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Self-disturbance as a Source of Spatiotemporal Heterogeneity: the Case of the Tallgrass Prairie

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Tallgrass prairies are characterized by high levels of litter production, which has a profound effect on live biomass. Litter introduces a delayed inhibition of biomass growth, generating nonlinear dynamics and chaos. In this paper, we study a model of biomass–litter interaction, and focus on the litter persistence rate. The observed dynamics depends largely on this rate of year-to-year persistence. Different scenarios are explored and discussed. A spatially extended counterpart of such a model is later on introduced to account for the effects of space. Temporal chaos introduces spatial heterogeneity in terms of gaps where the current year biomass is almost zero. Such gaps can be colonized by fugitive species. The inhibitory effect of litter on biomass is thus an important source of intrinsic, small-scale heterogeneities that may promote diversity. On the other hand, the huge amounts of litter produced by the competitive dominants in tallgrass prairies enhance the probability of fires. Fires benefit, rather than depress, the superior competitive species. This fact explains why the intermediate disturbance hypothesis (IDH) stating that the highest diversity levels should be observed at intermediate disturbance frequencies, does not work in these communities. We define self-disturbances as small-scale disturbances affecting the growth and survival of the individuals that have generated them (e.g. due to the effects of the litter mass they produce). In the absence of other disturbances, self-disturbances can induce high heterogeneity and diversity levels in tallgrass prairies. We discuss the general implications of self-generated disturbances for landscape heterogeneity and diversity of communities in which the main external perturbations benefit the dominant species.

1. Introduction

How high levels of diversity are supported in nature is one of the most intriguing questions in evolutionary ecology. Spatial heterogeneity has frequently been invoked as a major factor in controlling species diversity (e.g. Whittaker & Levin, 1977; Picket & White, 1985; Yodzis, 1986; Collins, 1992). In general, environments in which spatial heterogeneity is higher are expected to accommodate more species because they provide a greater variety of microhabitats, microclimates, resources, refuge from predators, etc.

Disturbances are a source of spatial heterogeneity for many communities (e.g. Connell, 1978; Pickett & White, 1985; Willig & Walker, 1999).

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A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Pickett & White, 1985). Disturbances open up spaces that can be colonized by other individuals and species. For example, for the case of a plant community this definition would include both externally generated disturbances (e.g. fire, storms, droughts, changes in salinity, grazing, etc.), and intrinsically generated disturbances (e.g. the fall of a tree that has died due to ageing). Within this later category, we also include what we call self-disturbance: small-scale perturbations affecting the growth and persistence of the individuals that have produced them (e.g. litter depression of subsequent biomass growth). Both extrinsic and intrinsic disturbances can have different consequences for community diversity (Pickett & White, 1985).

In this paper, we develop a hypothesis to explain the role of self-disturbances in promoting spatial heterogeneity. Since spatial heterogeneity is related to diversity, we extrapolate our discussion to diversity-related issues. We focus on tallgrass prairies as a specific example, and we develop a mechanistic model to understand some peculiarities of the dynamics of such prairies. In particular, we want to explain why tallgrass prairies do not obey the intermediate disturbance hypothesis (IDH) (Collins, 1992; Collins *et al.*, 1995) stating that within patch heterogeneity (and the highest diversity levels) is supported at intermediate levels of frequency and intensity of perturbations (Connell, 1978).

The process of litter production and accumulation in tallgrass prairies can potentially explain why tallgrass prairies do not behave according to the IDH. Tallgrass prairies are characterized by extremely high levels of litter production by the dominant grasses, and this is related to the frequent fires that affect these ecosystems (e.g. Knapp & Seastedt, 1986). Fire does not damage the dominant grasses but can kill their competitors. On the other hand, there exists evidence suggesting that, when litter accumulates in the absence of fires, litter may severely impair the growth of the dominant grasses (Hulbert, 1969; Knapp, 1985; Knapp & Gilliam, 1985; Knapp & Seastedt, 1986) but not that of other herbaceous and woody species (Bragg & Hulbert, 1976; Zimmerman & Kucera, 1977; Knapp, 1984; Towne & Owensby, 1984; Abrams *et al.*, 1986; Knapp & Seastedt, 1986). This suggests that accumulated litter can promote spatial heterogeneity (and diversity) in a similar way as that proposed for the IDH for extrinsic disturbances, i.e. by creating spaces within the community that are suitable for the colonization of less-competitive species. Nevertheless, the negative effects of litter on the species that generate it fall outside the range of situations accounted for by the IDH, as this hypothesis does not deal with self-disturbances. Here we present an alternative hypothesis to the IDH, the self-disturbance hypothesis (SDH) which is applicable to communities in which external perturbations benefit rather than depress the superior competitive species. In these situations, the highest diversity levels can be observed in the absence of external perturbations due to the role of such intrinsic, self-disturbances in generating heterogeneity and diversity. Thus, the SDH is an elaboration on two well-known observations. The first one is the observation that fire-dependent plant communities burn more readily than non-fire-dependent communities due to the accumulation of litter. The second observation is that these large amounts of litter may impair the growth of the dominant species generating spatial heterogeneity.

In a different context, the inhibitory effect of accumulated litter on biomass production has been proved to be the origin of oscillations and chaos in the dynamics of perennial grasses (Tilman & Wedin, 1991). In this important contribution, Tilman & Wedin (1991) combined experiments with analytical models to provide the first test of chaotic dynamics in perennial plants. Litter creates a temporal delay in biomass growth. This inhibition of growth can lead to nonlinear dynamics in productive habitats. An important issue that has not been explored is the implication of the inhibitory effect of litter on growth when space is taken into account. As Tilman & Wedin (1991) already suggested, litter-induced inhibition of biomass production is a local process, so chaos can be also a local phenomenon not observed at larger spatial scales.

This paper is organized as follows. We start by introducing an extension of the Tilman & Wedin

(1991) model for the dynamics of a perennial grass. We specifically study the effects of litter as a source of heterogeneity both in time and space. We first explore the non-spatial model to better determine the specific influence of litter on biomass dynamics. Specifically, we analyse how the temporal variability of biomass is affected by different values of litter persistence in various scenarios in which litter persistence is either independent or dependent on litter amount. In a subsequent section we study the spatial extension of this model. Our goals are two-fold: to analyse the relationship between biomass variability and spatial scales, and to investigate the emergence of spatial heterogeneity due to the litter inhibition of biomass growth. This provides a potential mechanism for the high heterogeneity and diversity observed in undisturbed prairies. From a more general perspective, our work also highlights the potential importance of self-generated disturbances for diversity in communities in which the dominant species benefit from external perturbations.

2. A Model for a Perennial Grass

Our goal in this section is to understand how litter inhibits biomass growth under different situations. We want to focus on litter persistence rate and on the relationship between such a rate and litter amount. Only after understanding the inhibitory effect of litter can we extend the model into a spatial dimension to ask how this inhibition can lead to spatial heterogeneity. Here we describe a slightly modified version of the Tilman & Wedin (1991) model for the dynamics of a dominant perennial grass,

$$B_{t+1} = cN \frac{e^{(a-bL_t)}}{1+e^{(a-bL_t)}}, \tag{1a}$$

$$L_{t+1} = pL_t + ckN \frac{e^{(a-bL_t)}}{1+e^{(a-bL_t)}}, \tag{1b}$$

where B_t and L_t are the living and litter biomass at year t (both measured in $\mathrm{g\,m^2}$). N is the total soil nitrogen (mg N per kg soil). The quantity k is the rate of conversion from biomass to litter and p is the litter persistence, the fraction of litter persisting from one year to the next ($p = 1 - d$, d being the decomposition rate). Quantities a, b and c are positive constants.

Model (1) describes a system in which biomass attains its N-determined equilibrium (cN) in a single year. The effect of litter is to reduce such a maximum value (Tilman & Wedin, 1991). Here we have written a simplified expression for the effect of litter decay (or persistence). We have just assumed a linear effect, i.e. litter persistence (p) is a constant independent of the amount of litter. Later on, we will explore more complicated scenarios. Tilman & Wedin (1991) explored the model for different N-values, showing that a well-defined route to chaos through a period-doubling scenario emerges. How do their results change for different litter decay rates?

In Fig. 1 we show a set of bifurcation diagrams. For a given nitrogen value we iterate model (1). After discarding transients, we plot biomass for the next iteration values. Figures 1(a)–(c) correspond to different persistence (p) values. As can be noted, in Fig. 1(b), corresponding to $p = 0.5$, steady states, cycles and chaos are observed as the total nitrogen is increased. This diagram is qualitatively similar to the one plotted in Tilman & Wedin (1991). However, both for high and low persistence values, chaos disappears and the system is more stable [see Fig. 1(a) and (c)]. This result is summarized in Fig. 2. For each persistence value, we plot the relative range of nitrogen values giving chaos in the corresponding bifurcation diagrams. That is, the amplitude of the N-interval producing chaos divided by the total range on total soil nitrogen (1600). As can be seen, there is a peak around $p = 0.5$. For this value, approximately 40% of the parameter space (from $N = 0$ to 1600) shows chaotic solutions. The fraction of the chaotic domain decreases as we either increase or decrease litter persistence. This can be interpreted as follows. For very low litter persistence values, litter almost disappears from one year to the next, and so does not exert an inhibitory effect on the next year's biomass growth. Without this inhibitory, delayed effect both cycles and chaos disappear and the dynamics are stable. A minimum persistence value is needed in order for the litter to induce such a nonlinear regulatory effect. However, if litter persistence is very high, the inhibitory effect on

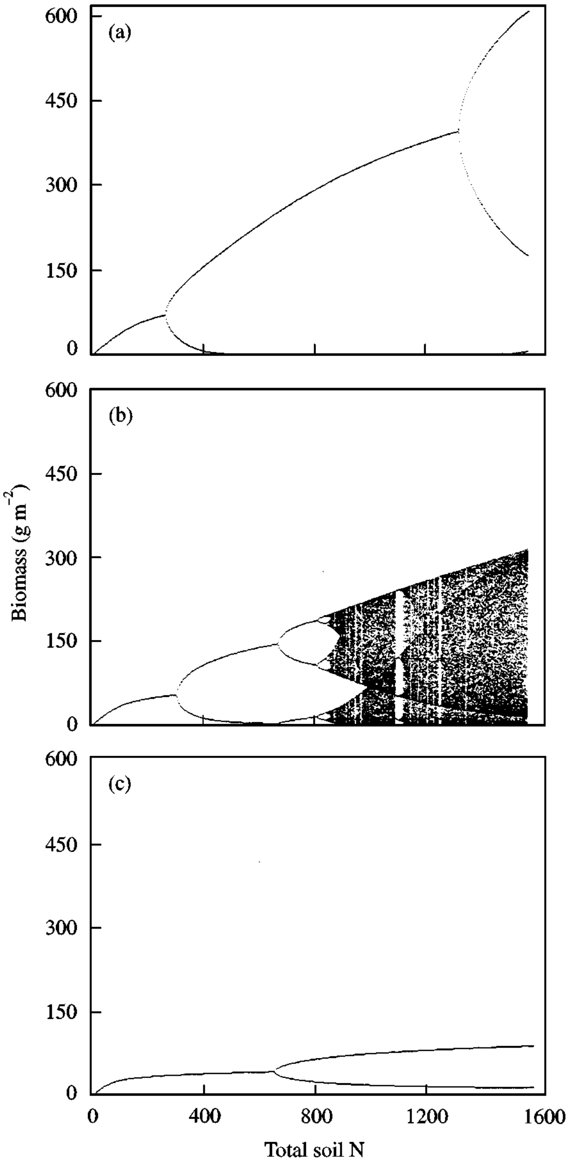

FIG. 1. Bifurcation diagrams for model (1). For a specific nitrogen value (mg N per kg soil), the model is iterated for 2000 time steps. After the first 1800 iterations are discarded to avoid transient behavior, the annual biomass values are plotted for the subsequent 200 iterations (years). Parameters are $a = 5$, $b = 0.1$, $c = 0.5$, $k = 0.4$ and litter persistence is $p = 0.2$(a), 0.5(b) and 0.7(c), respectively. By comparing the three bifurcation diagrams, a period-doubling route to chaos is observed as nitrogen is increased. However, chaos only appears for intermediate values of persistence. For both low and high values of persistence, chaos is absent.

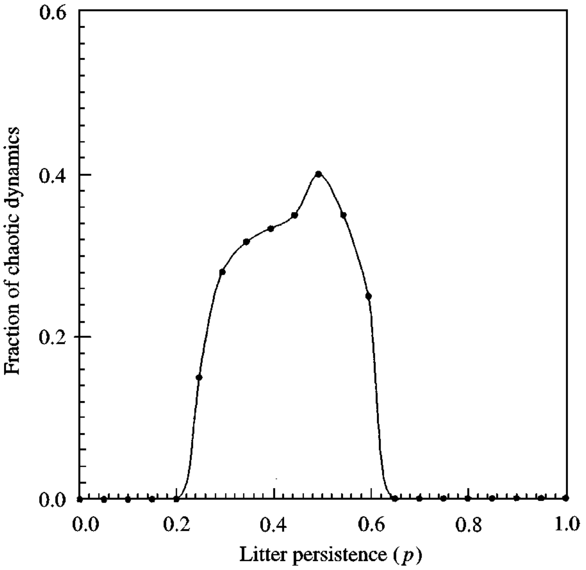

FIG. 2. The fraction of nitrogen values generating deterministic chaos in model (1) is plotted as a function of litter persistence (p). For each persistence value, a bifurcation diagram is generated by increasing total soil nitrogen from 0 to 1.600 mg N kg^{-1} soil. Three examples are plotted in the previous figure. From such bifurcation diagrams we then calculate the relative fraction of nitrogen values generating chaotic dynamics. This relative domain of chaotic solutions is plotted vs. p. Other parameters are as in the previous figure. From these parameter values, chaos is only observed for persistence values comprised between 0.2 and 0.65. This persistence values generate the delayed inhibition effect of litter on biomass necessary to observe chaotic oscillations.

biomass is too high and too long, and litter keeps biomass under low numbers.

Another way of presenting these results is by a bifurcation diagram in which persistence is changing for a given nitrogen value. This diagram is plotted in Fig. 3. An interesting pattern emerges. As p increases, there are a number of bifurcations from stationary to periodic and to chaotic dynamics. Then, suddenly there is a sequence of period-doubling reversals (e.g. Stone, 1993) until for high p-values the dynamics is again stationary. Both extremes are qualitatively similar in that the dynamics attain a steady state. However, the biomass is much higher at low p-values than for high p-values.

The amount of litter persistence is not likely to be constant but depends on the amount of litter. For example, the amount of litter is known to affect microenvironmental characteristics (e.g. temperature, humidity, aeration) which in turn may affect litter decomposition (see Facelli & Picket, 1991 and references therein). Hence, it can be adduced that the rate of litter persistence (or its inverse, i.e. litter decay) is not constant but depends on the amount of litter. How sensitive are the previous results to this assumption? The

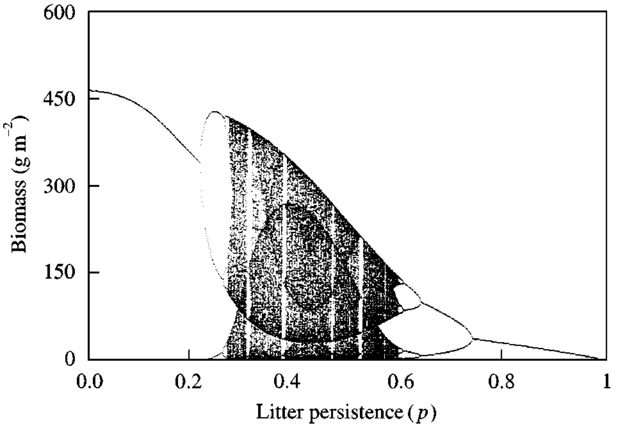

FIG. 3. Period-halving bifurcations (period-doubling reversals). In this bifurcation diagram, the annual biomass is plotted as a function of litter persistence. As usual, the first 1800 iterations are discarded to avoid transient behavior, and the posterior 200 iterations are plotted for each value of litter persistence. Parameters are $a = 0.5$, $b = 0.1$, $c = 0.5$, $N = 1, 200$, $k = 0.4$. The period-doubling route to chaos is reversed for higher persistence values.

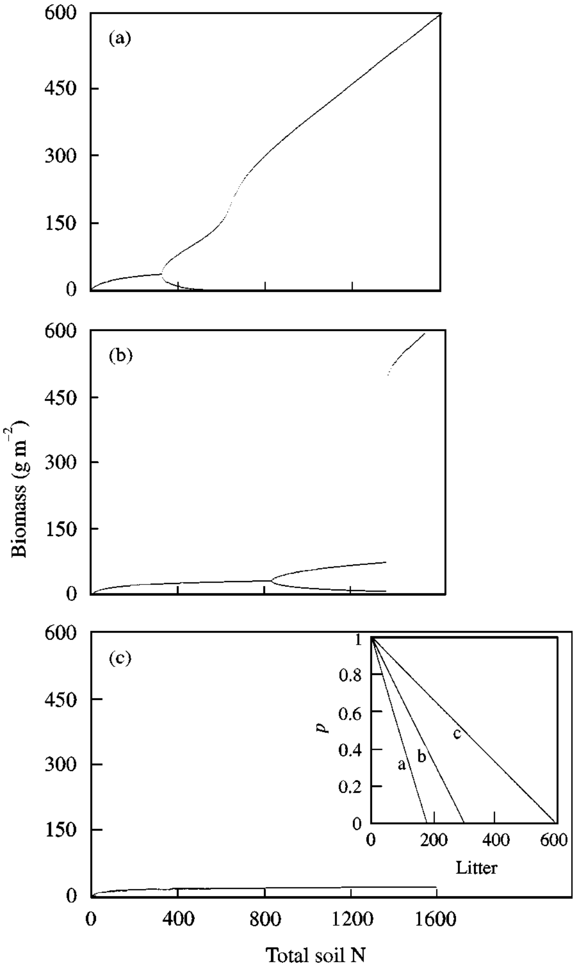

FIG. 4. Similar bifurcation diagrams as for Fig. 1. In this case, however, litter persistence is not a fixed rate but it changes linearly with litter amount. In this scenario, a negative relationship is assumed, i.e. persistence decreases with litter amount. Three particular relationships are shown in the inset. For each one of those, a bifurcation diagram (biomass vs. nitrogen) is plotted. Chaos is never observed. Note than in (b), a threshold in nitrogen exists at which biomass shows an abrupt transition. Parameters are as in Fig. 1 except for litter persistence, $p = 1 - bL_t$, where L_t is the annual amount of litter and $b = 0.0055$ (a), 0.0033 (b), and 0.0016 (c).

average lifetime of litter in tallgrass prairies before it is decomposed is about 3–4 years (Kucera *et al.*, 1967). However, it is not known whether the rate of litter decomposition varies with litter amount. Hence, we explored two scenarios: (i) litter persistence decreases with litter amount, and (ii) litter persistence increases with litter amount. Here we use simple relationships between litter amount and persistence. We do not intend these relationships to be realistic. We simply want to show the dependence of these two variables for different scenarios and the robustness of the results. Similar functions have been used with similar qualitative results, and overall the analysis show us the sensitivity of the model to changes in persistence.

Figure 4 is the equivalent of Fig. 1 for case (i). A linear relationship ($p = 1 - bL$) is assumed and three different slopes are illustrated. For each p–L relationship, we plot a bifurcation diagram by increasing the amount of total soil nitrogen. As observed, only periodic and stationary states are observed. Chaos has disappeared. The same qualitative result is observed when p declines with L is a nonlinear manner (data not shown). On the other hand, when litter persistence increases with the amount of litter ($p = bL$), chaos is again observed (see Fig. 5). An interesting phenomenon is noted in Fig. 5(a) and to a lower extent in Fig. 5(b). Once a critical N-value has been reached, biomass collapses to a very low value. This can be understood in the following way. In the chaotic domain, biomass, and hence litter increase. Since litter persistence increases with litter amount, there is even more litter in the next year. Litter persistence tends to one and so biomass is kept reduced at very low numbers. Litter also decreases, but not as fast as biomass does. These qualitative results remain unchanged

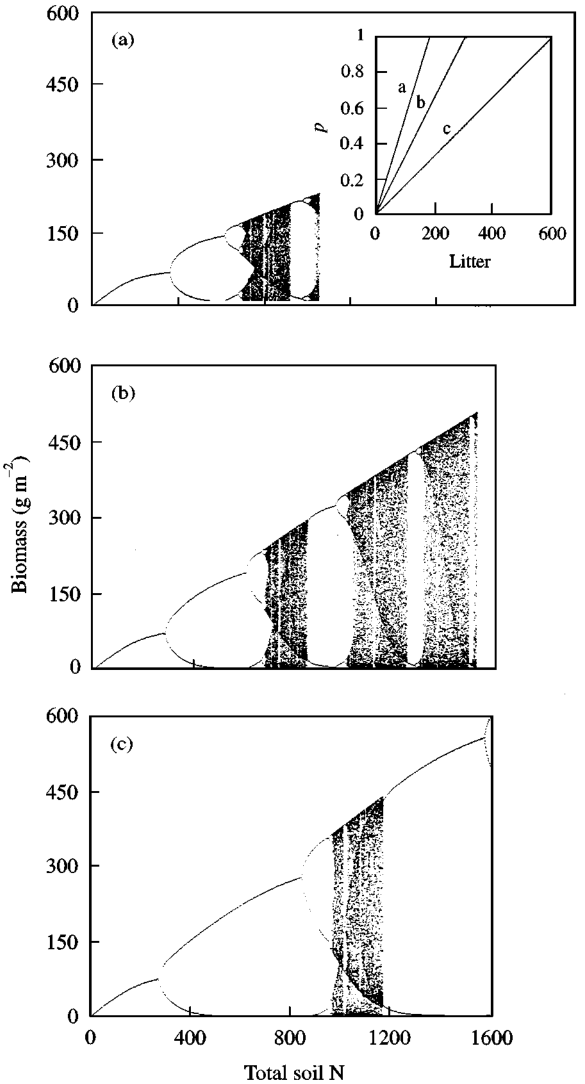

FIG. 5. Same as in Fig. 4, but now the relationship between litter persistence and litter amount is positive. Same parameters as before. The three examples (shown in the inset) correspond to $p = bL_t$, where L_t is the annual amount of litter and $b = 0.0055$ (a), 0.0033 (b), and 0.0016 (c). In contrast to the previous figure, chaos is observed for all three situations. In (a) and (b), a threshold in total soil nitrogen can be observed beyond which biomass almost disappears once litter amount is high enough for the persistence rate to be 1. Then, litter inhibition on biomass is very severe.

when the relationship between persistence and litter is made nonlinear (data not shown).

3. A Spatially Extended Counterpart

We turn now to the questions of how biomass variability (induced by the litter inhibitory effect studied in the previous section) depends on the spatial scale, and how this inhibitory effect can create spatial heterogeneity. We can explore the effects of space in the previous model by using the coupled map lattice (CML) formalism. A CML is a dynamical system with discrete space, discrete time and continuous state (Kaneko, 1992). CMLs have been recently used in ecology as a way to study spatiotemporal dynamics (Solé *et al.*, 1992; Bascompte & Solé, 1995, 1998).

The new model can be written as follows:

$$B_{t+1}(\mathbf{r}) = cN\frac{e^{(a - bL_t(\mathbf{r}))}}{1 + e^{(a - bL_t(\mathbf{r}))}}, \tag{2a}$$

$$L_{t+1}(\mathbf{r}) = pL_t(\mathbf{r}) + (1 - \varepsilon)ckN\frac{e^{(a - bL_t(\mathbf{r}))}}{1 + e^{(a - bL_t(\mathbf{r}))}} + \frac{\varepsilon}{4}\sum_{j=1}^{4} ckN\frac{e^{(a - bL_t(\mathbf{j}))}}{1 + e^{(a - bL_t(\mathbf{j}))}}. \tag{2b}$$

Here **r** represents the spatial coordinates of a site in the two-dimensional grid. The dynamics in each point in space is governed by model (1). But now each site is coupled to its four nearest neighbors. Such a coupling can be understood as follows. Each point in space corresponds to a plant. The biomass at this point becomes litter at the end of the growing season, and a fraction $1 - \varepsilon$ of such litter remains in the same site inhibiting plant growth the next year, while a fraction ε falls down to the nearest-neighbor sites affecting growth there. In eqn (2b), **j** indicates one of the four nearest-neighbor sites.

The first question we want to answer with model (2) is how the perception of chaos depends on the spatial scale. It is important to consider the relationships among spatial scales, as landscape-level patterns can be explained by local disturbance and patch dynamics (see Levin, 1992; Wu & Levin, 1994). As mentioned before, Tilman & Wedin (1991) have suggested that since litter inhibition is a local process, it may be difficult to detect it at larger scales even when the dynamics are chaotic. We address this question by calculating the coefficient of variation (CV = S.D./mean) of the dynamics of both biomass and litter for increasingly large clusters of sites, the smallest cluster containing 1 site, the next one 2 × 2 sites, 3 × 3 sites and so on. Parameters were in the region that generates chaos. In Fig. 6 we plot CV as a function of the size of the cluster for which

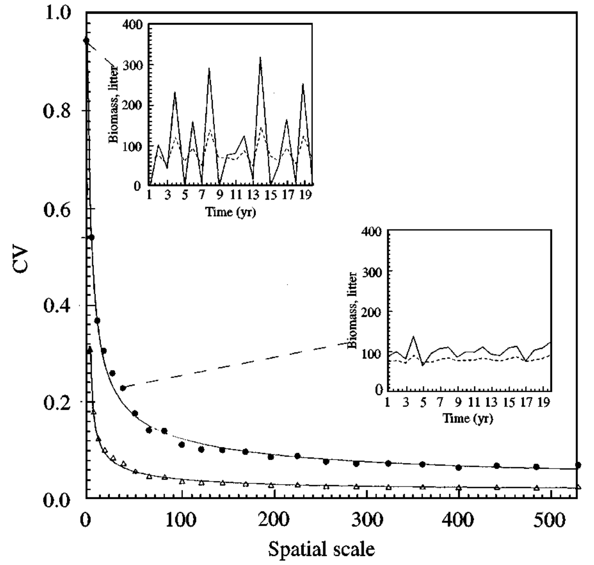

FIG. 6. CV (S.D./mean) of biomass (●●) and litter (△△) vs. the spatial scale of the temporal series for the spatially extended model (2). After 1500 transients are discarded we use the following 500 iterations to calculate the CV of the fluctuations in biomass and litter. The smallest spatial scale is that of one site. Then we repeat the process for the averaged biomass and litter at clusters of sizes 2×2, 3×3, and so on. Continuous lines are power-law fits of the data. The two insets are examples of the temporal series from which the CV is calculated at the scale of a single site, and of a cluster of 6×6 sites. Biomass (——), and litter (⋯⋯) are plotted as a function of time. The effect of space in stabilizing the dynamics is evident. Chaos introduces asynchronous fluctuations, and so a kind of stability due to an averaging effect of the fluctuations at different sites. Parameters are $a = 5$, $b = 0.1$, $c = 0.5$, $k = 0.4$, $p = 0.5$, and $\varepsilon = 0.1$. Lattice size is 50×50.

the dynamics are averaged. The observed points fit well with a power law. As noticed, there is a fast decay of the CV as the spatial scale is increased, followed by a *plateau*, a region with long tails where the CV is almost independent of further increases in area. In other words, the perception of the variation is highly dependent on the size of the cluster in which biomass is measured. Thus, even when highly unstable fluctuations are observed at a local site, one would have a perception of a stationary constancy with some deviations at a relatively larger (but still small) spatial scale (see insets of Fig. 6). This is due to the averaging effect of considering different sites together linked to the chaotic nature of local fluctuations.

The next question we want to answer is how the inhibitory effect of litter can create spatial heterogeneity: This is an important question since spatial heterogeneity could lead to the high levels of diversity observed in undisturbed grasslands. For different nitrogen values (and so different temporal regimes), we want to have some measurements of heterogeneity. In particular, we are interested in sites empty of living biomass. These litter-covered sites constitute gaps because they can be colonized by species which cannot grow under the biomass of the dominant grasses. In Fig. 7, we show two snapshots of our spatial system, each corresponding to one iteration after some transients have been discarded. Both snapshots differ in the nitrogen value used (one corresponding to the beginning of the chaotic region, and the other one well inside the chaotic domain). We consider that a site (or a cluster of sites) is a gap when its biomass is $\leq 1\ \mathrm{g\,m^{-2}}$. As can be seen, litter depression of biomass can generate gaps of different sizes, which are more frequent as the dynamics become more chaotic.

To further analyse the role of litter as a source of gaps, we plot the number of gaps, their total area within the grid, and the CV of their sizes over the range of nitrogen values [see Fig. 8(a)–(c)]. All these values are calculated for a single time step and then successive years are averaged. The persistence value ($p = 0.5$) is the same as in Fig. 1(b), so by comparing Fig. 8 and Fig. 1(b) we can compare the degree of spatial heterogeneity with the nature of the dynamics (stationary, periodic or chaotic). Note that Fig. 1(b) corresponds to the non-spatial model (1). While the local dynamics (i.e. the dynamics at a site) in a spatial counterpart are qualitatively similar to the non-spatial model for the same parameters (the same bifurcation scenario is observed), small differences exist. In particular, some of the periodic windows observed in the uncoupled map are destroyed in the spatial version.

For each nitrogen value we run model (2). After a certain number of transients are discarded, we calculate the number of gaps, total area of gaps and CV of gaps. What we plot in Fig. 8 is an average of such values for a given number of iterations. For stationary and periodic dynamics, the three variables are close to zero. Suddenly, once the chaotic domain has been entered, a well-defined transition takes place. The

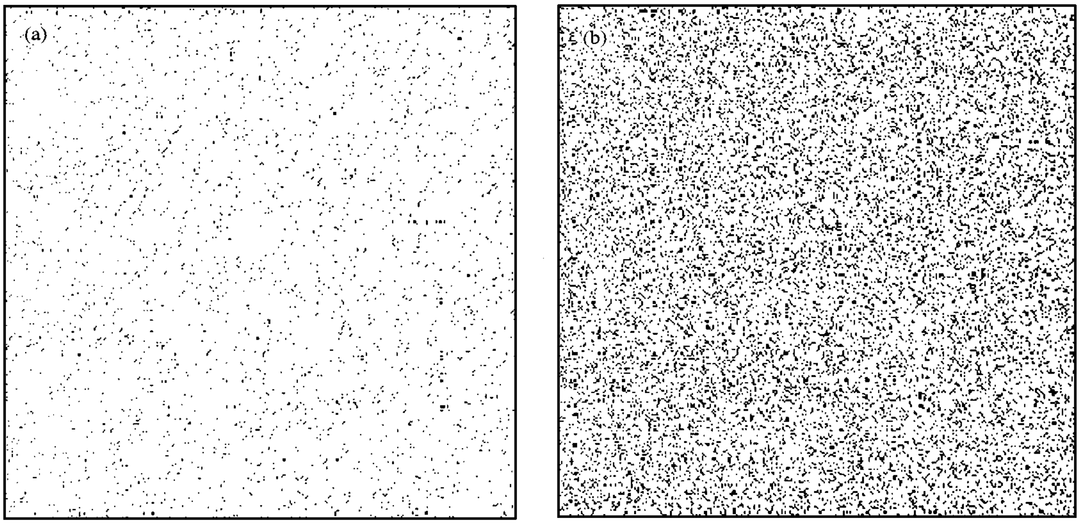

FIG. 7. Spatial heterogeneity generated by model (2). The snapshots correspond to a certain iteration after transients have been discarded. Black points are sites at which the inhibitory effect of litter has generated a local biomass $\leq 1\ \mathrm{g\,m^{-2}}$. Such sites can be colonized by other grasses. Both figures correspond to different nitrogen values. (a) $N = 1080$, corresponding to the beginning of the chaotic domain, and (b) $N = 1300$, corresponding to a more chaotic domain. Other variables as in Fig. 6 but lattice size is 300×300.

three variables increase suddenly. This behavior is similar to that of physical systems near a phase transition. There is a qualitative, discontinuous change in the properties of the system, which is identified with an order parameter (Schroeder, 1991; Solé *et al.*, 1996).

The previous result suggests that chaos is an important source of spatial heterogeneity in this model. Below the chaotic domain space is almost homogeneous. At a single iteration all the sites have similar biomass values, and these values are bigger than zero. But beyond the critical point (the edge of chaos), there is a qualitative change in behavior. On average, there are more gaps and their distribution is much more heterogeneous (there is more variability in gap size). The qualitative nature of these results does not depend on whether the particular value of the cutoff used to define a gap ($1\ \mathrm{g\,m^{-2}}$ in the present example) is changed.

To sum up, chaos can arise for some particular litter persistence rates and dependences between such rates and litter amounts. At a spatial scale, even when chaos can be hard to detect, it creates self-disturbances. The self-disturbances lead to spatial heterogeneity which is believed to be related to species diversity. Empirical information is still needed to determine whether litter persistence values are within the range of values inducing chaos, and hence capable of generating the type of spatial heterogeneity depicted in this paper. Our scenario is supported, though, by the results by Tilman & Wedin (1991) finding chaos in perennial grasses.

4. Discussion

Much progress has been made in understanding the role of disturbances in conditioning community diversity (e.g. Connell, 1978; Pickett & White, 1985; Willig & Walker, 1999). Disturbances are often viewed as discrete forces triggering a chain of events within the community which will ultimately determine its composition and diversity. For example, small-scale disturbances can be important mechanisms for maintaining species richness by producing a mosaic of patches at different stages of succession that vary in species composition (Wu & Levin, 1994). These patches often provide microsites for the establishment of fugitive species in areas otherwise dominated by superior competitors (e.g. Yodzis, 1986). As a consequence, community diversity and heterogeneity are enhanced (e.g. Picket & White, 1985).

Heterogeneity has frequently been attributed to external disturbances (Connell, 1978). While this happens to be true for a large number of systems, other systems may maintain high heterogeneity even in the absence of external perturbations. In other words, the intrinsic dynamics of a community can create heterogeneity and hence maintain high levels of diversity (Bascompte *et al.*, 1993). An excellent example is the application of critical phenomena to the study of gap formation in tropical forests. It seems that tropical forests behave as dynamic systems at a critical point at which "tree-avalanches" of all sizes are observed. Power laws in the size frequency of the gaps created by these avalanches are observed, and the suggestion is that such intrinsic dynamics is very important for the maintenance of diversity in the forest community (Solé & Manrubia, 1995a, b). Heterogeneity is still the key to the high diversity levels observed. But the crucial difference is that it is intrinsically rather than extrinsically generated.

Besides tropical forests, internal disturbances can occur in a number of other ecosystems (e.g. see Pickett & White, 1985; Frelich & Reich, 1998). For example, it is well known that litter accumulation can have profound effects on the dynamics and structure of many plant communities (reviewed by Facelli & Picket, 1991). In this paper, we have focused on a particular kind of internal disturbances, the self-disturbances, which have to do with the negative impacts that individuals of a particular species can cause themselves due to their own growth. Specifically, we have modeled the processes of biomass growth and litter production of the grass species that dominate the tallgrass prairies of North America. Our present results extend and generalize the importance of self-disturbances in promoting and maintaining spatial heterogeneity.

Litter has an inhibitory effect on subsequent biomass growth of the grasses that contribute to most of its production. This delayed inhibitory

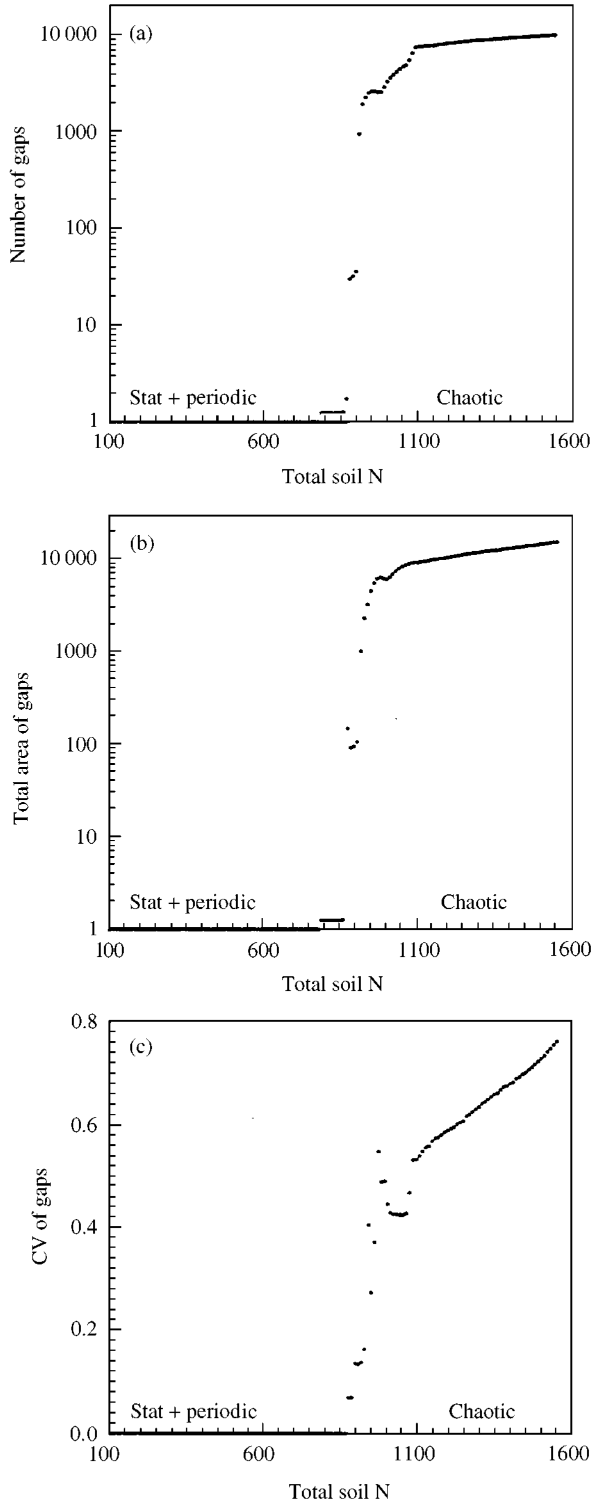

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FIG. 8. Number of gaps (a), total area of gaps (b), and CV of gaps (c) as a function of total soil nitrogen for the spatially extended model (2). All three variables are measures of spatial heterogeneity induced by the inhibitory effects of litter on biomass. Same parameters as in Fig. 7. Figure 1(b) shows the non-spatial model for these parameter values, so the behavior of the present figure can be compared with Fig. 1(b) to see how the structural properties are related to the kind of dynamics. The parameter domain giving place to steady state, cycles and chaos is delimited. The chaotic domain starts at a value for total soil nitrogen of $N = 855$. As observed, a well-defined transition takes place at the onset of chaos for all three parameters. The chaotic region is the one in which the highest heterogeneity values are observed.

effect has been proven to be a source of deterministic chaos and cycles (Tilman & Wedin, 1991, and this paper). The introduction of explicit space into these models allows us to explore spatial considerations. At higher spatial scales, local chaos is difficult to detect because of the asynchrony in the fluctuations at different local sites. The question now is why this averaging effect is so powerful in the present scenario. The answer is, because of chaos by itself. It has been proven that despite its instability at local scales, deterministic chaos is a powerful source of stability at higher scales (Allen *et al*., 1993; Bascompte & Solé, 1995). This counterintuitive property has been termed chaotic stability (Solé *et al*., 1992; Bascompte & Solé, 1995), and can be understood as follows. Due to its property of dependence on initial conditions, local sites fluctuate in total asynchrony even when biomass values were very close at some initial condition (Solé & Bascompte, 1994; Bascompte & Solé, 1995). Thus, the same mechanism producing instability at local scales is the source of stability at global ones.

One relevant question is whether or not the nitrogen levels necessary to generate chaos in our model are compatible with the values observed in nature. The Tilman and Wedin model shows chaos for nitrogen values higher than or equal to 700 mg per kg of soils [see Fig. 2(d) in Tilman & Wedin, 1991]. Similar results have been obtained here for appropriate litter persistence values [see Figs 1(b) and 5(b)]. Several unmanipulated experimental fields at the Cedar Creek Natural History Area, Minnesota, present soil nitrogen levels that are within the range of situations leading to chaos in the model. Specifically, four fields studied by Inouye *et al*. (1987), namely fields 32, 35, 47, and 72 have an average nitrogen content of 706–870 $\text{mg}\,\text{kg}^{-1}$ of soil (see Table 1 in Inouye *et al*., 1987). Moreover, in 18 out of the 22 unmanipulated fields analysed by these authors, the maximum value of soil nitrogen recorded was between 750 and 1873 $\text{mg}\,\text{kg}^{-1}$ of soil. Similarly, in relation to the tallgrass prairies, several studies also indicate that their soils present nitrogen levels within the range of values leading to chaos in the model. For example, Rosburg & Glenn-Lewin (1996) have estimated the amount of soil nitrogen in several native tallgrass prairies and found that they were within the range of 700–1400 $\text{mg}\,\text{kg}^{-1}$ of soil.

The same mechanism generating cycles and chaos, i.e. the inhibitory effect of litter, is also responsible for the generation of spatial heterogeneity, i.e. gaps within the community. Accordingly, the effects of litter on community structure seem to resemble those caused by small-scale disturbances that are out of phase to each other. This may account for the observation that tallgrass communities show higher community heterogeneity and diversity when left unburnt than when they are affected by frequent fires, in a conspicuous departure of the IDH (Collins *et al*., 1992, 1995). In the absence of fire, litter accumulation provides gaps for the establishment of inferior competitive species, such as forbs and woody perennials. The strong capacity of the dominant grasses to regrow after fire allows them to rapidly occupy the available space, leaving few opportunities for the growth of other less-competitive species (see Abrams & Hulbert, 1987; Gibson & Hulbert, 1987).

One has to keep in mind, however, that current patterns in tallgrass prairies are not necessarily the same as historical patterns. For example, the current accumulation of litter which occurs in the absence of grazing may have been very different when the Great Plains was populated with huge herds of grazing animals. This may complicate our understanding of the evolutionary forces relating patterns and processes in such communities.

When an external disturbance is highly likely in an ecosystem, some species may have evolved traits aimed at providing them with resistance to such disturbances (e.g. the capability of resprouting after fire). Such species would possess a clear advantage over other species that are sensitive to the disturbances, as long as these events occur with an adequate frequency. However, if there is a delay in the occurrence of the disturbances, the same traits enhancing the disturbance, and so benefiting to the most competitive species, can have a negative effect on them. These traits act as self-disturbances, perturbations generated by the dynamics of the species that dominate the community. The self-disturbance hypothesis (SDH) presented in this paper is aimed at communities where the dominant species have traits that either benefit them by enhancing the occurrence of external disturbances that are harmful to their competitors, or impair their own growth in the absence of such external disturbances. Specifically, SDH states that the observed levels of spatial heterogeneity (and diversity) in such situations will be determined by the relative contribution of self-disturbances and external disturbances. In this paper, we have simulated the dynamics of the dominant tallgrass prairies in the absence of external disturbances. However, self-disturbances can also generate high heterogeneity levels if external perturbations are sufficiently spaced in time, as can occur in communities experiencing a natural regime of external disturbances. Thus, as stated by the SDH defined here, the observed heterogeneity levels will depend on the relative importance of self-disturbances vs. other disturbances.

It is well known that diversity is associated with spatial heterogeneity, but usually an external source for such heterogeneity is assumed. Some systems, due to nonlinear interaction terms, are able to generate heterogeneity through time and space that can be of paramount importance for the maintenance of diversity. This, together with the fact that the results of external perturbations depend strongly on which species are the ones benefited, is important in understanding the interrelationship between diversity, heterogeneity, intrinsic dynamics, and responses to external perturbations.

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