

Coupling microscale vegetation–soil water and macroscale vegetation–precipitation feedbacks in semiarid ecosystems

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Abstract

At macroscale, land–atmosphere exchange of energy and water in semiarid zones such as the Sahel constitutes a strong positive feedback between vegetation density and precipitation. At microscale, however, additional positive feedbacks between hydrology and vegetation such as increase of infiltration due to increase of vegetation, have been reported and have a large impact on vegetation distribution and spatial pattern formation. If both macroscale and microscale positive feedbacks are present in the same region, it is reasonable to assume that these feedback mechanisms are connected. In this study, we develop and analyse a soil-vegetation-atmosphere model coupling large-scale evapotranspiration–precipitation feedback with a model of microscale vegetation–hydrology feedback to study the integration of these nonlinearities at disparate scales. From our results, two important conclusions can be drawn: (1) it is important to account for spatially explicit vegetation dynamics at the microscale in climate models (the strength of the precipitation feedback increased up to 35% by accounting for these microscale dynamics); (2) studies on resilience of ecosystems to climate change should always be cast within a framework of possible large-scale atmospheric feedback mechanism (substantial changes in vegetation resilience resulted from incorporating macroscale precipitation feedback). Analysis of full-coupled modelling shows that both type of feedbacks markedly influence each other and that they should both be accounted for in climate change models.

Keywords: alternative stable states, climate change, semiarid regions, vegetation dynamics

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Introduction

Vegetation distribution tends to be largely controlled by precipitation (Woodward, 1987) but in turn, vegetation distribution affects regional precipitation by modifying the atmospheric energy and water budget (Charney, 1975). In regions in the world where water is a limiting resource for vegetation, a stimulating effect of vegetation on precipitation would further stimulate vegetation, implying a positive feedback (Scheffer *et al.*, 2005). The strength of this so-called precipitation feedback depends on the amount of available energy and the

amount of soil moisture available for evaporation and transpiration (Zeng *et al.*, 1999; Koster *et al.*, 2004).

It has been shown by using coupled atmosphere–vegetation models how interactions between vegetation cover and the atmosphere influence climate variability in semiarid regions, such as the Sahel (Claussen, 1997; Zeng *et al.*, 1999). The positive effect of vegetation on the evapotranspiration flux can play an important role in land–atmosphere interaction, because vegetation can access deep soil water and groundwater by their roots. Also, relatively dark vegetation canopies have a low albedo and therefore absorb more radiation that can be used to transpire more water. Both these mechanisms increase atmospheric water content and thereby the probability of rain. Owing to this precipitation feedback the dynamics of vegetation are now explicitly included

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into models that predict effects of climate change on vegetation distribution (e.g. Cramer *et al.*, 2001). Although these atmosphere–vegetation models have high resolutions up to $0.5^\circ \times 0.5^\circ$ (e.g. Gerten *et al.*, 2004), it is widely recognized that microscale variability of land surface properties (e.g. vegetation type and soil texture) strongly influence hydrological processes at the macroscale (e.g. Pitman *et al.*, 1990; Ghan *et al.*, 1997). This is because such microscale variability significantly affects the partitioning between evapotranspiration and runoff, as well as the partitioning of the radiative energy input between sensible and latent heat fluxes at the land surface (Wang & Eltahir, 2000). At mesoscales, surface inhomogeneity causes changes in the surface-energy budget, which can generate mesoscale atmospheric circulations (Pielke *et al.*, 1998) that may optimize cumulus convective precipitation (Anthes, 1984) and trigger thermal circulations (Avisar & Liu, 1996).

Although microscale variability by itself causes differences in absolute amounts of water and energy fluxes at macroscale, it may not have a dramatic effect on the qualitative nature of the precipitation feedback. However, if at the microscale additional positive feedback mechanisms are present between vegetation and water resources, nonlinear responses could be observed such as self-organized patchiness and bistability of ecosystem states (Klausmeier, 1999; von Hardenberg *et al.*, 2001; Rietkerk *et al.*, 2004). In turn, this could have large impact on vegetation cover, evapotranspiration, and precipitation feedback at macroscale (e.g. Dekker & Rietkerk, 2005).

Moreover, the precipitation feedback at macroscale and the feedback between vegetation and water resources at microscale could work synergistically, thereby disproportionately affecting atmosphere–vegetation interactions. Recently, Scheffer *et al.* (2005) reviewed these macro- and microscale feedback mechanisms and conclude that it is important to integrate these nonlinearities at disparate scales. They argue that by incorporating the synergistic effects of these feedbacks at different scales, models would produce more realistic predictions of the effects of climate change and deforestation.

In this study, we demonstrate the effects of coupling the precipitation feedback at macroscale with the feedback between vegetation and water resources at the microscale in a simplified, spatially explicit soil–vegetation–atmosphere model. We show how positive feedback at microscale can influence the precipitation feedback at macroscale, and how this affects the resilience of the ecosystem. Positive feedback between vegetation and water resources at the microscale is modelled by incorporating the positive relation between plant biomass and water infiltration rate

(HilleRisLambers *et al.*, 2001; Rietkerk *et al.*, 2002). Hereafter, we call this the infiltration feedback at microscale. This mechanism is only one of the many possible feedbacks between vegetation and water resources at the microscale. Other examples are the redistribution of soil water due to positive feedback between plant biomass, extent of root system, and water uptake (Klausmeier, 1999; von Hardenberg *et al.*, 2001) or by short-range facilitation and long-range competition for limiting water (Lejeune *et al.*, 2004).

The precipitation feedback at macroscale is modelled by the positive relation between evapotranspiration and precipitation rate (Entekhabi *et al.*, 1992). This model is only based on advection and atmospheric water balance considerations while the feedback is only related to bulk evapotranspiration. Hereafter, this will be called the precipitation feedback at macroscale. Other biosphere–atmosphere feedback mechanisms caused by mesoscale changes in the surface energy budget or effects of surface inhomogeneity (Pielke *et al.*, 1998) are not considered.

Models

Precipitation feedback at macroscale

The modelled interaction between the atmosphere and the land surface is based on the model by Entekhabi *et al.* (1992). The atmospheric water balance is calculated over a large landmass of size L [m] (area per unit width) (Fig. 1). The advection of atmospheric moisture is given by wu , with w the vertical integral of precipitable atmospheric moisture (m) and u the average wind speed (ms^{-1}), assuming full mixing over the atmosphere, and no correlation between vertical soil moisture and wind variation. The precipitation P (m yr^{-1}) that falls over the region comes from advected moisture (P_a) and local evaporative sources (P_1)

$$P = P_a + P_1. \quad (1)$$

Evapotranspiration ET (m yr^{-1}) is the sum of transpiration from plants and evaporation from soils and open water. As it is assumed that full mixing occurs in the atmosphere over such a large landmass, a relationship can be derived between precipitation, advection, and evapotranspiration (Budyko, 1974; Entekhabi *et al.*, 1992):

$$P = P_a \left(1 + \frac{LET}{2wu} \right). \quad (2)$$

As the evapotranspiration ET depends on soil wetness and plant biomass, and these variables themselves

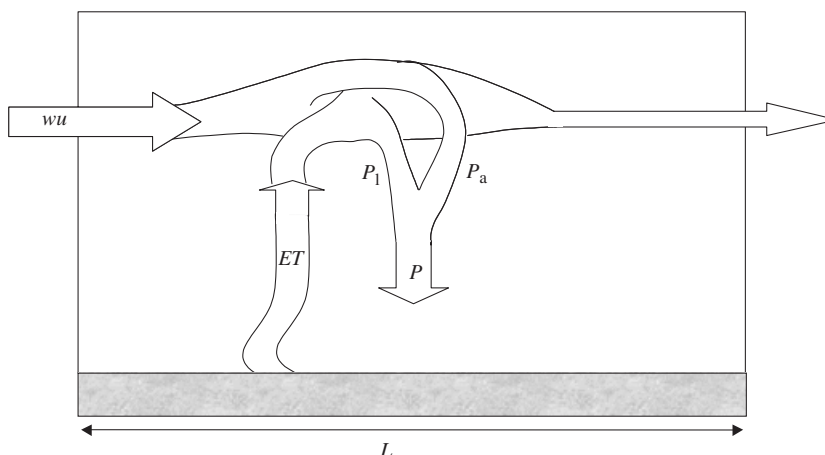


Fig. 1 Macroscale atmospheric water balance (after Entekhabi *et al.*, 1992), wu is advection, ET is evapotranspiration, P is total precipitation formed by P_1 , precipitation derived from local evaporative sources, and P_a , precipitation derived from advected moisture. L is total land region.

depend on precipitation (see next section), there is a feedback between the land surface and the atmosphere.

Clearly, the model of Entekhabi *et al.* (1992) is based on simple atmospheric water balance equations. It does not consider albedo feedback and additional boundary layer dynamics (e.g. Pielke *et al.*, 1998; Ek & Holtslag, 2004). However, at the larger temporal and spatial scales at which this model claims to operate, the average effect of increased evapotranspiration over a large region will be an increase in precipitation. This simple model should thus be viewed as a tendency equation showing this effect.

Entekhabi *et al.* (1992) provide parameters for Eqn (2) for semiarid and semihumid climate zones, which correspond with the northern and southern parts of the Sahel. In their parameterization, both P_a and w increase when moving from a semiarid to a semihumid climate zone. The amount of rainfall coming from advection P_a and advected precipitable atmospheric moisture w are strongly related and are therefore both connected to the position in the Inter Tropical Convergence Zone (ITCZ). If we denote this position as Z with $Z = 0$ the most northern part (approximately 20° north) of the ITCZ with an arid climate, and with $Z = 1$ the southern part (approximately 10° north) with a semihumid climate, then, based on the parameter settings of Entekhabi *et al.* (1992), P_a and w are:

$$P_a = 0.1 + 0.5Z, \quad (3)$$

$$w = 0.00455 + 0.094((Z + 0.1)0.5)^2. \quad (4)$$

By this parameterization, changing Z means considering a different latitude (i.e. moving southward or

northward toward a different climate zone). However, changing Z may also mimic a change in zonal climate for a given latitude, for instance due to a multiyear change in the strength of the Monsoon and the associated position of the ITCZ. With $L = 2.5 \times 10^6$ (m) (e.g. between $W 5^\circ$ and $O 25^\circ$) and $u = 0.04 \text{ m s}^{-1}$ (Entekhabi *et al.*, 1992), the macroscale precipitation feedback parameter $L/2wu$ changes from 2.07 to 0.30 when moving from an arid to semihumid climate.

Infiltration feedback at microscale

The spatially explicit model of infiltration feedback at microscale is adopted from HilleRisLambers *et al.* (2001) and Rietkerk *et al.* (2002). The ecological mechanisms and assumption of this model concept are from Rietkerk *et al.* (1997). Here, we briefly review this model. Soil water availability is limited by low intrinsic infiltration rate of water into the soil. The vegetation itself, however, promotes the rate of infiltration, invoking a positive feedback between increased plant growth and enhanced infiltration. Vegetation improves the structural and water holding properties of the soil by forming root channels, by preventing crust formation through the interception of raindrops, and by stimulation of biological activity in the soil, resulting in higher infiltration rates (references in Rietkerk & van de Koppel, 1997). During rain showers, some rainwater will infiltrate into the soil, while the remainder will run off as surface water to other areas. With increasing plant density, the rate of infiltration of surface water into the soil will asymptotically approach a maximum. The vegetation takes up part of the infiltrated water and the rest will evaporate or move out of reach of plant roots by drainage or lateral subsurface flow due to capillary

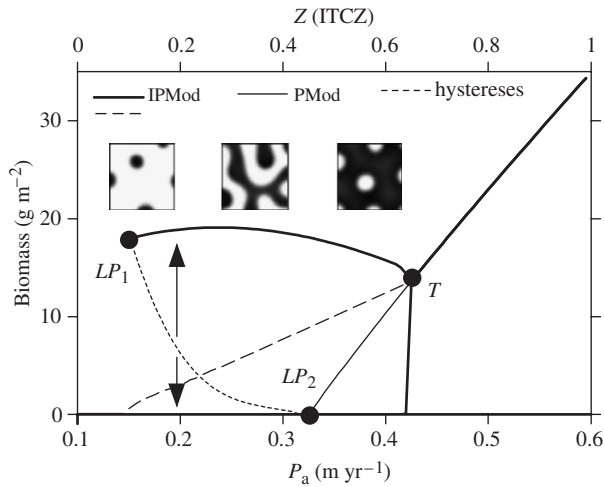


Fig. 2 Bifurcation analysis of the IPMod (microscale infiltration and macroscale precipitation feedback model, thick line) and the Pmod (macroscale precipitation feedback model, thin line). Between limit point LP_1 and T , the IPMod simulated vegetation, which goes through a variety of vegetation patterns. Dashed line is the average vegetation density of the grid during pattern formation with the IPMod. Dotted line between LP_1 and LP_2 (hysteresis) represents breakpoint values indicating alternative stable equilibria (homogeneous stable equilibrium with no plants and nonhomogenous stable equilibrium where plants can persist); arrows indicate direction of change.

forces. Soil water uptake and plant growth rate are both assumed to be saturation functions of soil water availability. Plants can disperse through seeds or vegetative propagation. For the current analysis, we further assume homogeneous flat terrain. The model consists of a set of three partial differential equations describing the dynamics of three state variables: plant density (B ; $g\ m^{-2}$), soil water storage (S ; mm) and surface water storage (O ; mm):

$$\frac{\partial B}{\partial t} = c g_{\max} \frac{S}{S + k_1} B - dB + D_B \nabla^2 B, \quad (5)$$

$$\frac{\partial S}{\partial t} = \alpha O \frac{B + k_2 S_0}{B + k_2} - g_{\max} \frac{S}{S + k_1} B - r_S S + D_S \nabla^2 S, \quad (6)$$

$$\frac{\partial O}{\partial t} = P - \alpha O \frac{B + k_2 S_0}{B + k_2} + D_O \nabla^2 O. \quad (7)$$

where P ($mm\ day^{-1}$) is rainfall and described by Eqn (1), c ($g\ mm^{-1}\ m^{-2}$) is the conversion of water uptake by plants to plant growth, g_{\max} ($mm\ g^{-1}\ m^{-2}\ day^{-1}$) is the maximum specific water uptake, k_1 (mm) is a half-saturation constant of specific plant growth and water uptake, d (day^{-1}) is the specific loss of biomass due to mortality, D_B ($m^2\ day^{-1}$) is plant dispersal, α (day^{-1}) is the maximum infiltration rate, k_2 ($g\ m^{-2}$) is the saturation

constant of water infiltration, S_0 (–) is the fraction of water that infiltrates in the absence of biomass relative to the maximum infiltration rate, r_S (day^{-1}) is the specific soil water loss due to soil evaporation and drainage, D_S ($m^2\ day^{-1}$) is the diffusion coefficient for soil water, D_O ($m^2\ day^{-1}$) is the diffusion coefficient for surface water (HilleRisLambers *et al.*, 2001). Parameter values are obtained from HilleRisLambers *et al.* (2001) and Rietkerk *et al.* (2002).

The model of Rietkerk *et al.* (2002) does not include interception losses. This is because rain events are very intense in semiarid regions, resulting in a small percentage of rainfall intercepted during such events (Ramirez & Senarath, 2000).

Coupling feedbacks

The precipitation feedback was coupled with the spatial vegetation model by soil evaporation and plant transpiration. Transpiration equals the second term of Eqn (6) and soil evaporation was parameterized with values of Wallace & Holwill (1997), resulting in sixty percent of the third term of Eqn (6). The remaining 40% is drainage.

All evapotranspiration fluxes from microscale grid cells were aggregated. This aggregated evapotranspiration flux was input for the macroscale precipitation feedback model, which in turn calculated the new total rainfall which was subsequently equally distributed on the microscale grid cells. Through this coupling it is implicitly assumed that total atmospheric mixing occurs and that the area for which the new total rainfall was calculated is representative for a much larger area. This assumption is corroborated by the fact that the vegetation patterns occur over much larger areas throughout the Sahel than the area for which we calculated the new total rainfall (Rietkerk *et al.*, 2002).

Analysis

To investigate the effects of the infiltration feedback at the microscale and the precipitation feedback at macroscale, as well as their interactions, four models were used: (1) both infiltration feedback model at microscale and precipitation feedback model at macroscale (IPMod), (2) infiltration feedback model at microscale only (IMod), (3) precipitation feedback model at macroscale only (PMod) and (4) no feedback model (Mod).

In the models without infiltration feedback at microscale (PMod and Mod), the amount of infiltration is constant, meaning that it is not dependent on biomass. In the models without precipitation feedback at macroscale (IMod and Mod), the amount of rainfall P is used as fixed rainfall rate without dependence on evapotranspiration.

For simulations, the program Matlab (MathWorks) was used. The two-dimensional coupled numerical simulations were performed using forward Euler integrations of the finite-difference equations. The spatial mesh consisted of a rectangular grid of 200×200 elements with periodic boundary conditions with grid sizes of 2 m. So, we consider a $400 \text{ m} \times 400 \text{ m}$ area as representative for a much larger region, in the order of 1000 km width (Fig. 1). This area is a valid spatial scale to evaluate the effects of the infiltration feedback at microscale (Rietkerk *et al.*, 2002) yielding evapotranspiration and precipitation values that are typical for a certain position in the ITCZ, and therefore, those values can subsequently be extrapolated to the larger region. This means that if the infiltration feedback at microscale leads to systematic differences in evapotranspiration, this will have a regional impact through the precipitation feedback at macroscale.

Simulations were started by randomly seeding 1% of the grid elements with biomass. The model could not be solved analytically and therefore, we performed a numerical bifurcation analysis to explore under which conditions pattern formation occurs in the models and the possibility of alternative stable states. For every Z between 0 and 1, with steps of 0.01 (about 0.1°), simulations were run until stability was reached. From the steady-state output of the model (i.e. at equilibrium) for a specific Z , we calculated the ranges of rainfall values for which the vegetation cover consists of a homogeneous equilibrium or of a vegetation pattern, and for which vegetation goes extinct. We plotted this in a so-called bifurcation diagram (cf. Rietkerk *et al.*, 2002; see caption Fig. 2 for details). With this bifurcation analysis, we demonstrate how plant biomass is affected by changing advective moisture (wu and P_a) or location within the ITCZ.

The resilience of the IPMod and IMod systems was compared. Resilience is defined as the magnitude of disturbance that can be absorbed before the system switches to a different equilibrium (Gunderson, 2000). We run simulations initialized with a stable vegetation pattern nearby extinction (cf. Fig. 2 left panel with spot patterns of vegetation). For 1 year rainfall intensity was decreased or grazing intensity increased and after this year, the rainfall or grazing intensity were set back to initial values. Resilience was measured as the decrease of rainfall or increase of grazing necessary for plants to become extinct, which means that recovery to the original equilibrium, was not possible.

Results

Effect of the infiltration feedback at microscale

To analyse the effect of the infiltration feedback at microscale, the model was first analysed by switching

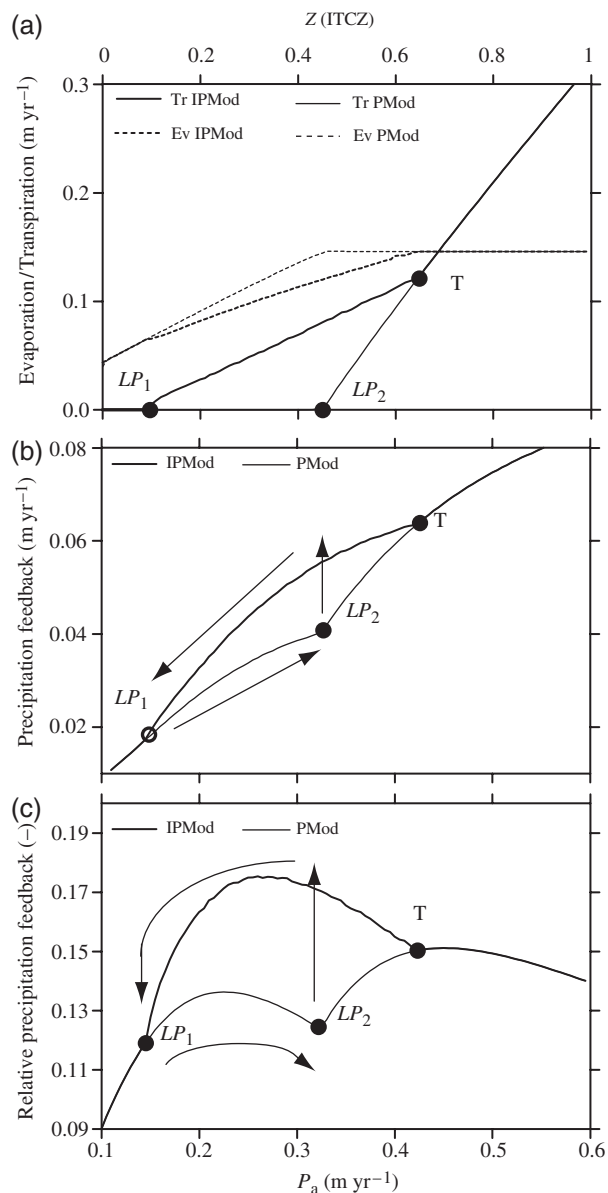


Fig. 3 (a) Simulated evaporation and transpiration rates of IPMod (thick lines) and PMod (thin lines); continuous lines are transpiration and dotted lines are soil-evaporation rates. (b) Precipitation feedback of the IPMod vs. PMod. (c) Relative precipitation feedback, that is precipitation feedback divided by the sum of P_a and P_v of both models. Arrows indicate the range of bistability of the IPMod.

this feedback on and off, while the macroscale precipitation feedback is on. Figure 2 shows the results of numerical bifurcation analysis of IPMod (thick line, with microscale infiltration feedback) and PMod (thin line, without microscale infiltration feedback). The PMod predicts a high homogeneous equilibrium of plant biomass at high P_a . With decreasing P_a , homogeneous plant biomass decreases linearly until it be-

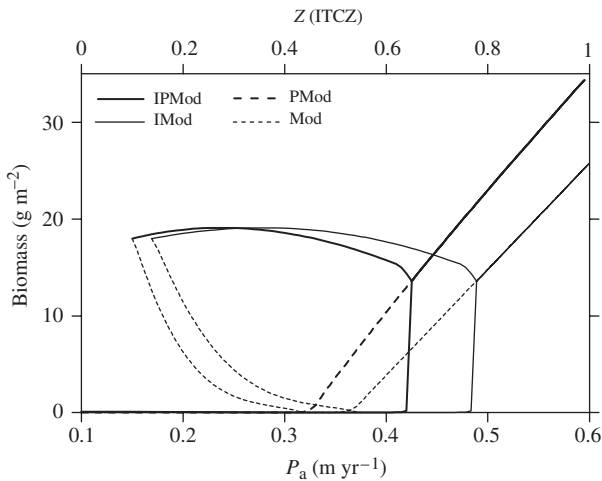


Fig. 4 Bifurcation analysis of the IPMod (microscale infiltration and macroscale precipitation feedback model, thick lines) and the PMod (macroscale precipitation feedback model, thick dashed line), IMod (microscale infiltration model, hair line), and Mod (without feedback, dashed line). Dotted lines represent breakpoint values indicating alternative stable states.

comes extinct at ITCZ is 0.42 (or $P_a = 0.32$). So, the model with only the precipitation feedback shows no multiple equilibria meaning that vegetation is always homogeneous distributed.

The IPMod predicts the same high homogeneous equilibrium of plant biomass at high P_a , but in contrast it becomes unstable at point T , the Turing instability point (Turing, 1952). From point T , as P_a decreases further, the homogeneous equilibrium does not exist and stable nonhomogeneous equilibria occur that are illustrated by maximum and minimum plant biomass (thick lines), which reflect spatial vegetation patterns as shown in Fig. 2. Mean plant biomass is depicted by the dotted line. With further decreasing P_a , plants survive in spatial patterns until limit point LP_1 is reached, beyond which all plants go extinct. Once extinct, P_a must be increased above limit point LP_2 before plants recover again. This limit point LP_2 of the IPMod is exactly at the same position of P_a 0.32 m yr^{-1} where the vegetation, simulated by the PMod, goes extinct. With values above LP_2 , plants can recover again without the use of the positive feedback, meaning that they do not need to reach a threshold density to survive. This is why from this point vegetation can recover in the PMod as well. At P_a rates between LP_1 and LP_2 , plant biomass will recover only if their initial values are carried over the breakpoint values indicated by the dotted line connecting these two points. So, between point T and LP_1 , the vegetation goes through a variety of spatial patterns, ranging from gaps, to labyrinths and spots (Fig. 2).

The two models both simulate soil evaporation and transpiration (Fig. 3a). Maximum average actual soil

evaporation is 146 mm yr^{-1} , which is in the same order as found by Wallace & Holwill (1997). Maximum actual evapotranspiration, at $Z = 1$ is 1.3 mm day^{-1} , which is far less than the potential evapotranspiration reported by Entekhabi *et al.* (1992). This entails that evapotranspiration is water limited for all values of Z . For the IPMod, plant transpiration occurs between LP_1 and LP_2 due to the occurrence of vegetation patterns. For the PMod vegetation and therefore transpiration is absent for this parameter range. Here, soil evaporation is lower while evapotranspiration is higher for the IPMod as compared to the PMod.

So, for given atmospheric moisture advection, microscale feedback increases evapotranspiration, which in turn results in a larger simulated macroscale precipitation feedback (up to 35%, Fig. 3b). Also, between limit points LP_1 and LP_2 , alternative stable equilibria occur for the IPMod between a relatively high and low precipitation feedback, because of the alternative stable equilibria of a homogenous stable equilibrium with no plants and nonhomogenous stable equilibrium where plants can persist. Moreover, the largest relative precipitation feedback (i.e. precipitation feedback divided by the sum of P_a and P_l) of the IPMod is found at intermediate values of Z (i.e. $Z = 0.36$, Fig. 3c).

Thus, the relative strength of the macroscale precipitation feedback (i.e. precipitation feedback divided by the sum of P_a and P_l , first increases from semihumid climate to arid climate), which can be expected if moisture advection wu decreases at the same time. However, when moving further towards the arid climate zone, the absolute value of the precipitation feedback diminishes again because there is no moisture to evaporate. So, a relatively strong feedback is found in the transition zones between wet and dry climates (Koster *et al.*, 2004). With PMod, two peaks in relative precipitation feedback can be found, the first only due to soil evaporation, because vegetation is absent, and the second due to evapotranspiration.

This analysis clearly shows that microscale variability can cause large differences in predicted macroscale precipitation feedback if vegetation patterns are a manifest of microscale feedback. It also shows that it is important to account for spatially explicit vegetation dynamics and microscale feedbacks at the subgrid scale of climate models when predicting climate change.

Effect of precipitation feedback at macroscale

The same analysis is repeated but now by comparing the models with and without precipitation feedback (IPMod and IMod). The IPMod and IMod models show qualitatively similar behaviour, although IMod simulates vegetation patterns across larger ranges of lati-

tudes (Fig. 4). Owing to precipitation feedback, vegetation patterns can exist for lower P_a values where they would otherwise go extinct.

Although the model behaviours are qualitatively similar, marked differences in resilience after drought or biomass removal by grazing are found. Starting with a characteristic spot pattern of vegetation, precipitation was decreased during 1 year. Initial rainfall equilibrium was 0.195 m yr^{-1} with P_a as 0.170 m yr^{-1} . It is found that P_a can be decreased for the IPMod with 0.107 m yr^{-1} during 1 year before plants become extinct. However, for the IMod, plants only become extinct with a decrease of 0.137 m yr^{-1} during 1 year, or during 475 days with the decrease of 0.107 m yr^{-1} , having the same initial rainfall equilibrium.

Not only the resilience due to changes in precipitation can be calculated but also due to an increase of grazing (i.e. as a sudden decrease in biomass). It is found that grazing can be increased with 37% during 1 year before the biomass goes extinct with the IPMod, while in the IMod this can be increased with 39%, or during 390 days instead of 365 days. This analysis shows that due to the existence of precipitation feedback, vegetation is more sensitive to drought and grazing. The reason is that rainfall is dependent on evapotranspiration, which in turn depends on soil moisture and biomass. So any changes (such as drought and grazing) affecting soil moisture and biomass have an accelerating effect.

Discussion

This study shows how feedbacks at different scales interact to affect both regional climate and microscale vegetation patterns. In particular it is shown that a model with microscale positive infiltration feedback mechanisms simulating vegetation patches, produces higher evapotranspiration rates resulting in higher macroscale positive precipitation feedback. An incorrect incorporation of the partitioning between evapotranspiration, runoff, and drainage in climate models has significant influence on the terrestrial biosphere–atmosphere system through the precipitation feedback.

It is interesting to note that the model with only positive precipitation feedback (Pmod) shows no multiple equilibria contrary to what was suggested by for instance Scheffer *et al.* (2005). They argue that due to the stimulating effect of vegetation on precipitation a strong positive feedback is implied. From this, Scheffer *et al.* (2005) imagine that this could cause a vegetated wet state and a barren dry state to be both stable and self-reinforcing. Although in our coupled model the increase of precipitation does result in higher biomass and higher evapotranspiration, the resulting positive feedback is not strong enough to cause multiple stable

states. The reason is that in our model two counteractive mechanisms are at play. First, the growth of additional biomass and associated evaporation is limited by soil moisture status. Second, not all additional evaporation will be returned to the surface as precipitation. The atmosphere in our model is an open system, allowing some of the additional evapotranspiration to be lost (Budyko, 1974) by advection. This results in only a limited increase in rainfall. Indeed, also the model of Entekhabi *et al.* (1992) in an equilibrium setting does not show alternative stable equilibria. Only through sufficient stochastic forcing of this system a *stochastic* bistability occurs in the form of a bimodal probability distribution. So, in our equilibrium model bistability only occurs due to microscale positive feedbacks, which at the same time affect the strength of the macroscale precipitation feedback.

It is known that self-organization of vegetation is a result of positive feedback mechanisms. The microscale positive infiltration feedback mechanism results in large ranges of pattern formation, while the precipitation feedback mechanism decreases this range. So vegetation tends to self-organize itself in regular patterns due to local accumulation of infiltrated water but at the same time tends to increase the precipitation rate. These results show that it is important to account for spatially explicit vegetation dynamics at the microscale of climate models if positive feedbacks are involved.

Resilience of ecosystems, defined as the magnitude of disturbance that can be absorbed before the system switches to a different equilibrium (Gunderson, 2000), was calculated for the microscale infiltration feedback models with and without macroscale precipitation feedback. It is found that the precipitation feedback influences the resilience of the vegetation, such that a model without macroscale precipitation feedback is more resilient against variation of precipitation and the effects of grazing. These results show that resilience studies of ecosystems should always be cast within a framework of possible macroscale atmospheric feedback mechanisms.

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