback ratios will tell us the size and orientation of the hyperbolic arc

- $\gamma_A \gamma_B > 1$: species specific (within) feedback benefits are stronger than non-specific (cross) feedback benefits. As shown in Figure 6.1 $\kappa_B / \kappa_A$ is maximum if $S_A = 0$ and $\kappa_A / \kappa_B$ is maximum if $S_A = 1$ ($S_A$ increases along $xy = 1$ from lower-right to upper-left). A consequence of this is that a plant species is less vulnerable to invasion when
its associated soil biota is dominant (i.e. the difference \( x - c_A \) decreases as \( S_A \to 1 \) and \( y - c_B \) decreases as \( S_A \to 0 \)). In other words the (geometric) average or **net feedback is positive**, i.e. \( \log(\gamma_A \gamma_B) > 0 \).

- \( \gamma_A \gamma_B < 1 \): non-specific (cross) feedback benefits are stronger than specific (within) feedback benefits. This time (6.1b) shows that \( \kappa_B/\kappa_A \) minimum \( S_A = 0 \) and \( \kappa_A/\kappa_B \) is minimum at \( S_A = 1 \) (\( S_A \) increases along \( xy = 1 \) from upper-left to lower-right). In this case, plants become more prone to be invaded when its associated soil biota is dominant (i.e. the difference \( x - c_A \) increases as \( S_A \to 1 \) and \( y - c_B \) increases as \( S_A \to 0 \)). In this case the (geometric) average or **net feedback is negative**, i.e. \( \log(\gamma_A \gamma_B) < 0 \).

We can envision the plant competitive system as “moving” along the feasibility arc of the hyperbola \( xy = 1 \) as we vary the soil community composition. If the net feedback is positive the system moves “up” if we raise \( S_A \), or “down” if we raise \( S_B \). If the net feedback is instead negative, these directions are reversed. Such changes in \( S_A \) and \( S_B \) are driven by the abundance of the plants, meaning that there is a feedback that drives the system up or down these arcs in the combined plant-soil system.

The size of the feasibility arc increases with the absolute magnitude of the net feedback, \( |\log(\gamma_A \gamma_B)| \). Thus, in the absence of net feedback effects (\( \alpha_A = \alpha_B = \beta_A = \beta_B \to \gamma_A \gamma_B = 1 \)) the arc degenerates into a point of the unit hyperbola, and the plant community becomes a soil-independent Lotka-Volterra system, as if feedbacks were zero as discussed at the beginning.

6.3.4 **Combining plant and soil dynamics**

Combining the plots in Figures 6.3 and 6.2 provides us with a graphical method that is often sufficient for a rather complete characterization of the dynamics of the coupled plant-soil community described by equations (6.1a), (6.1b) and (6.2). As Figure 6.4 shows, there are 20 different ways or “cases” in which the feasibility arc can intersect the invasion zones. We will highlight two particular cases to illustrate the derivation of coexistence and invasion conditions in terms of competition coefficients and feedback ratios, and in the next section we treat more complex but interesting cases. See the Appendix A for a complete overview of the cases. Our graphical method is in the same spirit as the “recovery plane” analysis of Eppinga et al. (2006), in which the factors on the left-hand-side of inequality (6.5) are plotted against each other.

Figure 6.5a depicts case 12, where all feasible systems fit entirely in the region where only species B invades (II). As there are no other equilibria to consider (since the arc does not intersect III or IV), we conclude that independently of the state of the soil, only species B can grow in this system. Thus, species B and the system converges to the monoculture equilibrium \( B_B \) in which \( S_A = 0 \). In fact, in all cases where the feasibility arc lies within zones I or II (cases 1, 2, 11 and 12), one of the plants always wins, independently of the initial conditions. When the arc lies in zone III (cases 3 and 13) both can invade and coexist. And when it lies in zone IV (cases 4 and 14) neither can invade when rare, and the winner depends on the initial conditions, an outcome that is called **founder control** (Bolker et al., ...
Figure 6.4: Intersection of the feasibility arc of Fig. 6.3 with the invasion zones of Fig. 6.2. The arc is represented as an arrow, thus indicating its orientation: the "head" \((x = \gamma_A^{-1}, y = \gamma_A)\) corresponds to \(S_A = 1\) and the "tail" \((x = \gamma_B, y = \gamma_B^{-1})\) to \(S_A = 0\). A monoculture of species A will follow the orientation of the arc \((S_A\) increases), whereas a monoculture of plant B will move in the opposite sense \((S_B\) increases). There are 20 intersection "cases", differing in the relative position and arc orientation with respect to the invasion zones. The location of the end points (head & tail) with respect to the invasion zones determines if a species can invade or not.
Figure 6.5: Graphical analysis of two cases depicted in Fig. 5.4. (a) In case 12 the feasibility arc occurs in a zone where only species B can invade (II) and a coexistence equilibrium is not possible, thus species B always wins. (b) In case 15 the monoculture of species A would evolve towards the $S_A = 1$ end of the arc, which lies in a zone where species B can invade (III). The monoculture of B will instead evolve towards the $S_A = 0$, located in the zone where species A can invade (I). As a consequence both can grow when rare and coexist.

Thus, whenever the feasibility arc lies completely inside an invasion zone, the qualitative outcomes of plant competition do not depend on the net direction of the feedback, positive or negative.

In Figure 6.5b we show case 15, which is a bit more complex because the feasibility arc spans two invasion zones. In a monoculture of plant A, the soil composition will change towards the $S_A = 1$ end of the arc, which lies in the invasion zone of species A and B (III). In contrast, in the monoculture of species B, the soil composition change towards the $S_A = 0$ end of the arc, which lies in the invasion zone of species A (I). We conclude that in this case, soil community effects enable coexistence of the two plant species.

As indicated by Figure 6.5, the position of the arc’s end points with respect to the invasion zones tell us whether a plant can invade or not. Whenever plant A is a monoculture, it will attain the equilibrium state $A_A$ which corresponds to the $S_A = 1$ end of the arc. Thus $A_A$ can be invaded plant B if only if

$$c_A < \gamma_A^{-1}$$

(6.7)

and by symmetry, the monoculture of plant B attains the equilibrium state $B_B$ corresponding to the $S_A = 0$ end of the arc, which can be invaded by plant A if and only if

$$c_B < \gamma_B^{-1}$$

(6.8)

Combining both inequalities, we obtain a necessary condition for mutual invasion

$$\frac{(c_A c_B)}{\gamma_A \gamma_B} < 1$$

(6.9)
which coincides with the requirement for stable coexistence in Lotka-Volterra models \((c_{ACB} < 1)\) in the absence of net feedback \((\alpha_A = \alpha_B = \beta_A = \beta_B)\). This lead to the prediction that the more negative the feedbacks (low \(\gamma_{AB}\)) the higher the chances of coexistence via mutual invasion. On the other hand if feedbacks are strongly positive (high \(\gamma_{AB}\)), co-existence via mutual invasion demands lower competition strength (low \(c_{ACB}\)). Back to the graphs in Figure 6.4, when the feedback is negative, further decrease of the product \(\gamma_{AB}\) widens the feasibility arc, until the end points fall in the zones where monocultures can be invaded. When feedback is positive, further increase of the product \(\gamma_{AB}\) also widens the feasibility arc, but this time the arc has the reverse orientation and in consequence the end points will end up in zones where monocultures cannot be invaded; to make coexistence possible again, \(c_A\) or \(c_B\) must be lowered such that the arc is forced to lie inside the mutual invasion zone III.

Although quite similar with standard Lotka-Volterra theory, conditions (6.7,6.8) and (6.9) only tells us about invasion. As we will show, neither conditions (6.7,6.8) are sufficient, nor condition (6.9) necessary, for plant coexistence in general.

6.4 Results and Discussion

In this section, we employ the graphical method presented in section 3 to address some important aspects of the plant-soil interaction. First of all, we justify our definition of net positive and net negative feedbacks. Second, we study the mechanism by which competitive oscillations emerge in Bever’s model. Third, we discuss the consequences of competitive oscillations for the maintenance of plant diversity. And lastly, we critically examine the generality of results obtained by means of invasion analysis and our graphical methodology.

6.4.1 Positive and negative feedbacks

As seen in Figure 6.3, we use the product \(\gamma_{AB}\) to unequivocally discriminate between scenarios in which the net plant-soil feedback is positive or negative. If \(\gamma_{AB} > 1\) the net feedback is positive, i.e. self-enhancing, because each plant attains its highest relative abundance –as measured by ratios of soil dependent carrying capacities \(k_A/k_B\)– when its associated soil biota is dominant. On the other hand, if \(\gamma_{AB} < 1\) the net feedback is negative, i.e. detrimental, because the pattern is the absolute opposite.

In contrast with us, Bever employs the soil feedback interaction coefficient \(I_S = \alpha_A - \alpha_B - \beta_A + \beta_B\) to distinguish between net positive \(I_S > 0\), and net negative \(I_S < 0\), plant-soil effects. In previous works \(I_S\) was originally meant to be used in models without density dependence (Bever et al., 1997, Bever, 1999), and its extrapolation for the present system requires to consider equivalent competitors (Bever, 2003), e.g. parameter symmetry.

In most cases our criterion and Bever’s coincide, but it is very easy to find examples where it does not. Let for example have \(\alpha_A = -0.06, \beta_B = 0.52, \alpha_B = -0.41, \beta_A = 0.95\), this results in \(I_S = -0.08\) indicating negative feedback according to Bever and \(\gamma_{AB} = 1,242\) indicating positive feedback according to us. Discrepancies in the opposite direction are possible too, e.g. \(\alpha_A = 0.76, \beta_B = -0.95, \alpha_B = 0.18, \beta_A = -0.62\) results in \(I_S = 0.25\) (Bever positive) and \(\gamma_{AB} = 0.196\) (us negative). Since \(I_S\) cannot tell apart net positive or
negative feedback in all cases as \( \gamma_A \gamma_B \) does, we consider our choice the most appropriate in the present context.

We can reconcile both approaches, by deriving a net interaction coefficient that relaxes the assumption of parameter symmetry:

\[
I_S = \log(\gamma_A \gamma_B) = \log(1 + \alpha_A) - \log(1 + \alpha_B) - \log(1 + \beta_A) + \log(1 + \beta_B)
\]  

Equation (6.10) only converges to \( I_S \approx \alpha_A - \alpha_B - \beta_A + \beta_B \) for small values of the feedback coefficients. This suggests that when relatively strong plant-soil community effects are measured in empirical home vs. away experiments, it is necessary to use equation (6.10) to predict the consequences of plant-soil feedbacks for the plant community.

### 6.4.2 When do oscillations occur?

Perhaps one of the most interesting results in Bever (2003) is a numerical example showing that species that cannot coexist in the absence of feedback, can do so by means of competitive oscillations under net negative feedbacks. When trying to run the same example, we found instead that a coexistence equilibrium is rapidly achieved. We concluded that the example provided is a numerical artifact due to the use of inappropriate integration methods. As a consequence we tried to figure out how and under which conditions are oscillations possible.

Population cycles are frequently associated with predator-prey dynamics. Competitive oscillations however, are a common feature in Lotka-Volterra equations (Gilpin, 1975; May and Leonard, 1975) and resource competition models (Huisman and Weissing, 2001; Revilla and Weissing, 2008). In these models, oscillations require at least three competitors such that species \( P \) outcompetes species \( R, S \) outcompetes \( P \) and \( R \) outcompetes \( S \), as in the Rock-Paper-Scissors game. Mathematically, the monocultures of \( R, P \) and \( S \) are connected by means of heteroclinic orbits, i.e. a sequence of paths \( R \rightarrow P \rightarrow S \rightarrow R \) forms a cycle. Although the Bever model involves only two plant competitors, it has in fact four monocultures: \( A_A, A_B, B_B, B_A \), and this allows us to construct an heteroclinic cycle as follows.

First, let us assume that conditions (6.7) and (6.8) hold. This means that both plants monocultures can be invaded when their associated soil biotas are dominant, in other words \( A_A \) and \( B_B \) are unstable against invasion. Second, let us assume each monoculture cannot be invaded when the invader’s soil biota is dominant, in other words \( A_B \) and \( B_A \) are stable against invasion. The conditions that allow this to happen can be easily found. Consider the monoculture \( A_B \) of plant A where \( N_A = K_A(1 + \beta_A), N_B = 0, S_A = 0 \); substituting it in equation (6.1b) shows that plant B cannot invade this equilibrium \( dN_B/dt|_{A_B} < 0 \) if

\[
c_A > \gamma_B \tag{6.11}
\]

on the other hand in the monoculture \( B_A \) of plant B we have \( N_B = K_B(1 + \alpha_B), N_A = 0, S_A = 1 \); and its substitution in equation (6.1a) shows that plant A cannot invade this equilibrium \( dN_A/dt|_{B_A} < 0 \) if

\[
c_B > \gamma_A \tag{6.12}
\]
Figure 6.6: Competitive oscillations. (a) The monoculture of species A evolves from a non-invadable (I) to an invadable (II) condition, and the monoculture of B from non-invadable (II) to invadable (I); in both directions, the system passes through the zone of unstable community equilibria (IV). (b) The parameter space is mapped into a phase space where circles represent equilibria (white: unstable, gray:saddle) at the corresponding invasion zones (this mapping is explained in Appendix A). The diagonal line represents the A-B nullcline (species A grows towards the right B grows towards the left), and the dashed line is the soil nullcline ($S_A$ increases in the right, and decreases in the left); their intersection corresponds to the internal equilibrium predicted in (a). Monocultures are competitively or soil stable, but not both: they are saddle points forming a heteroclinic cycle around the internal equilibrium $AB$ which is competitively unstable. The system oscillates permanently.

In a the graphical representation of Figure 6.6, conditions (6.4) can simultaneously occur if and only if: the $S_A = 1$ end point of the feasibility arc lies in the zone where only plant B invades (II), and if the $S_A = 0$ end point of the arc lies in the zone where only plant A invades (I); in other words only for cases 19 and 20. Let see what happens in case 20, shown in detail in Figure 6.6b:

1. at $S_A = 1$ plant B invades $A_A$: the system moves towards $B_A$ ($A_A \rightarrow B_A$)
2. $B_A$ is soil unstable: the system moves towards $B_B$ ($B_A \rightarrow B_B$) and $S_A \rightarrow 0$
3. at $S_A = 0$ plant A invades $B_B$: the system moves towards $A_B$ ($B_B \rightarrow A_B$)
4. $A_B$ is soil unstable: the system moves towards $A_A$ ($A_B \rightarrow A_A$) and $S_A \rightarrow 1$

Thus the four monoculture equilibria are saddle points connected through heteroclinic orbits in the sequence $A_A \rightarrow B_A \rightarrow B_B \rightarrow A_B \rightarrow A_A$. That is how oscillations originate, and Figure 6.6b shows a representation of the corresponding dynamics, where plants A and B take turns trying to outcompete each other.
Figure 6.7: Competitive oscillations for increasing competition strength $c_A c_B$. Top row shows plants A (solid line) and B (dashed line) densities, bottom row indicates the soil composition. In (a) $c_A = 0.858$ and $c_B = 0.98$, oscillations damped out. In (b) $c_A = 1.005$ and $c_B = 0.98$, oscillations persist as limit cycle. In (c) $c_A = 1.055$ and $c_B = 0.98$, oscillations are heteroclinic. The other parameters are as in Bever (2003): $r_A = 0.7$; $K_A = 100$; $r_B = 0.5$; $K_B = 120$; $\alpha_A = -0.03$; $\beta_A = 0.1; \alpha_B = 0.1; \beta_B = -0.2$ and $\nu = 0.8$.

Figure 6.7 shows the temporal evolution of such oscillations. Using Bever’s parametrization the system always converges to a coexistence equilibrium (Fig. 6.7a). By increasing the strength of competition, $c_A c_B$, this equilibrium becomes unstable and give rise to limit cycles (Fig. 6.7b). With further increases in competition strength the cycles become heteroclinic, i.e. oscillations attain very low minima for increasingly longer times (Fig. 6.7c). Heteroclinic oscillations are considered mathematical artifacts: sooner or later one plant species will get extinct in real life scenarios. If $c_A$ or $c_B$ become too large, one of the conditions, (6.7) or (6.7), is no longer fulfilled. At this point, the heteroclinic cycle driving the oscillations no longer exists.

As indicated by this numerical example, the local stability of the community equilibrium changes from stable to unstable when the product $c_A c_B$ is smaller than 1 ($c_A c_B \approx 0.975$), which is in contrast with the standard Lotka-Volterra stability threshold $c_A c_B = 1$. This is a consistent result and it can be explained by our graphical method as follows. Competitive
oscillations require that the arc end points \( S_A = 0 \) and \( S_A = 1 \) lie in zones I and II respectively; consequently, the arc joining them must pass through zones III or IV which explains the existence of an “internal” coexistence equilibrium \( \textbf{AB} : \hat{N}_A > 0, \hat{N}_B > 0, 0 < \hat{S}_A < 1 \) (and the non-existence of “border” equilibria, i.e. with \( \hat{S}_A = 0 \) or 1). If the arc intersects zone IV (Fig. 6.6a), the internal equilibrium is competitively unstable (\( c_{ACB} > 1 \)); thus oscillations will persist. On the other hand, if the arc intersects zone III instead, the internal equilibrium is competitively stable (\( c_{ACB} < 1 \)), which is necessary but not sufficient to guarantee stability; thus oscillations can persist or vanish. Summarizing: the equilibrium \( \textbf{AB} \) is always unstable if \( c_{ACB} > 1 \), but cannot guaranteed to be stable if \( c_{ACB} < 1 \). Conclusion: the \( c_{ACB} \) stability threshold of an internal equilibrium is lower than 1 (Appendix B), i.e.

\[
c_{ACB} = 1 - \epsilon \tag{6.13}
\]

where \( \epsilon \) is a positive quantity. If the soil equilibrium composition \( \hat{S}_A \) happens to be very close to 0 or 1, or if there is parameter symmetry for \( r_A = r_B, K_A = K_B, \gamma = 1 \) and \( c_A = c_B = c \) (but not for \( \alpha_A, \alpha_B, \beta_A, \beta_B \)), we recover the standard Lotka-Volterra stability threshold.

Since it is geometrically impossible to place \( \textbf{A}_A \) in the exclusive invasion zone of B (II) and \( \textbf{B}_B \) in the exclusive invasion zone of A (I) when \( \gamma_A \gamma_B > 1 \), oscillations cannot develop under net positive feedback. We conclude that persistent competitive oscillations, that means limit cycles, require: 1) net negative feedback \( \gamma_A \gamma_B < 1 \), 2) mutual invasion, and 3) unstable community equilibria.

### 6.4.3 Does negative soil feedback enhance coexistence?

An important conclusion of Bever (2003) is that net negative feedbacks enhance coexistence and promote high diversity, while net positive feedbacks leads to exclusion and low diversity. This can be understood graphically: it is easier to conceive soil-stable monocultures \( \textbf{A}_A(S_A = 1) \) and \( \textbf{B}_B(S_A = 0) \) inside the invasion zones of plants B (II) and A (I) respectively if the feasibility arc in Figure 6.2 is oriented according to the pattern of net negative feedbacks as in Figure 6.3b, compared with the opposite orientation under net positive feedbacks as in Figure 6.3a.

But since negative feedbacks can in theory lead to competitive oscillations, we have to evaluate their consequences for the long term dynamics of the community. On the one hand, coexistence through oscillations is coexistence after all: no species can be excluded (in a mathematical sense). On the other hand, coexistence through oscillations is a relatively uncertain mode of coexistence: populations can be driven close to very low densities in which case extinction may occur due to demographic stochasticity (as in the enrichment paradoxi of Rosenzweig 1971). Thus, successful invasion (6.7, 6.8) does not imply the realization of long term coexistence.

To get an idea why this is an important issue, let us compare the occurrence of limit versus heteroclinic cycles using the pattern seen in Figure 6.6 as an example. There, oscillations develop above \( c_{ACB} = 0.975 \) (i.e. between Figs. 6.6a,b) and must end somewhere below \( c_{ACB} = 1.559 \) the point where the requirement for mutual invasion (6.9) does not hold anymore. If we consider \( c_{ACB} = 1.029 \) (Fig. 6.6c) as the switching point between limit cycles and heteroclinic cycles, then limit cycles occur for a rather small region
In parameter space in comparison with heteroclinic cycles. In other words, a small increase in the strength of competition results in a very large increase in the amplitude of oscillations, and thus the risk of extinction.

In addition, equation (6.13) predicts that oscillations may occur in a system for which the plants would otherwise coexist at stable densities in the absence of net feedback (i.e. when $1 - \epsilon < c_A c_B < 1$ and $\alpha_A = \alpha_B = \beta_A = \beta_B$). Unfortunately, the extent of destabilization brought by negative feedbacks cannot be evaluated in the present model, since we do not have an explicit algebraic expression for the quantity $\epsilon$ appearing in (6.13).

If competitive oscillations turn out to be a common feature, Bever’s conclusion regarding the role of negative feedbacks in the maintenance of diversity could be considered premature, because of the destabilizing effects on stable communities. On the other hand, in a spatial context the risks associated with large amplitude oscillations can be compensated by migration; and heteroclinic cycles could also mean local opportunities for invasion, and regional persistence.

### 6.4.4 Invasion requirements and coexistence requirements

Invasion analysis is a powerful technique for the analysis of dynamical systems in ecology and evolution (Case, 2000). When properly used, invasion criteria are very useful to predict the range of dynamics that a dynamical system can possibly display. In the present context, by considering (6.7) and (6.8), and the direction of the net feedback, we can list all possible dynamics of Bever’s model as in Table 6.1.

However, there can be some limitations using invasion analysis which can be illustrated by the following example. Consider a scenario of net positive feedback ($\gamma_A \gamma_B > 1$) as in Figure 6.8a (case 5), where the feasibility arc of the competitive system is such that $c_A > \gamma_A^{-1}$ and $c_B < \gamma_B^{-1}$, and mutual invasion criterion (6.9) does not hold: plant species A is able to grow when rare since (6.8) holds, but plant species B cannot since (6.7) does not hold.

However, coexistence may still be possible. As indicated in Figure 6.8h, the $S_A = 0$ end point of the arc lies in zone III, which means that there is a competitively stable plant community equilibrium when $S_A = 0$. Following our previous notation, let call this equilibrium $AB_B$ since the soil is dominated by B’s soil biota. If the ratio of plant equilibrium densities is $N_A/N_B < \nu$ then according to (6.2) $dS_A/dt < 0$, thus for small fluctuations vanish and $AB_B$ is soil stable. Thus, $AB_B$ is a local attractor because is competitively stable and soil stable. The other end point of the arc $S_A = 1$ lies in zone I, where a coexistence equilibrium is not possible and plant A attains a competitively stable and soil stable monoculture $A_A$, i.e. another local attractor. As a consequence, the system has two alternative stable states: the coexistence equilibrium $AB_B$ dominated by B’s soil community and the soil-stable monoculture $A_A$ dominated by A’s soil community, as shown in Figure 6.8a.

In contrast if at $AB_B$ the density ratios are $N_A/N_B > \nu$ then $dS_A/dt > 0$ and small fluctuations of $S_A$ increase, making $AB_B$ soil unstable, while $A_A$ remains stable in both senses (soil and competitively). In this case A always wins, as predicted by the invasion criterion.

This example illustrates two things. The first is a limitation in our graphical analysis, which cannot address soil stability in all the cases, like it does with respect to competitive
Figure 6.8: Alternative stable states. (a) In this configuration a monoculture of species A evolves from an invadable (III) to a non-invadable zone (I), whereas a monoculture of B can be invaded always: coexistence by means of mutual invasion is ruled out. However, there are coexistence equilibria because the feasibility arc intersects the zone of mutual invasion (III). (b) The phase space shows the equilibria (white: unstable, black: stable, gray: saddle) and the invasion zones. The diagonal line representing the A-B nullcline (both species grow towards it) intersects $S_A = 0$ giving rise to the coexistence equilibrium $AB$ predicted in part (a). If the vertical dashed line representing the soil-nullcline ($S_A$ increases to the right, and decreases to the left) intersects the A-B nullcline there will be an internal equilibrium $AB$ that is a saddle point; and depending on the initial conditions the system moves towards the monoculture of $A_A$ dominated by A's soil biota, or towards the coexistence equilibrium $AB_B$ dominated by B's soil biota.
### Table 6.1: The sign of the net feedback and the invasion criteria determine the outcomes of the model. In case of stable coexistence the soil composition is indicated. In case of exclusion, the soil composition consists entirely to the one associated with the winner ($S_A = 1$ if $A$ wins, $S_A = 0$ if $B$ wins).

<table>
<thead>
<tr>
<th>Positive net feedback $\gamma_{AB} &gt; 1$</th>
<th>Negative net feedback $\gamma_{AB} &lt; 1$</th>
</tr>
</thead>
</table>
| **Both invade** $c_A \gamma_A < 1$  
$c_B \gamma_B < 1$ | 1. Stable coexistence ($S_A = 1$)  
2. Stable coexistence ($S_A = 0$)  
3. Stable coexistence ($S_A = 0$ or $S_A = 1$, depends on initial conditions) |
| **A invades** $c_B \gamma_B < 1$  
B does not $c_A \gamma_A > 1$ | 1. A wins  
2. A wins or stable coexistence (depends on initial conditions) |
| **B invades** $c_A \gamma_A < 1$  
A does not $c_B \gamma_B > 1$ | 1. B wins  
2. B wins or stable coexistence (depends on initial conditions) |
| **None invade** $c_A \gamma_A > 1$  
$c_B \gamma_B > 1$ | A or B wins (depends on initial conditions)  
A or B wins (depends on initial conditions) |

stability (in other words we cannot infer the magnitude of $\gamma$ in the graphs). Second, it shows the limitations of invasion analysis. Invasion analysis is a powerful technique for the analysis of dynamical systems in ecology and evolution [Case, 2000], perhaps the best example is the classical Lotka-Volterra model where mutual invasion and stable coexistence are synonymous. But if the model being considered displays multiple equilibria and alternative stable states, as is the present case, it is erroneous to state that mutual invasion is a requisite for coexistence.

Nevertheless, when properly used, invasion criteria remain very useful for predicting the range of dynamics that a dynamical system can possibly display. In the present context, invasion conditions (6.7) and (6.8), and the direction of the net feedback, allow us to list all the possible dynamics of Bever’s model as shown in Table 6.1.
6.5 General Conclusions

In this paper we performed a more complete analysis of the Bever (2003) model to get more insight in plant species coexistence and dynamics and the potential role of plant-soil feedback affecting those. We found that plant species coexistence could be explained by an interaction between net soil feedback \( (\gamma_i) \) and competition strength \( (c_i) \) between the plants, i.e. when feedback becomes more positive competition coefficients have to be lower in order to allow plant coexistence. This means that more negative plant soil feedback result in higher chances for coexistence. Negative soil feedback has been suggested previously as one of the mechanisms to explain plant species coexistence and consequently to maintain plant diversity (Bever et al., 1997; van der Heijden et al., 2008). Results of different recent empirical studies, as well as a meta-analysis of more than 300 plant-soil feedback experiments, indeed provide evidence for this hypothesis (Bever, 1994; Mills and Bever, 1998; De Deyn et al., 2003; Kulmatiski et al., 2008; Bradley et al., 2008).

We addressed four important issues concerning plant-soil feedback effects. First, we discussed the definition of feedback in a mathematical model. We showed that the assumption of parameter symmetry that is needed to calculate Bever’s interaction coefficient \( (I_S) \) can be relaxed when introducing the relative feedback coefficient, \( \log(\gamma_A, \gamma_B) \). Our results show that especially in experiments where large soil community effects are measured, it may be important to use the relative feedback coefficient to assess plant community consequences.

Second, we found that negative soil feedback can drive oscillations in plant abundances, but only under different conditions than presented by Bever. Stability of soil-driven plant dynamics was dependent on the competition strengths between the plants, i.e., the more competitive the plants were, the less stable coexistence was. We do not know how realistic it is that oscillations in plant abundances in nature are driven by soil feedback, because the range in which we found oscillations was very narrow and cycles quickly resulted in heteroclinic cycles, which in real life scenarios will probably result in extinction of one of the two plant species. We are not aware of any empirical study directly testing the effect of negative soil feedback on plant oscillations. However, there are suggestions that soil-borne pathogens may play an important role determining plant community dynamics (Olff et al., 2000). Moreover, different studies showed that soil feedback can enhance succession (van der Putten et al., 1993; De Deyn et al., 2003) and thus, can drive plant community dynamics. However, these dynamics are not necessarily oscillations of the same plant species, but may be different plant species succeeding each other.

Third, we discussed the consequences of oscillations for plant community diversity. We found that in the presence of negative soil feedback plant coexistence was possible under conditions that would otherwise lead to competitive exclusion of one of the two plant species. This was coexistence by means of oscillations of plant abundances, i.e., soil feedback increased the range in which oscillations occurred. Thus, in the presence of soil feedback oscillations would occur in situations that would otherwise allow stable coexistence between the plant species. Therefore, we can conclude that net negative plant-soil feedback can either promote or limit plant community diversity, depending on the role of oscillations on plant diversity. On the one hand, negative feedback enlarged the range in which plants could coexist, thus in that sense coexistence and consequently diversity was enhanced by
soil feedback. On the other hand, soil feedback can be viewed as a factor destabilizing plant species coexistence, because it causes oscillations in situations that otherwise would allow stable coexistence between the plant species. In real life scenarios the oscillations, especially the heteroclinic cycles may enhance chances for exclusion of one of the plant species, thereby reducing plant diversity.

Fourth, we presented an overview of the dynamics of the model analyzed with our new graphical method. The Bever model, relatively simple at first sight, already showed quite complex dynamics, however, this new graphical technique provided a rather complete analysis of equilibria and their stability and is still relatively easy to perform and understand. Results obtained by the graphical analysis agree with results from the mathematical analysis. Although our new technique was very useful in providing a full model analysis and overview of all scenarios, we have to conclude that there were some limitations because it could not address soil stability in all cases.

Most of our general conclusions agree with Bever, i.e., that plant species coexistence is dependent on an interplay between net plant-soil feedback and competition strength and that negative soil feedback can drive plant community dynamics. However, some of our results disagreed with Bever’s findings. First, we found that it was better to express net soil feedback as the relative feedback coefficient $\log(\gamma_A \gamma_B)$, instead of the interaction coefficient $I_S$. Second, we found that even under positive feedbacks, in general associated with species exclusion and loss of plant diversity, plant species are able to coexist if competition coefficients are low enough. Therefore, we conclude that mutual invasion is not a necessary requirement for coexistence, yet it does increase chances a lot. Third, soil feedback driven oscillations as presented by Bever were probably caused by the use of inappropriate integration methods, since redoing the simulations with similar parameter settings resulted in stable coexistence between the two plant species. However, we were able to find a range of parameters under which plant-soil interactions led to sustained oscillations.

Although most of the insights gained from the Bever model and our new analysis coincide, we still think we have to be careful translating these findings to the real world. On the one hand because the model is relatively simple. For example, one assumption of the model is that the soil community is always saturated, i.e. $S_A + S_B = 1$. In old-field ecosystems this assumption may hold (Bever, 1994), but extrapolation to other systems may be difficult. To get better insight in plant-soil interactions and their consequences for community dynamics and diversity, it would be useful to develop a more mechanistic model. On the other hand, oscillations in plant abundances occurred in a very narrow range and may result in exclusion of one of the plant species easily. Therefore, we cannot be sure whether it is likely to discover a phenomenon like the oscillations in nature. Finally, the oscillations extended the range where plant coexistence was possible, which led to the important conclusion that soil feedback may enhance plant diversity. However, this form of non-equilibrium coexistence may lead to stochastically driven extinction of plant species in real ecosystems. An outstanding challenge is to examine whether plant oscillations occur in nature under the conditions predicted by the model, and their role in maintaining plant diversity.
Appendix A: Graphical analysis

**APPENDIX A: GRAPHICAL ANALYSIS**

Figure 6.4 is useful for classifying and describing the main features of the dynamics in terms of the invasion conditions. For example in cases 1, 2, 11 and 12 it is easy to see that only one species A or B always wins, because only one of them is able to grow for any soil composition. In cases 4 and 14 we have that any resident species will be protected against invasion, and any equilibrium that may exist will be competitively unstable, for any soil composition.

However, cases 3, 5-10, 13, 15-20 are more complicated. In these situations, it is sometimes useful to have a graphical representation in the familiar form of a phase space and nullclines. Although this is possible for three-dimensional system like the Bever mode, the following two-dimensional representation is more convenient:

The phase space is constructed according to the following rules:
The horizontal axis indicates the plant composition: plant A is dominant on the right, plant B on the left. The vertical axis indicates soil composition: A’s soil biota is dominates on the top, B’s soil biota dominates on the bottom.

The corners represent the plant monocultures, with $A_B, B_B$ corresponding to $S_A = 0$, and $A_A, B_A$ corresponding to $S_A = 1$. Depending on the competitive stability conditions (6.7, 6.8, 6.11, 6.12) and their soil stability, the corners are classified as stable, unstable or saddle points.

The invasion zones intersected by the feasibility arc become the domains of attraction in the phase plot, placed in the same order as they are encountered by traversing the arc from $S_A = 0$ to 1 (and using the same fill patterns).

If the arc intersects zones III or IV the corresponding domain of attraction in the phase plot is divided by a diagonal line. This line, representing coexistence equilibria, is the plant nullcline, i.e. a nullcline for the plant composition, not the plant densities. In case of intersecting zone III, the plant composition moves towards the line (communities are competitively stable). In case of intersection with zone IV, the plant composition moves away from the line (communities are competitively unstable).

The plane is divided by vertical that represents the non trivial soil nullcline: $S_A$ increases at the right of the line ($N_A > \nu N_B$ in eq. 6.2), and decreases at the left ($N_A < \nu N_B$ in eq. 6.2). The smaller the $\nu$ the bigger the portion of the plane where $S_A$ increases, and viceversa. The top ($S_A = 1$) and the bottom ($S_A = 0$) sides of the plane are trivial soil nullclines.

A coexistence equilibrium corresponds to the intersection of the plant nullcline with a soil nullcline, trivial or not. For this reason, there can be border equilibria where $S_A = 0, S_A = 1$ or an internal equilibrium where $S_A$ is intermediate. Depending on its location with respect to the attraction domains and the non trivial plant nullcline, an equilibrium is declared stable, unstable or a saddle point.

Because of symmetry, we do not show cases 6, 8, 16 and 18 because they are qualitatively equivalent to cases 5, 7, 17 and 18 (by swapping the “A” and “B” labels). Cases 3 and 13 are very similar in the stability of their monocultures, and because of having border equilibria. However, they display qualitatively different dynamics. Under net positive feedbacks (case 3) the system can display alternative stable states: coexistence with dominance of plant A and its soil community or coexistence with dominance by plant B and its soil community. On the other hand, under net negative feedbacks (case 13) there can not be alternative stable states, and oscillations may develop (though we suspect they dampen out given the geometry of the nullclines).

The majority of cases under net positive feedback result in competitive exclusion. However, some can display alternative stable states, and coexistence depending on the initial conditions (5 and 6). On the other hand, the majority of scenarios under net negative feedback promote mutual invasion and coexistence (17 and 18 are the exceptions), including non-equilibrium coexistence through oscillations (19 and 20).
Consider an internal equilibrium $A_B$, where $N_A > 0, N_B > 0$ and $0 < S_A > 1$. We already know that if the net feedback is positive ($\gamma_A \gamma_B > 1$) $A_B$ lies in the zone of competitive instability (zone IV in 6.6b). Thus, under net negative feedback the community equilibrium will be always unstable, and the oscillations will persist.

Thus, from here onwards we will consider that the net feedback is negative ($\gamma_A \gamma_B < 1$). In this case $A_B$ is locally stable if and only if all eigenvalues $\lambda$ of the jacobian matrix of the dynamical system (6.1a, 6.1b, 6.2) evaluated at $A_B$

$$J = \begin{bmatrix}
-\frac{r АN_A}{K_A} & -\frac{c_Аr АN_A}{K_A} & \frac{r АN_A(\alpha_A - \beta_A)}{1 - S_A} \\
-\frac{c_АT МN_B}{K_B} & -\frac{r_ТМN_B}{K_B} & \frac{r_ТМN_B(\alpha_B - \beta_B)}{1 - S_A} \\
\frac{S_А(1 - S_A)}{N_A + N_B} & -\frac{\gamma S_А(1 - S_A)}{N_A + N_B} & 0
\end{bmatrix} \quad (6.14)$$

have negative real parts. The eigenvalues of $J$ are the solutions of the characteristic equation

$$\lambda^3 - T(J)\lambda^2 + M(J)\lambda - D(J) = 0 \quad (6.15)$$

where $T(J) = \frac{\partial F}{\partial N_A} + \frac{\partial G}{\partial N_B}$, $M(J) = \frac{\partial F}{\partial N_A} \frac{\partial G}{\partial N_B} - \frac{\partial F}{\partial N_B} \frac{\partial G}{\partial N_A} - \frac{\partial F}{\partial N_A} \frac{\partial H}{\partial N_B} - \frac{\partial F}{\partial N_B} \frac{\partial H}{\partial N_A}$ and $D(J) = \frac{\partial F}{\partial N_A} \frac{\partial G}{\partial N_B} \frac{\partial H}{\partial N_A} + \frac{\partial F}{\partial N_A} \frac{\partial G}{\partial N_B} \frac{\partial H}{\partial N_B} - \frac{\partial F}{\partial N_B} \frac{\partial G}{\partial N_A} \frac{\partial H}{\partial N_A} - \frac{\partial F}{\partial N_B} \frac{\partial G}{\partial N_A} \frac{\partial H}{\partial N_B}$ are respectively the trace, the sum of the principal minors and the determinant of the jacobian matrix. According to the Routh-Hurwitz criterion all eigenvalues have negative real parts if and only if:

1. $T(J) < 0$
2. $D(J) < 0$
3. $M(J) > 0$
4. $-T(J)M(J) + D(J) > 0$

where

$$D = \frac{S_А(1 - S_A) r_А r_ТМ N_A N_B}{N_A + N_B} \left\{ \frac{(\beta_A - \alpha_A)(1 + c_A \nu)}{K_B} + \frac{(\alpha_B - \beta_B)(c_B + \nu)}{K_A} \right\} \quad (6.16)$$

$$M = \frac{r_А r_ТМ N_A N_B (1 - c_A c_B)}{K_A K_B} + \frac{S_А(1 - S_A)[r_ТМ(\alpha_B - \beta_B) + r_А(\beta_A - \alpha_A)]}{1 + \nu} \quad (6.17)$$

$$-TМ + D = \left\{ \frac{r_А N_A}{K_A} + \frac{r_ТМ N_B}{K_B} \right\} \left\{ \frac{r_А r_ТМ N_A N_B (1 - c_A c_B)}{K_A K_B} + \frac{S_А(1 - S_A)[r_А\delta_A + r_ТМ\delta_B]}{1 + \nu} \right\}$$

$$- \frac{S_А(1 - S_A) r_А r_ТМ N_A N_B}{N_A + N_B} \left\{ \frac{\delta_A(1 + c_A \nu)}{K_A} + \frac{\delta_B(c_B + \nu)}{K_A} \right\} \quad (6.18)$$

Simple inspection of (6.14) shows that the first condition always holds. Before continuing with 2, 3 and 4, let assume Assumption 1: that the net feedback is negative because $\alpha_B, \beta_A >
Appendix B: Stability of the internal equilibrium

\(\alpha_A, \beta_B\) and define \(\delta_A = \beta_A - \alpha_A > 0\) and \(\delta_B = \alpha_B - \beta_B > 0\). Thus condition 2 holds since \(D\) is negative. Condition 3 holds if and only if

\[
c_{ACB} < 1 + \frac{K_\alpha K_\beta S_A (1 - S_A) [r_A \delta_A + r_B \delta_B]}{r_A r_B (N_A + N_B)}
\]  
(6.19)

and for condition 4 we will employ two more assumptions in order to check its validity.

Assumption 2: consider an equilibrium in which \(S_A\) is very close to 0 or 1, such that the product \(S_A (1 - S_A)\) is very small. These circumstances allows to approximate equation (6.18) by

\[-TM + D \approx \left\{ \frac{r_A N_A}{K_A} + \frac{r_B N_B}{K_B} \right\} \left\{ \frac{r_A r_B N_A N_B (1 - c_{ACB})}{K_A K_B} \right\}
\]  
(6.20)

and condition 4 holds if and only if \(c_{ACB} < 1\), which already validates condition 3.

Assumption 3: let consider the symmetry \(r_A = r_B = r\), \(K_A = K_B = K\), \(\nu = 1\) and \(c_A = c_B = c\) (but not for \(\alpha_A, \alpha_B, \beta_A, \beta_B\)). As a result, plant equilibrium densities must be \(\hat{N}_A = \hat{N}_B = N\) and \(-TM + D\) can be easily factored as follows

\[-TM + D = \frac{2rN}{K} \left\{ \frac{r^2 N^2 (1 - c^2)}{K^2} + \frac{S_A (1 - S_A) r (\delta_A + \delta_B)}{2} \right\}
\]

\[-S_A (1 - S_A) r^2 N (1 + c) (\delta_A + \delta_B)
\]

\[
= \frac{rN}{K} \left\{ \frac{2r^2 N^2 (1 - c^2)}{K^2} + S_A (1 - S_A) r (\delta_A + \delta_B) - \frac{rS_A (1 - S_A) (1 + c) (\delta_A + \delta_B)}{2} \right\}
\]

\[
= \frac{rN}{K} \left\{ \frac{2r^2 N^2 (1 - c^2)}{K^2} + S_A (1 - S_A) r (\delta_A + \delta_B) \left[ 1 - \frac{1 + c}{2} \right] \right\}
\]

\[
= \frac{rN}{K} \left\{ \frac{2r^2 N^2 (1 - c) (1 + c)}{K^2} + S_A (1 - S_A) r (\delta_A + \delta_B) \frac{1 - c}{2} \right\}
\]

\[
= \frac{rN (1 - c)}{K} \left\{ \frac{2r^2 N^2 (1 + c)}{K^2} + S_A (1 - S_A) r (\delta_A + \delta_B) \frac{1 - c}{2} \right\}
\]  
(6.21)

The quantity in curly braces is positive, so the sign of \(TM - D\) is that of \(1 - c\). Thus for \(c < 1\) both condition 4, and also condition 3, holds and the internal equilibrium is locally stable.

Only under after making three assumptions we obtain the result that the stability of \(AB\) changes exactly at \(c_{ACB} = 1\). Thus in general, the stability threshold cannot be \(c_{ACB} = 1\). Since we already know that any equilibrium is competitively unstable if \(c_{ACB} > 1\) (6.21b), we must conclude that under net negative feedbacks the internal equilibrium remains stable as long as

\[c_{ACB} < 1 - \epsilon\]

where \(\epsilon\) is a positive quantity smaller than 1.
Appendix B: Stability of the internal equilibrium