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JANZEN-CONNELL EFFECTS ARE WIDESPREAD AND STRONG ENOUGH TO MAINTAIN DIVERSITY IN GRASSLANDS

Jana S. Petermann,[1] Alexander J. F. Fergus, Lindsay A. Turnbull, and Bernhard Schmid

Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland

Abstract. Crop rotation schemes are believed to work by preventing specialist soil-borne pests from depressing the future yields of similar crops. In ecology, such negative plant–soil feedbacks may be viewed as a type of Janzen-Connell effect, which promotes species coexistence and diversity by preventing the same species from repeatedly occupying a particular site. In a controlled greenhouse experiment with 24 plant species and using soils from established field monocultures, we reveal community-wide soil-based Janzen-Connell effects between the three major functional groups of plants in temperate European grasslands. The effects are much stronger and more prevalent if plants are grown in interspecific competition. Using several soil treatments (gamma irradiation, activated carbon, fungicide, fertilizer) we show that the mechanism of the negative feedback is the buildup of soil pathogens which reduce the competitive ability of nearly all species when grown on soils they have formerly occupied. We further show that the magnitude of the change in competitive outcome is sufficient to stabilize observed fitness differences between functional groups in reasonably large communities. The generality and strength of this negative feedback suggests that Janzen-Connell effects have been underestimated as drivers of plant diversity in temperate ecosystems.

Key words: biodiversity; coexistence; community ecology; density dependence; functional groups; grassland; home-away effect; Janzen-Connell effect; negative soil feedback; stabilizing mechanism.

Introduction

A revolution in agriculture occurred when crop rotation was introduced to combat what became known as "soil sickness," or the faltering productivity of crops sown recurrently on the same site. For example, typical European crop rotations in the nineteenth century involved wheat, barley, turnips, and clover or peas (Overton 1996). These crops belong to what we now recognize as three different functional groups: grasses, forbs, and legumes. These plant functional groups have a taxonomic basis, and as closely related species are likely to share pests and pathogens (Gilbert and Webb 2007), the success of crop rotation schemes could be due to the avoidance of negative soil feedbacks (Bever 1994). Here, we explore negative soil feedbacks among the same three functional groups in natural grassland. If pathogens accumulate in the soil, they may reduce the chance that a related species will capture the site once a plant dies, potentially leading to natural rotations analogous to those imposed by farmers.

Studies in temperate grasslands have already shown that species can negatively affect the growth of conspecifics via the soil compartment (van der Putten et al. 1993, Bever 1994, De Deyn et al. 2003) and demonstrated a relationship between the size of such negative feedbacks and species abundances (Klironomos 2002). However, much of the work on negative soil feedbacks has focused on exotic invasions and community succession (but see Bever 1994, Olff et al. 2000, Bonanomi et al. 2005). For example, such studies have demonstrated that native–invasive interactions are strongly influenced by soil-mediated feedbacks acting via fungi or other soil organisms (Reinhart and Callaway 2006); although allelochemicals can sometimes be involved (Callaway and Aschehoug 2000). A further substantial part of the plant–soil feedback literature deals with successional dynamics, where negative soil feedbacks help to explain directed species change (van der Putten et al. 1993, van der Putten and Peters 1997, De Deyn et al. 2003).

We studied a native nonsuccessional grassland and examined how negative soil feedbacks can potentially facilitate the coexistence of species and the maintenance of diversity by acting in a similar way to the Janzen-Connell effect (Bever 2003). Janzen (1970) and Connell (1971) suggested that adults, by harboring host-specific predators and herbivores, could locally reduce the recruitment success of conspecific juveniles. However, the importance of the Janzen-Connell effect as a coexistence mechanism remains in question, because it has only been shown to operate for a single or few species within any particular community (Augspurger and Kelly 1984, Condit et al. 1992, Packer and Clay 2000, Bell et al. 2006). The prevalence and strength of the effect was therefore deemed insufficient as a

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[1] E-mail: peterman@uwinst.uzh.ch

mechanism of diversity maintenance (Gilbert 2005). The Janzen-Connell effect has also been exclusively associated with tropical ecosystems (Freckleton and Lewis 2006) or, very rarely, with temperate forests (Packer and Clay 2000, Hille Ris Lambers et al. 2002). However, negative soil feedbacks involving species-specific pathogens in grasslands can maintain diversity in a fundamentally similar way to Janzen-Connell effects: negative soil feedbacks reduce the chance of conspecific juveniles capturing sites following the death of adults, while Janzen-Connell effects reduce the chance of conspecific juveniles capturing sites close to existing adults.

We performed a controlled greenhouse experiment using common species from temperate grassland and soil collected from established field plots. We grew each species alone; but in contrast to other studies, we additionally grew each species in competition with other functional groups (Bever 2003). The influence of negative feedbacks on competitive ability has rarely been studied, potentially leading to an underestimation of their magnitude and relevance to natural communities. We concentrated on functional groups because pathogen-related effects may be more likely to maintain diversity at higher phylogenetic levels than at the species level (Gilbert and Webb 2007). In order to explore possible mechanisms behind observed effects, we applied a number of soil treatments that selectively excluded certain groups of potential feedback agents. Finally, we put our measured effect sizes into a community context by modeling how such effects interact with the inevitable fitness differences which exist between species, both within this particular community and more generally.

Materials and Methods

Soil origin and preparation

Field monocultures of 24 common European grassland species, eight grasses, eight forbs, and eight legumes (see legend of Fig. 2 and Appendix A: Table A2), were grown for three growing seasons near Zurich, Switzerland (Wacker et al. 2008). In autumn 2005, we removed four subsamples of soil per monoculture, pooled them and added 20% of washed and autoclaved sand.

We subdivided soils into a control and four treatments to investigate the general causes of potential plant–soil feedbacks. The treatments were (1) sterilization by gamma irradiation to remove all soil organisms, (2) fungicide to remove only fungi, (3) activated carbon to remove allelochemicals, and (4) fertilizer to serve as an additional control for nutrient flushes that may result from the killing of soil organisms (Troelstra et al. 2001). Fertilizer-treatment pots received a liquid NPK fertilizer once at the beginning of the experiment. There was no fertilization in any of the other treatments (see Appendix A for more details).

Experiment

The same 24 species that had conditioned the soil in the field were then grouped into eight sets, each containing one forb, one grass, and one legume species (Appendix A: Table A2). Species were reciprocally grown on their own soils ("home") and on soils from the two other species in the set ("away") in the glasshouse. We sowed seeds in monocultures on the respective home and away soils that had been subjected to the five soil treatments. There were five replicates of each combination (1800 0.2-L pots), and we recorded germination percentages after 12–20 days, depending on germination behavior of the species.

For the main experiment, seedlings were transplanted into 0.6-L pots filled with the treated soils. Communities with one of two types of competition were assembled. The first type of competition involved planting three individuals of the same species together on both the home soil and the two away soils within the set, without competition from other species (24 species × 3 soils × 5 soil treatments = 360 pots; Appendix C: Fig. C1). The second competition type involved planting one individual from each of the three species in the set together in the same pot on each of the three soils. Thus, on each soil one species was always growing "at home" while the other two were growing "away" (Appendix A: Table A2). There were three replicates per multi-species combination (8 multispecies sets × 3 soils per set × 5 soil treatments × 3 replicates = 360 pots). When the first plants started to flower after eight weeks, the experiment was stopped, all aboveground plant parts were harvested and weighed after drying at 70°C for 48 hours (see Appendix A for more details).

Data analysis

Dry mass of single plants growing on home soil was divided by the dry mass of single plants growing on away soils to get a proportional measure of feedback that is independent of plant size (in contrast to the measure used by Klironomos (2002)). For example, for species i,

$$\text{Feedback}_i = \log\left[\frac{\text{biomass}_i(\text{home})}{\text{biomass}_i(\text{away})}\right]$$

where biomass_i (home) = biomass of species i on its own soil and biomass_i (away) = biomass of species i on soil of species j (in the interspecific competition treatment, the average mass of individuals across the three replicates was used). Because each species was grown on two different away soils, each belonging to a different functional group, this resulted in two values of the feedback measure for each species per competition type and soil treatment (480 degrees of freedom in the main experiment). The ratio was log-transformed to achieve normality and homogeneity of variances. At the same time, the log transformation returns zero when there is no difference between home and away soils, and negative values for "negative feedbacks" (biomass at home smaller than biomass away) and vice versa. The log-ratio was then used as the response variable in a mixed-model ANOVA (Table A1). A similar analysis was done with germination percentage instead of biomass for the germination experiment (Table A3).

Modeling

Our intention was to see whether a typical grass, forb, and legume could coexist given the strengths of negative soil feedbacks measured in the experiment. Thus, we modeled a simplified community consisting of three different functional groups, each containing one average or typical species. Rather than use a deterministic framework (Bever 2003), we chose a stochastic formulation to assess the impact of demographic stochasticity on persistence times. We assumed that adult individuals die at rate d and a new individual of species i is recruited to fill a site formerly occupied by an individual of type j with probability. $P_{ij} = N_i c_{ij} / \Sigma N_i c_{ij}$. Here N_i is the population size of the ith species and c_{ij} is the competitive weighting for species i at a site formerly occupied by species j. If $c_{ii} < c_{ij}$ then negative feedbacks operate, because species are less competitive when recapturing sites which they have formerly occupied.

Suitable values for the competition coefficients can be determined from our experiment, as we can assess the competitive ability of each species against identical competitors on different soil types. We can average over the eight sets to obtain robust "typical" values for each functional group. Suitable values for the death rates, d_i were estimated from field monocultures of 52 species (the entire original species pool from which our 24 species were randomly selected for this experiment). These values should typify the kind of fitness differences found between the functional groups, although some important processes are inevitably missing.

In addition to simulations including specific values estimated from the data, we also explored a range of other scenarios to examine the general relationships between fitness differences, negative feedback strengths and community size. We used four community sizes (99, 501, 999, and 5001 plant individuals) where each of the three functional groups had equal population sizes in generation 1. A proportion d_i of individuals belonging to species i was randomly selected and removed each generation during a single mortality episode (to mimic episodic mortality such as that induced by summer drought or winter cold) followed by a single episode of recruitment restoring the initial community size. We considered the persistence of the three functional groups over the long term (10 000 generations) in two ecological scenarios: (1) all functional groups had the same adult mortality rate $d_i = 0.2$ for all i and (2) there were differences in mortality rates for each functional group of either 10% ($d_1 = 0.2$, $d_2 = 0.9 \times d_1 = 0.18$, and $d_3 = 0.9 \times d_2 = 0.162$) or 20% ($d_1 = 0.2$, $d_2 = 0.8 \times d_1 = 0.16$, $d_3 = 0.8 \times d_2 = 0.128$). In each case, the probability of persistence of all three functional groups was calculated from 1000 runs each of 10 000 generations. Dispersal was global so that each functional group had the same chance of arriving at a site, although we analyzed a subset of models with local dispersal (see Appendix A).

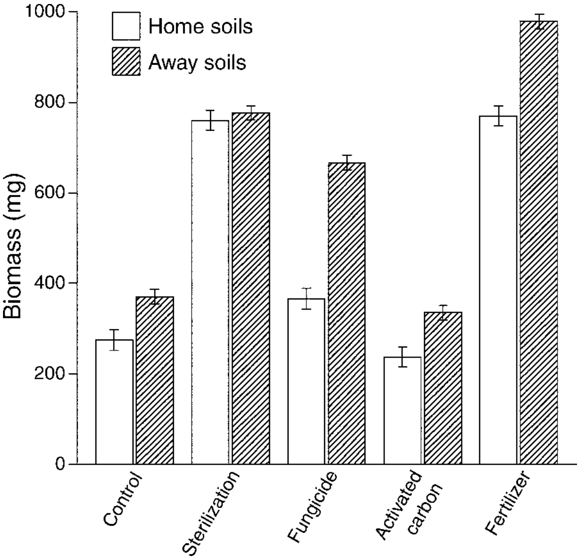

FIG. 1. Absolute biomass per plant individual (mean ± SE) on home soils (open bars) and away soils (hatched bars) for controls and the four soil treatments; data are from monocultures and three-species competition treatments combined. Only soil sterilization eliminates the disadvantage of growing on home soils.

RESULTS

We found strong negative plant–soil feedbacks throughout our study community ($F_{1,23} = 35.69$, $P < 0.001$; Appendix A: Table A1). On average, plants produced 30% less biomass when growing on home rather than on away soils (Fig. 1, "Control"), with the effect being considerably more severe when plants were grown in competition with the other two functional groups ($F_{1,23} = 16.68$, $P < 0.001$). In the pots with interspecific competition, 23 out of 24 species suffered a negative feedback (Fig. 2a, left) and plant mass was on average halved on home compared with away soils. In monocultures, fewer species experienced negative feedbacks and the effects were much weaker than in interspecific competition (Fig. 2a left vs. right). Species from each functional group grew equally well on soil from either of the other two functional groups ($F_{2,22} = 0.47$, $P = 0.634$). Furthermore, species from each functional group suffered the same magnitude of negative feedback ($F_{2,21} = 0.53$, $P = 0.595$). Within functional groups, the size of the effect varied between species ($F_{21,215} = 12.86$, $P < 0.001$). For example, the biomass reduction when growing on home vs. away soils in competition with the other two functional groups ranged from 90% in *Echinochloa crus-galli* to around 4% in *Centaurea jacea*. Only one out of 24 species, *Trifolium incarnatum*, had a higher biomass (+6%) on home soil. When grown in monoculture, the effect size ranged from

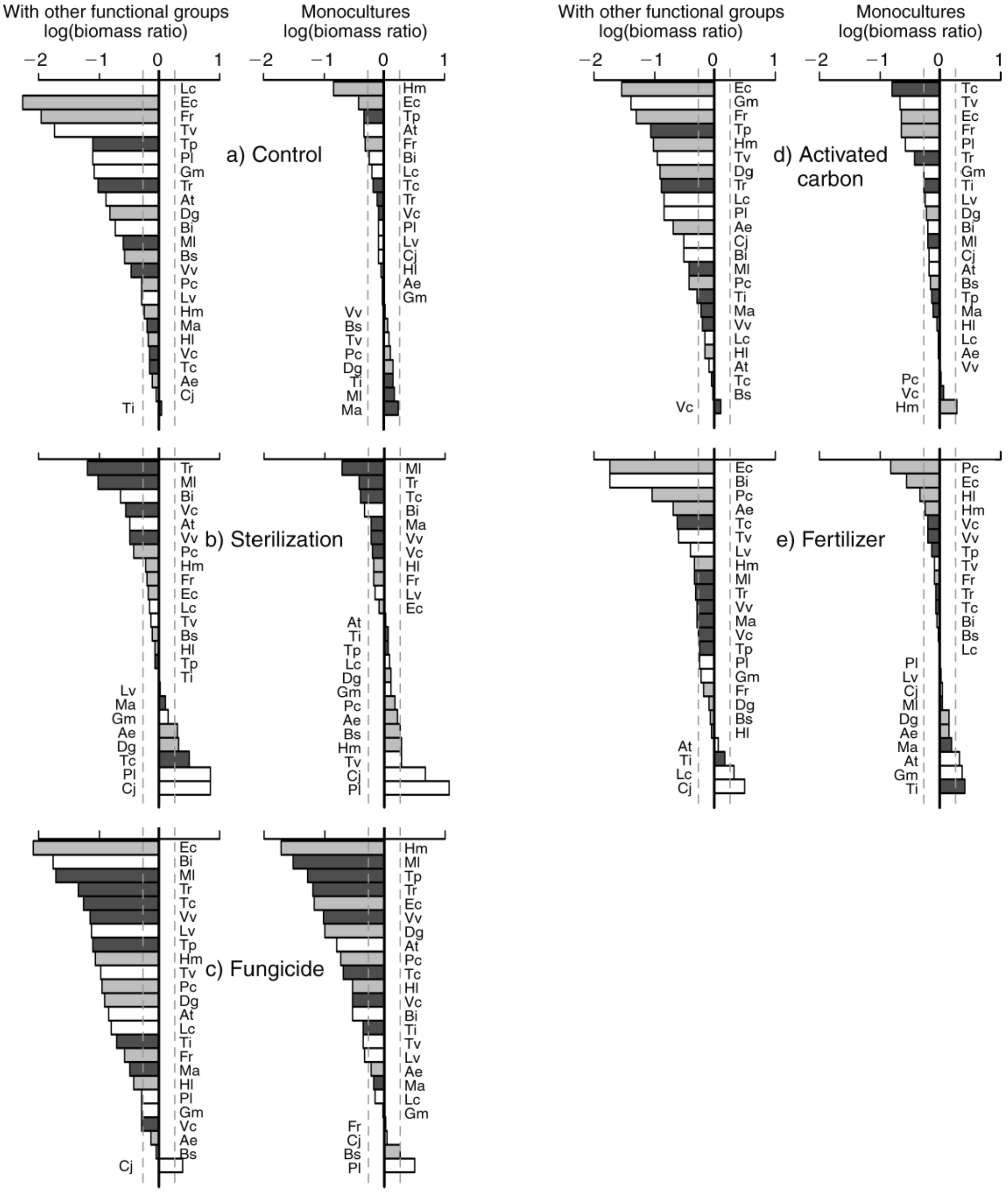

FIG. 2. Mean soil feedbacks for all 24 species of European grassland plants: biomass of individual plants on home soils was divided by biomass of individuals on away soils for each species, then log-transformed. Negative values correspond to a net disadvantage on home soils (negative feedback); positive values to a benefit on home soils (positive feedback). The left-hand column shows plants grown with competition from other functional groups; the right-hand column shows monocultures. Dashed lines show ±SE around zero. Forbs are represented by white bars, grasses by light gray bars, and legumes by dark gray bars. Abbreviations: At, *Arctium tomentosum*; Ae, *Arrhenaterum elatius*; Bi, *Berteroa incana*; Bs, *Bromus sterilis*; Cj, *Centaurea jacea*; Dg, *Dactylis glomerata*; Ec, *Echinochloa crus-galli*; Fr, *Festuca rubra*; Gm, *Galium mollugo*; Hl, *Holcus lanatus*; Hm, *Hordeum murinum*; Lc, *Lepidium campestre*; Lv, *Leucanthemum vulgare*; Ml, *Medicago lupulina*; Ma, *Melilotus albus*; Pc, *Panicum capillare*; Pl, *Plantago lanceolata*; Tv, *Tanacetum vulgare*; Tc, *Trifolium campestre*; Ti, *T. incarnatum*; Tp, *T. pratense*; Tr, *T. repens*; Vc, *Vicia cracca*; Vv, *V. villosa* (Lauber and Wagner 1996). Lc indicates the control (outlier excluded).

a 55% biomass reduction (*Hordeum murinum*) to a 25% increase (*Melilotus albus*) on home soil. In contrast to the effects on growth, there was no general home vs. away effect on seedling emergence ($F_{1,23} = 0.24$, $P = 0.627$; Appendix A: Table A3; Appendix B: Fig. B1).

Our experiment also included soil manipulation treatments designed to investigate potential mechanisms. These treatments differed significantly in their impact ($F_{4,92} = 4.68$, $P = 0.002$). Gamma irradiation removed the negative feedback almost completely (Fig. 1), particularly when species were grown in competition with the two other functional groups (Fig. 2b left). The fungicide treatment of the soil resulted in a net increase of the negative feedback compared with controls (Fig. 1, Fig. 2c left and right). The activated carbon treatment had little effect in our experiment (Fig. 1, Fig. 2d left and right), and the fertilization treatment reduced the negative feedback effect, although not as effectively as the gamma irradiation (Fig. 1, Fig. 2e left and right).

Modeling

The model parameters are particularly simple: we can use the same value of c_{ii} for each functional group as the magnitude of the negative feedbacks suffered by each functional group was the same ($F_{2,21} = 0.53$, $P = 0.595$). In addition, we can use a single value of c_{ij} for all i and j, as each functional group grew equally well when "away" on soils belonging to either of the other two functional groups ($F_{2,22} = 0.47$, $P = 0.634$). By setting the competitive weighting when capturing away sites (c_{ij}) to unity for all i and j we can vary the size of the negative feedback on home soils by choosing values for the competitive weighting when trying to capturing home sites (c_{ii}) in the range 0–1. In our experiment, species from all functional groups had roughly half the biomass when grown with the same competitors on home rather than on away soils; therefore we would estimate $c_{ii} = 0.5$ for all i. In the special case of $c_{ii} = 1$, the model becomes neutral and the only force in the community is drift. In contrast, when $c_{ii} = 0$, a species has no chance of recruiting on a home site, and the model is deterministic in the case of two species. However, there will always be stochasticity in the three-species case because species from the remaining two functional groups have an equal chance of capturing any site vacated by the third.

The model revealed that even weak negative soil feedbacks ($c_{ii} \leq 0.9$) lead to stable coexistence when different functional groups have equal fitness ($d_i = d_j$), but that stronger feedbacks are necessary to ensure coexistence when species differ in fitness ($d_i \neq d_j$, Fig. 3a). Fitness differences between species lead to unequal equilibrium population sizes and therefore increase the probability that the functional group with the lowest fitness becomes extinct. Much stronger negative feedbacks are therefore required to reduce fluctuations around the equilibrium and hence stabilize the interaction (Fig. 3a–d). The strength of negative feedback estimated here ($c_{ii} = 0.5$) would stabilize fitness differences among functional groups of around 10%, but not of 20%, even in a large community (5000 individuals; Fig. 3a). Using observed death rates of the three functional groups from field monocultures (legume $d = 0.466$, grass $d = 0.450$, forb $d = 0.364$) reveals that this value ($c_{ii} = 0.5$) is sufficient to ensure persistence of all three functional groups in communities of $\geq$500 individuals (Fig. 3, dashed lines). However, this only holds if a sufficiently high proportion of the seeds produced (more than about 50%) disperse away from the parent site (see Appendix D: Fig. D1).

DISCUSSION

In our communities, feedback effects were strong and pervasive, and species from all three functional groups were similarly disadvantaged when competing for sites which they had formerly occupied. The effects were considerably weaker when plants were grown only with conspecifics, indicating that it is competitive ability that is primarily affected. Negative feedbacks affecting competitive ability, rather than growth in the absence of competition have rarely been directly investigated and this might have lead to a significant underestimation of the incidence and strength of Janzen-Connell effects in natural communities. We also failed to find effects on germination and seedling survival, although many studies of Janzen-Connell effects only examine these measures (Hyatt et al. 2003).

The almost complete removal of the negative feedback across the community by soil sterilization strongly suggests that soil biota were the primary agents causing the observed effects. These soil organisms must be host-specific (Freckleton and Lewis 2006) as generalist pathogens would be expected to affect plants growing at home and away equally. Pathogenic fungi are most often specifically examined in feedback studies and in some cases their effect has been directly demonstrated (Mills and Bever 1998, Packer and Clay 2000, Klironomos 2002). However, pathogenic fungi can be very variable in their host range (Augspurger and Wilkinson 2007) and very often information about host-specificity is lacking (Freckleton and Lewis 2006). In our study, we were unable to attribute the effect to soil fungi. While absolute plant biomass increased on both home and away soils with the addition of fungicide, it increased more strongly on away soils, intensifying the net negative feedback (Fig. 1). The most likely explanation is that generalist pathogenic fungi constrained other, even more detrimental, soil organisms (e.g., bacteria, or specific fungicide-tolerant fungi or fungus-like organisms such as Oomycetes). In a separate experiment, Zeller et al. (2007) showed that the biomass of the species with the greatest negative soil feedback, *Echinochloa crus-galli*, is reduced by 90% when infected with a cyanide-producing *Pseudomonas* bacterial strain. Other soil organisms that could be responsible for the negative feedback include nematodes and larger invertebrates such as insect larvae (De Deyn et al. 2003).

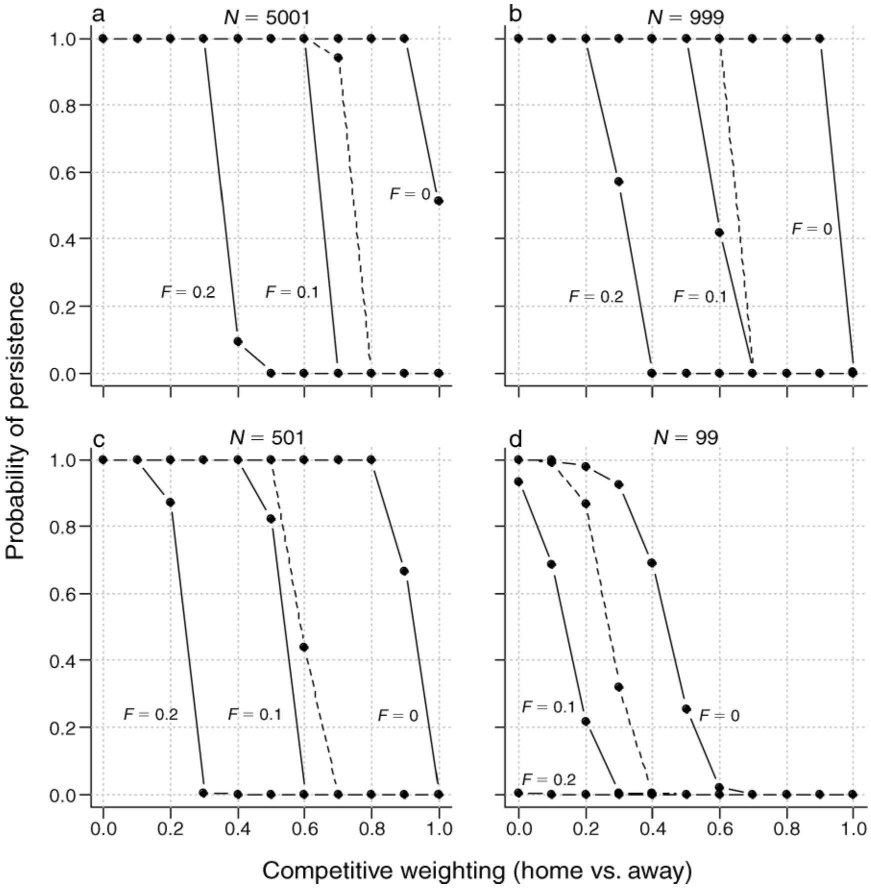

FIG. 3. Community dynamics with and without negative soil feedbacks: in a community of fixed total size (N), the probability of all three functional groups persisting for 10 000 years decreases as the competitive weighting (home vs. away) increases, and as fitness differences (F) between functional groups increase from zero ($F = 0$) to 10% ($F = 0.1$) and 20% ($F = 0.2$). As the community size decreases from ~5000 to ~100 (a–d) a lower weighting (home vs. away) is needed to ensure persistence. Fitness differences are incorporated as differences in death rates. Model simulations using observed fitness differences between functional groups (average death rates over the summer) are also shown (dashed line). The competitive weighting (home vs. away) estimated in this experiment is 0.5.

In contrast to previous studies which have demonstrated dramatic negative effects caused by allelochemicals released by exotic plant invaders on native plant species (Callaway and Aschehoug 2000), we found no consistent chemically mediated effects. Thus, chemical weapons do not seem to play an important role in structuring communities of native species with a common evolutionary history. The fact that the negative feedback was to some extent reduced in samples treated with fertilizer implies that part of the negative soil feedback could have been due to specific nutrient depletion. This represents abiotic density dependence (Ehrenfeld et al. 2005) and corresponds to predictions from classical resource niche theory (Tilman 1982). On the other hand, fertilizer addition could simply have mitigated the detrimental effect of pathogenic soil organisms by removing nutrient limitation (van der Putten and Peters 1997).

Several studies have examined feedback effects and their impact on community processes using deterministic models and have identified conditions for successful exotic invasion and the coexistence of species (e.g., Eppstein and Molofsky 2007). Here, we investigated the potential consequences of measured feedbacks on the persistence of three species each belonging to a different functional group in communities of different total size. In a community without negative feedbacks, the population dynamics are characterized by pure ecological drift and there is no stable equilibrium (Chesson 2000, Hubbell 2001). Although populations can persist for long periods under drift, this is only true when fitness differences are minimal (Zhang and Lin 1997). When fitness differences are present, stabilizing mechanisms, for example resource niches, are required (Chesson 2000); and the stronger the fitness inequalities, the stronger the stabilizing forces needed (Adler et al. 2007, Harpole and Suding 2007). We show that soil-mediated negative feedbacks can be potent stabilizing forces. The size of the measured feedbacks, coupled with information on typical fitness differences between the functional groups, indicates that negative soil feedbacks could play an important role in the maintenance of functional diversity in grasslands, providing that seeds are dispersed sufficiently far from the parent sites.

In traditional niche theory, the number of species able to coexist in a community increases with the number of niche dimensions (Hutchinson 1978). Recently, this concept of "high-dimensional" coexistence has again gained favor (Clark et al. 2007). Here we show that Janzen-Connell effects could be an important source of niche-dimensionality, with "pathogen niches," or rather pathogen-free space, providing the resource axes. Similarly, studies of biodiversity and ecosystem functioning often conclude that resource partitioning causes diverse communities to outperform monocultures; however, Janzen-Connell effects could be an equally likely explanation of why monocultures "under perform" compared to mixtures (Mwangi et al. 2007). Soil-mediated Janzen-Connell effects might furthermore be the reason that monocultures are much more easily invaded than mixtures, as has been shown in numerous previous experiments (Hector et al. 2001, Mwangi et al. 2007).

Our results demonstrate that Janzen-Connell effects are widespread among the three major functional groups in European grasslands. Each functional group is consistently disadvantaged when competing for sites that it has formerly occupied, leading to natural rotations of site occupancies, similar to those traditionally imposed by farmers. Under a neutral model, a monoculture functions just as well as a diverse community; but if low-diversity communities quickly accumulate specialist soil pathogens, these depauperate communities may develop the same "soil sickness" which continues to plague some farmers today.

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APPENDIX A

Supplementary materials, methods, and tables (*Ecological Archives* E089-135-A1).

APPENDIX B

Mean soil feedback on seedling emergence (*Ecological Archives* E089-135-A2).

APPENDIX C

Design of the main experiment (*Ecological Archives* E089-135-A3).

APPENDIX D

The effect of seed dispersal on persistence time (*Ecological Archives* E089-135-A4).