Direct evidence for this is provided by the finding that serum stimulation of quiescent cells induces the phosphorylation of PKCδ (Fig. 3), but not of PKCζ (*8*); this parallels the mitogen responsiveness defined by membrane association (*19*).

PKC isotypes are regulated by allosteric activation. The demonstration here that like cPKCs, both nPKCs and aPKCs are subject to phosphorylation in their activation loop sites, establishes an additional level of physiological control. The definition of the PI 3-kinase/PDK1 pathway leading to this phosphorylation would account for the role of a PI 3-kinase pathway in triggering n/aPKC-dependent responses (*9*, *10*). This pathway may thus operate in concert with the allosteric input to control PKC.

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Metapopulation Dynamics, Abundance, and Distribution in a Microecosystem

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The experimental fragmentation of landscapes of a natural ecosystem resulted in declines in the abundance and distribution of most species in the multispecies animal community inhabiting the landscapes and the extinction of many species. These declines caused the deterioration of the positive interspecific relation between local population abundance and distributional extent in this community. However, when patches were connected by habitat corridors, an immigration "rescue effect" arrested declines in both abundance and distribution and maintained the observed positive relation between them. These results demonstrate the importance of metapopulation dynamics and landscape connectivity for the persistence of populations in fragmented landscapes.

The observation that locally abundant species tend to be widespread, whereas locally rare species tend to be narrowly distributed, is one of the most pervasive patterns in ecology (*1*–*3*). At present, there are at least eight explanatory hypotheses, ranging from niche breadth (*4*) to sampling artifact (*5*), but each lacks conclusive evidence (*3*, *6*). A positive abundance-distribution relation is a prediction of metapopulation theory (*1*, *3*, *7*–*9*). One formulation of this theory, the rescue effect hypothesis (*8*), assumes that immigration decreases the probability of a local population becoming extinct (the "rescue effect") and that the rate of immigration per patch increases as the proportion of patches that are occupied increases. This rescue effect results in a positive relation between local abundance and one measure of distribution, namely the number of occupied patches. An important, but hitherto experimentally untested, consequence of this mechanism is that a reduction in the distributional extent of a species, for example, by habitat destruction, will result in a lower per patch immigration rate and thus a decline in the species' local abundance in remaining unaltered patches (*10*). A further prediction is that reduction or elimination of immigration between habitat patches inhibits the rescue effect and should result in declines in both abundance and occupancy in patches. We tested the rescue effect hypothesis for an entire animal community using a miniature, moss-based ecosystem. Moss landscapes are ideal because they are easy to manipulate in the field at a scale that is large relative to the size and dispersal abilities of the animal populations that live in them and because they contain an easily sampled, well-known, diverse community of microarthropods living at high densities (*11*). To date, experimental tests of extinction and immigration processes have been predominantly laboratory-based (*12*).

The first experiment (*13*) (Fig. 1A) examined the effects of habitat fragmentation on the distribution and abundance of species in the moss fauna. One year from the start of this experiment, species in nonfragmented control patches exhibited a strong abundance-distribution relation (Fig. 1B). However, in identically sized samples, there was a significant difference in the species richness of control and fragmented communities (*14*) [means of 17.0 ± 1.03 versus 10.3 ± 0.66 (±SEM); $F(1,11) = 27.9$, $P < 0.001$], a decline in mean species richness per patch of 40%. Surviving species still showed a positive relation between abundance and distribution in the fragments (Fig. 1C), but, as predicted by theory (*7*, *8*, *10*), the average patch occupancy and abundance of these species had both declined significantly (paired t tests: patch occupancy, $t = 8.43$, df = 20, $P < 0.001$; $\log_{10}$ abundance, $t = 4.09$, df = 20, $P < 0.001$; Fig. 1D). This experiment demonstrates how large-scale fragmentation of a landscape can result in a near universal decline in both the distribution and the abundance of the species inhabiting that landscape; even species surviving in the fragments declined in abundance,

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exactly as theory predicts (*10*).

Although the results of the first experiment are exactly as predicted by metapopulation dynamics theory, they may conceivably have been generated by changes in the microclimate of fragmented patches. Accordingly, a second experiment (*15*) (Fig. 2A) tested the hypothesis that the decline in abundance and patch occupancy observed in the first experiment was due to the reduction or elimination of interpatch movement and consequently the lack of a rescue effect. To test this hypothesis, we again fragmented the landscape but maintained corridors between some habitat patches. We also created "pseudocorridors" to control for the slight increase in area due to the corridors. After 6 months, species in the continuous control patches exhibited a strong abundance-distribution relation. However, 41% of the species present in the isolated fragments and in the pseudocorridor treatments had suffered extinction. Surviving species in the pseudocorridor treatment still showed a significant abundance-distribution relation (Fig. 2B) but declined in both abundance (paired *t* test: $t = 4.98$, df = 20, $P < 0.001$; Fig. 2C) and distribution (paired *t* test: $t = 4.50$, df = 20, $P < 0.001$) relative to the controls. Species surviving in the pseudocorridor and fragmented treatments did not differ in distribution (paired *t* test: $t = 0.66$, df = 20, not significant), but the abundances of species were significantly lower in the pseudocorridor treatment (paired *t* test: $t = -2.46$, df = 20, $P = 0.02$). Thus, changes in the moss fauna in the pseudocorridor treatment mirror both those in the completely isolated patch treatment and, importantly, those in the fragmentation treatment of the first experiment. In contrast, only 14.5% of the species in the communities inhabiting the landscapes connected by corridors became extinct. Although extant species in the corridor treatment also showed significant declines in both abundance (paired *t* test: $t = 4.92$, df = 20, $P < 0.001$; Fig. 2C) and distribution (paired *t* test: $t = 3.19$, df = 20, $P < 0.001$) relative to the controls, these declines were significantly less than those in the pseudocorridor treatment (paired *t* tests: patch occupancy, $t = 2.90$, df = 20, $P = 0.009$; $\log_{10}$ abundance, $t = 4.31$, df = 20, $P < 0.001$).

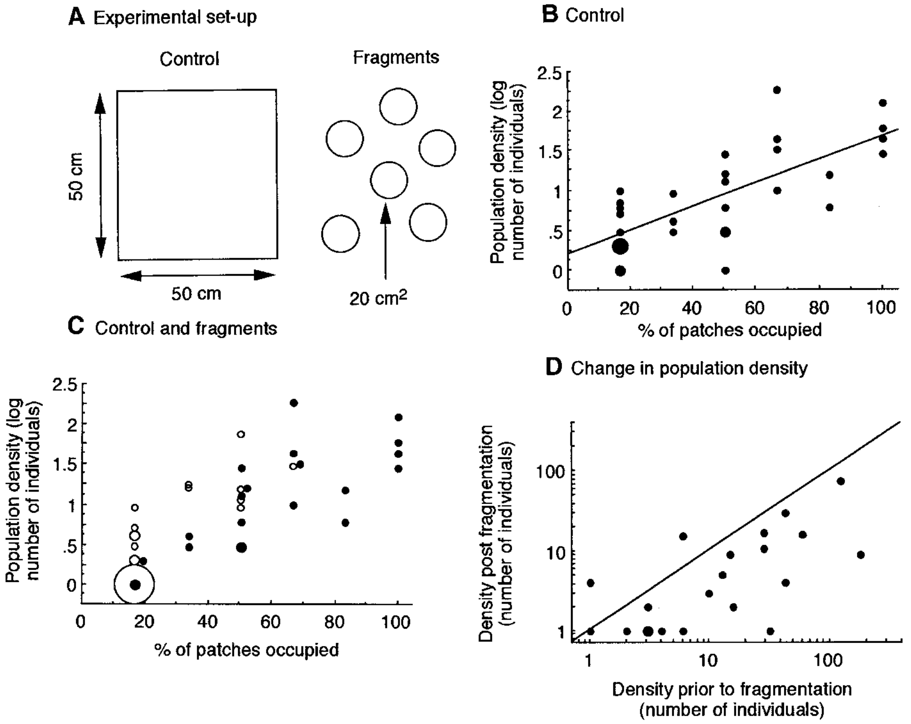

Fig. 1. (**A**) Schematic representation (not to scale) of a single replicate of the treatment design used in the first experiment (*13*). (**B**) The positive relation between abundance and distribution (proportion of patches occupied) for the microarthropods inhabiting the control moss fragments at 12 months [$F(1,28) = 30.3$, $P < 0.001$]. (**C**) Plot of population density against proportion of patches occupied for the species surviving fragmentation after 12 months (open circles) and for the same species in the control samples (filled circles). For clarity, three control points have been displaced horizontally. (**D**) Change in population density for the species surviving fragmentation illustrated by plotting population density after fragmentation against density before fragmentation. The 1:1 line has been added to better show that most species decline on fragmented patches. Coincident points are represented on all graphs by larger plot symbols, the largest indicating the coincidence of seven points.

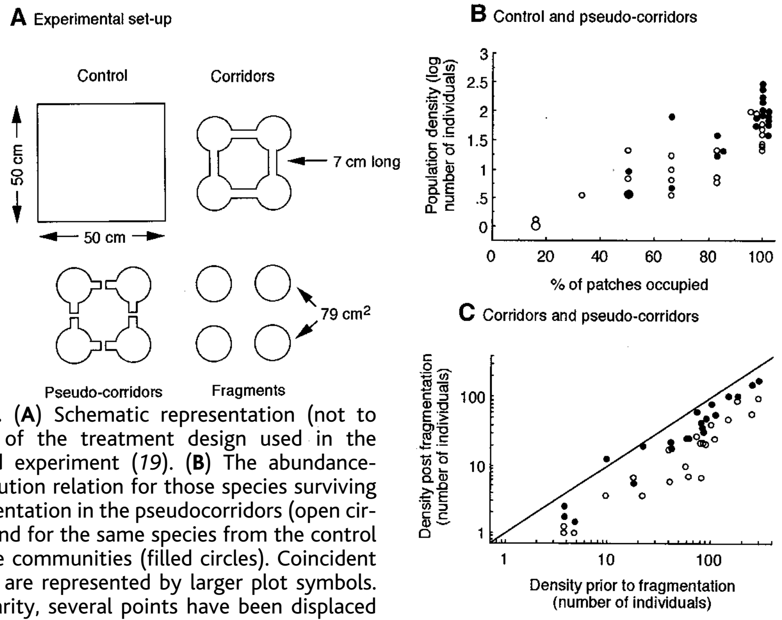

Fig. 2. (**A**) Schematic representation (not to scale) of the treatment design used in the second experiment (*19*). (**B**) The abundance-distribution relation for those species surviving fragmentation in the pseudocorridors (open circles) and for the same species from the control sample communities (filled circles). Coincident points are represented by larger plot symbols. For clarity, several points have been displaced horizontally. (**C**) The difference in the abundance of each species in the corridor (filled circles) and pseudocorridor (open circles) communities after and before fragmentation. Points below the 1:1 line show a decline due to fragmentation.

These experiments show that, at the landscape scale, habitat fragmentation results in a near universal decline in the distribution and abundance of animal species, with abundances declining even on surviving habitat patches. Exactly as theory predicts, these declines are a consequence of reducing or eliminating immigration between patches in the fragmented landscape. The creation of corridors (but not pseudocorridors of similar area) significantly ameliorates the effects of fragmentation. We suggest that real corridors facilitate dispersal between patches, creating a metacommunity and thereby maintaining the distribution and abundance of species within patches through the rescue effect (*16*).

A positive abundance-distribution relation is the null expectation if the distribution of individuals follows some stochastic process (*5*). However, in the absence of immigration, species in fragmented landscapes "slide down" the relation observed in the control communities; many species become extinct and most become rarer. Stochastic processes alone cannot generate these significant differences between treatments. Moreover, the different responses of species to the corridor and pseudocorridor treatments count against hypotheses based on interspecific variation in environmental tolerance. Thus, these results corroborate the rescue effect metapopulation model predicting the near universal relation between abundance and distribution (*4*, *17*). The scale of fragmentation and the dispersal distances of the organisms in this system are likely to be appropriate for observing metapopulation dynamics, and we do not necessarily expect the metapopulation mechanism to pertain at biogeographical scales (*4*). The results of these experiments emphasize that, at the landscape level, maintaining dispersal is imperative for maintaining the abundance-distribution relation. They also starkly demonstrate how population persistence in the face of habitat fragmentation is critically dependent on the maintenance of landscape connectivity (*18*).

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