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EFFECTS OF FOREST FRAGMENTATION ON POPULATION ATTRIBUTES OF WHITE-FOOTED MICE AND EASTERN CHIPMUNKS

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We examined differences between populations of white-footed mice (Peromyscus leucopus) and eastern chipmunks (Tamias striatus) in woodlot fragments and unfragmented forests and attempted to discriminate among potential causal mechanisms. White-footed mice showed increased population density and body mass in woodlots but otherwise no differences in population attributes between woodlots and forests. Eastern chipmunks showed decreased survival rates in woodlots but no other differences in population parameters between woodlots and forests. Mast production was variable among sites but showed no differences between woodlot and forest sites. Likewise, total biomass of mammalian granivores was similar between woodlot and forest sites, but woodlots contained an impoverished community of granivores. White-footed mice and eastern chipmunks may be affected differentially by forest fragmentation, presumably due to differences in their life-history strategies. Our results suggest that white-footed mice thrive in woodlot fragments due to increased mast availability resulting from decreased biomass of competing granivores. In contrast, eastern chipmunks may be influenced negatively by forest fragmentation, possibly because they are more susceptible to increased rates of predation occurring in woodlots than white-footed mice.

Key words: Peromyscus leucopus, Tamias striatus, agriculture, forest, fragmentation, Indiana

Humans have altered ecosystems worldwide, but the magnitude of change wrought by agriculture in the midwestern United States has been particularly acute. As an example, Indiana’s landscape in the early 1800s consisted of >85% forest, with lesser areas of wetlands and prairie (Petty and Jackson, 1966). With the advent of land clearing and drainage, the landscape lost part of these native habitats. The inception of intensive agricultural production after World War II led to further conversion of idle land for agricultural uses and a reduced diversity of crop types, primarily corn and soybeans (Sheperd, 1994). As a consequence of this shift in land use, and a more recent trend toward increasing urbanization, the extent of Indiana’s forest, wetland, and prairie habitats has been reduced by ca. 78, 86, and 99%, respectively (Hartman, 1994; Miller, 1993). Similar changes have occurred elsewhere in the midwestern United States. (Andersen et al., 1996; Iverson, 1988).

Native habitats in a predominantly agricultural landscape often persist as fragmented patches. The process of fragmentation, by reducing the amount of available habitat while simultaneously increasing its insularization (Collinge, 1996; Wilcox and Murphy, 1985), has the potential to alter aspects of the ecology of organisms at an individual (e.g., Nixon et al., 1991; Sheperd and Swihart, 1995), population (Robinson, 1992; Verboom et al., 1991), and community (Blake and Karr, 1987; Laurance, 1991) level.
There are at least three ways that fragmentation can elicit changes in a population's dynamics and ultimately its persistence. Specifically, fragmentation may affect populations directly, by restricting rates of dispersal, or indirectly by altering levels of predation or availability of resources. Species most likely to be affected negatively by agriculturally induced fragmentation are those that require large tracts of undisturbed habitat, are extreme habitat specialists, or experience difficulty dispersing through agricultural lands surrounding isolated habitat fragments (Faaborg et al., 1993; Lord and Norton, 1990; Meffe and Carroll, 1994; Temple and Cary, 1988). Species that are less likely to be affected by fragmentation, or even derive benefits from it, include those with broad habitat tolerances, well-developed vagility, or affinities for edge habitats and disturbed areas created by farming practices (Hansson, 1987; Mumford and Whitaker, 1982).

Although progress has been made in understanding effects of fragmentation on vertebrates, studies that compare demographic characteristics of species occupying fragmented and unfragmented habitats are rare. We explored effects of forest fragmentation on white-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*), which occupy forest remnants in agricultural landscapes of the midwestern United States. These species differ somewhat ecologically, which could lead to differences in their sensitivities to agriculturally induced fragmentation of forest. White-footed mice are generalist granivores that exhibit an affinity for deciduous forest habitat but are found in a variety of other types of habitat, including old fields, hedgerows, grasslands, and occasionally cultivated fields (Iverson et al., 1967; Whitaker, 1967). Thus, they might be expected to thrive in highly fragmented landscapes due to their small spatial requirements, generalist nature, and tolerance of marginal habitats (Linzey and Kesner, 1991). On the other hand, eastern chipmunks are larger granivores that also occupy deciduous forest habitats but are largely intolerant of non-forested habitat (Bennett et al., 1994; Mumford and Whitaker, 1982; Snyder, 1982). Therefore, we expected eastern chipmunks to be affected more negatively by forest fragmentation than white-footed mice. We examined attributes of populations of white-footed mice and eastern chipmunks to document differences between populations in fragments and forests and attempted to identify possible mechanisms that could generate responses that we observed.

**Materials and Methods**

Our study was conducted on the Indian Pine Natural Resources Area in west-central Indiana. The 259-km² area encompassed two major watersheds in Tippecanoe and Warren counties; 82% of the landscape was cultivated, primarily for production of corn and soybeans. Within this agricultural landscape, woodlands comprised 16% of the area and consisted of small, more or less isolated, farmland woodlots and larger wooded riparian areas (Sheperd and Swihart, 1995). Four farmland woodlots (0.8, 0.9, 2.8, and 4.9 ha) were selected for study based on the criteria of relatively mature woody vegetation and separation from other wooded areas. Woodlots were 30, 60, 95, and 870 m from their nearest neighboring forest patch with no intervening fencerow connections. Additionally, three sites representative of more extensive wooded areas (>150 ha) were selected for comparison. To avoid sampling biases associated with comparisons of sites in forests and fragments (Williamson, 1981:241), we sampled areas within continuous forests that were structurally comparable to fragments (Nupp, 1997) and similar in size to our mid-sized fragments (2.0, 2.2, and 2.7 ha).

Live-trapping and marking of granivorous rodents were performed during capture sessions in 3 seasons: spring (April–May), summer (August–September), and autumn (November–December). Trapping was conducted during spring and autumn 1992 at two woodlots and one forest site. Trapping was conducted in all seasons during 1993 and 1994. In 1993, two woodlots were trapped during spring, four in summer, and three in autumn. In 1994, all four woodlots were trapped during spring and summer, and three in autumn. All three forest sites were trapped dur-
ing all seasons in 1993 and 1994. Sampling grids were established 10–100 m from edges of continuous forest sites and >5 m from edges of woodlots, except for the two smallest woodlots where grids were kept under the tree canopy. Sherman traps (7.5 by 9.0 by 30 cm) were placed at 15-m intervals and Tomahawk traps (15 by 15 by 60 cm) at 30-m intervals on sampling grids established at each study site. Trapping grids covered the entire area of the woodlots (34–194 stations/grid), and the area indicated previously in the larger stands of continuous forest (85–120 stations/grid). All traps were prebaited for 2 nights, followed by 5 nights of trapping. Sherman traps were baited with a mixture of rolled oats, sunflower seeds, and peanut butter, and Tomahawk traps were baited with English walnuts. Trapped mice and chipmunks were examined to determine sex, reproductive condition, and body mass, and were individually marked by placing a numbered tag in one ear. Males were categorized as sexually active if they had descended testes at the time of capture. Females were categorized as sexually active if they were pregnant or lactating, or if they had enlarged nipples and an open pubic symphysis.

Estimates of abundance of adult mice (≥18 g—Cummings and Vessey, 1994) were calculated using both minimum number known alive (MNKA—Krebs, 1966) and program CAPTURE (Otis et al., 1978). CAPTURE estimates were used to compute density; MNKA was used to determine survival rates. Captures of adult chipmunks (>90 g—Bennett et al., 1994) were insufficient to obtain estimates of abundance using CAPTURE, so abundance was estimated using MNKA. Density estimates were calculated subsequently using the entire area of woodlots (0.8–4.9 ha) and the area of the trapping grid plus a 7.5-m buffer on all sides for the continuous forest sites (2.0–2.7 ha).

Capture-history profiles were constructed for individuals captured at each site (Burnham et al., 1987:29), and these were used to estimate minimum survival rates. Survival rates from session i to i+1 were calculated as a/N, where a was the number of individuals known to survive the interval and N was the MNKA estimate of abundance for session i. Capture-recapture estimates of abundance and survival are preferable to the enumerator estimates that we used, because the latter are biased low (Nichols and Pollock, 1983; Pollock et al., 1990). However, our trapping was too infrequent and our captures of chipmunks too few to enable use of capture-recapture estimates at most sites (Kesner and Linzey, 1997; Pollock et al., 1990). Empirical evidence indicates a high correlation between MNKA and capture-recapture estimates and thus similar patterns for fluctuations, at least on a crude scale (Nupp and Swihart, 1996; N. A. Slade, pers. comm.). Because we could not trap all sites during the same 5-day period, some variation in interval length existed between sites and across years. To enable comparison among sites, we calculated daily survival rates based on actual interval lengths and computed a standardized seasonal survival rate based on mean interval lengths of 121, 96, and 147 days for spring-to-summer, summer-to-autumn, and autumn-to-spring, respectively. Our fall trapping sessions coincided with onset of hibernation for chipmunks and thus yielded few capture records. Therefore, we calculated survival rates over only two intervals for chipmunks, spring-to-summer, and summer-to-spring.

Yield of hard mast was estimated using seed traps placed at 30-m intervals throughout the woodlots and within the trapping grids on the forest sites. Mast traps were constructed of circular plastic bags (1 m² area) that were elevated off the ground. Traps were placed in woodlands before mast began to fall in late August or early September. Mast was collected from traps in October, sorted by species, oven-dried, and weighed.

Repeated-measures analysis of variance was used to test for effects of woodland type (forest or woodlot) on survival rate, population density, mass of adult males, proportion of males, proportion of juveniles, proportions of reproductively mature males and females, mast yield, and biomass (kg/ha) of potentially competing grani- vores (MNKA × adult mass/trapping grid area). Variables expressed as proportions were subjected to arcsine-square root transformations before analysis (Zar, 1974:185). In the event of significant time effects, we conducted an additional three-way analysis of variance using habitat, season, and year as main effects. Newman-Keuls multiple comparisons were used to examine differences among levels of season or year. We report results from multiple statistical tests, and one concern of such testing is that a proportion α of all tests may, by chance alone, result in rejection of the hypothesis of no dif-
difference between forest and fragment populations (Type I error). When examining impacts of fragmentation and its implications for conservation, however, we believe that failure to reject such a hypothesis when false (Type II error) is more serious (Shrader-Frechette and McCoy, 1992; Steidl et al., 1997; Swihart and Slade, 1986). When Type II error is an important consideration in ecological studies, or when sample size is small, strict adherence to an arbitrary guideline such as \( \alpha = 0.05 \) is inappropriate, and an increase in \( \alpha \) to reduce the Type II error rate may be warranted (Scheiner, 1993; Shrader-Frechette and McCoy, 1993). Determining relative importance of Type I and II errors is a subjective process. We report exact \( P \)-values for all tests except those resulting in values <0.001, thus permitting readers to make their own determinations on the importance of Type I and Type II errors and draw their own conclusions regarding statistical and biological significance.

\section*{Results}

We captured 1,608 white-footed mice 3,232 times and 263 eastern chipmunks 808 times at the seven study sites. Other granivorous rodents captured included 95 fox squirrels (Sciurus niger), 65 gray squirrels (Sciurus carolinensis), 13 red squirrels (Tamiasciurus hudsonicus), and 59 southern flying squirrels (Glaucomys volans).

\textbf{White-footed mice.}—Mean density (number/ha) of adult white-footed mice was greater in woodlot sites than forest sites (woodlots, 34.6 ± 5.23, 95\% CI; forests, 15.5 ± 5.72; \( F = 18.10; d.f. = 1, 28; P < 0.001 \)). Densities in both woodlots and forests increased from spring through autumn (\( F = 2.72; d.f. = 7, 28; P = 0.03 \); Fig. 1). On average, adult male mice were 5\% heavier in woodlot sites than in forest sites (\( F = 29.98; d.f. = 1, 28; P < 0.001 \)). Temporal fluctuations were evident in mean adult weight (\( F = 7.75; d.f. = 7, 28; P < 0.001 \)); males in spring were 8\% heavier than males in autumn (Fig. 2).

Mean seasonal survival rates of mice from fragments (0.22) and forests (0.20) did not differ (\( F = 0.42; d.f. = 1, 23; P = 0.53 \)). However, mean survival rates varied seasonally (\( F = 5.24; d.f. = 2, 27; P = 0.01 \)), and Newman-Keuls multiple comparisons (\( \alpha = 0.05 \)) indicated that survival from autumn to spring (0.13 ± 0.03 \( SE \)) was significantly lower than for either
spring to summer (0.22 ± 0.02) or summer to autumn (0.24 ± 0.03). Estimates of survival were biased low, and the extent of bias could vary seasonally if capture probability also varied over time (Nichols and Pollock, 1983). However, it seemed unlikely that variation in capture probability produced differences in survival that we observed because trapping in summer (0.19 ± 0.03) and autumn (0.17 ± 0.02) yielded lower capture probabilities than spring (0.28 ± 0.02) but bracketed the season with the highest rate of survival.

Mean proportion of sexually active individuals did not differ between woodlots or forests for either males (F = 0.08; d.f. = 1, 28; P = 0.77) or females (F = 1.41; d.f. = 1, 28; P = 0.25). Temporal fluctuations did occur; proportions of sexually active individuals were lower in autumn for males (F = 23.06; d.f. = 7, 28; P < 0.001) and females (F = 4.28; d.f. = 7, 28; P = 0.005). The proportion of the population comprised of juveniles did not differ between woodlots and forests (F = 0.03; d.f. = 1, 26; P = 0.87) but showed a marginal increase from spring to autumn (F = 2.23; d.f. = 7, 26; P = 0.08). The proportion of males was similar in woodlots and forests (F = 1.16; d.f. = 1, 28; P = 0.29) and over time (F = 1.62; d.f. = 7, 28; P = 0.17).

Eastern chipmunks.—Unlike white-footed mice, mean densities of chipmunks in forests (5.8/ha) and fragments (5.5/ha) did not differ (F = 0.01; d.f. = 1, 19; P = 0.91), nor did densities fluctuate much through time (F = 1.11; d.f. = 4, 19; P = 0.38). Mean body mass of adult males in forests (112.6 g) and fragments (116.6 g) did not differ (F = 0.02; d.f. = 1, 13; P = 0.89). Likewise, temporal changes in mean body mass of adult males were small (F = 0.78; d.f. = 4, 13; P = 0.56).

Mean survival rates for chipmunks in fragments tended to be lower than rates for chipmunks in forests (F = 3.54; d.f. = 1, 12; P = 0.08; Fig. 3). When converted to annual values, survival rates were 0.05 for chipmunks in fragments and 0.22 for chipmunks in forests. Populations of chipmunks in forests and fragments did not differ in the mean proportion of males (F = 0.05; d.f. = 1, 18; P = 0.83), nor were temporal fluctuations evident in this parameter (F = 0.64; d.f. = 4, 18; P = 0.64).

Mast production and biomass of other mammalian granivores.—Overall mean production of mast was 246 kg/ha during the study. Sites varied in mast production, with a range of 7–819 kg/ha. Mast production did not differ between forests and fragments (F = 0.22; d.f. = 1, 6; P = 0.65) or between years (F = 0.06; d.f. = 1, 6; P = 0.81). Because size of black walnuts (Juglans nigra) likely precludes their use by white-footed mice (J. S. Ivan, pers. comm.), we also examined production of mast without walnuts, but no differences in yield were noted between forests and fragments (F < 0.01; d.f. = 1, 6; P = 0.95) or between years (F = 0.08; d.f. = 1, 6; P = 0.79).

Mean biomass of squirrels, chipmunks, and white-footed mice was similar in forests (2.81 kg/ha) and fragments (2.21 kg/ha—F = 1.31; d.f. = 1, 28; P = 0.26). There was a marginal tendency for mean biomass to increase from 1992 to 1994 (F =
When mean biomass of granivorous mammals other than white-footed mice was considered (i.e., gray squirrels, fox squirrels, red squirrels, southern flying squirrels, and eastern chipmunks), levels in forests (2.39 kg/ha) were greater than those in fragments (1.39 kg/ha—$F = 5.74$; $d.f. = 1, 28$; $P = 0.02$). In contrast, mean biomass of mammalian granivores other than chipmunks did not appear to differ between forests (2.34 kg/ha) and fragments (1.83 kg/ha—$F = 1.60$; $d.f. = 1, 28$; $P = 0.22$). As with total biomass per ha, the mean biomass of species other than white-footed mice increased from 1992 to 1994 ($F = 2.64$; $d.f. = 7, 28$; $P = 0.03$); a similar trend was noted for the biomass of species other than eastern chipmunks ($F = 2.32$; $d.f. = 7, 28$; $P = 0.05$).

**DISCUSSION**

Agriculturally induced fragmentation of forests produced measurable effects on populations of white-footed mice and eastern chipmunks in our study area. White-footed mice, a generalist species, appeared to flourish in remnant woodlots relative to extensively forested sites (Nupp and Swihart, 1996:figs. 1 and 2). In contrast, eastern chipmunks, a more specialized species, exhibited lower survival rates in woodlots, suggesting a negative impact of fragmentation (Fig. 3). We considered the potential role of three causative and potentially overlapping mechanisms (dispersal, predation, resource availability) in producing patterns that we observed. Because species differed in their responses to fragmentation, we considered white-footed mice and chipmunks separately.

Isolation of woodlots from other forested habitat may restrict rates of emigration, and produce increases in density relative to continuous forest sites (e.g., the “fence effect”; Krebs, 1996; Krebs et al., 1969). Rates of loss, which measure death and dispersal, also should decline if there are no strong density-dependent effects on survival. Elevated densities of mice that we observed in woodlots are consistent with this explanation. However, rates of loss did not decline as expected if relatively fewer individuals disperse from fragments. Evidence regarding movement of white-footed mice through agricultural habitat is mixed. Use of crop fields occurs during periods of the year when crops provide overhead cover (Cummings and Vessey, 1994; Whitaker, 1967). When white-footed mice were removed from a woodlot in Canada, recolonization was rapid (Middleton and Merriam, 1981). In at least one study, white-footed mice were as prevalent in corn fields as wooded habitat, based on records of nestbox use (Wegner and Merriam, 1990). These findings suggest that effects of agriculturally induced fragmentation on emigration of white-footed mice may be small.

Populations of rodents on small oceanic islands often experience lower risk of predation due to a decreased complement of predators compared with mainland sites (Alcover and McMinn, 1994). Reduced levels of predation may lead to increased rates of survival and greater densities on small islands, which in turn favors selection for competitive abilities culminating in a population skewed toward older, and larger individuals (Adler and Levins, 1994; Kawasaki, 1993). In our study, white-footed mice showed increased density and body mass, but none of the other changes expected if predation pressure had been reduced following fragmentation. In the midwestern United States, numerous species of predators appear capable of incorporating several woodlots into their home range (e.g., Petersen, 1979; Pils et al., 1978). Moreover, photographic evidence indicates that woodlots are visited by the full complement of mammalian predators found in more heavily forested sites (L. K. Page and T. M. Gehring, pers. comm.), and some of these predators may attain higher densities in landscapes with a variety of land uses than in continuous forests (Brown and Litvaitis, 1995). Evidence suggests that in terrestrial systems, populations of small mammals in for-
est fragments may experience elevated levels of predation, in contrast to the pattern on oceanic islands (Andrén and Angelstam, 1988; Brown and Litvaitis, 1995; Villafuerte et al., 1997). Thus, we doubt that our results for white-footed mice can be explained by reduced rates of predation in woodlots.

The amount of resources available to granivorous rodents could be influenced by fragmentation directly through changes in the composition or productivity of trees. Production of hard mast is correlated positively with tree-bole diameter and crown size (Goodrum et al., 1971), both of which might be expected to increase at edges of forest where competition for light is lessened. Increased levels of light along edges also favors establishment of species of trees with low to moderate shade tolerances (Palik and Murphy, 1990), such as *Quercus* and *Carya* (Harlow and Harrar, 1969). Fluctuations in population densities of granivorous rodents are tied closely to production of mast (Nixon et al., 1975; Wolff, 1996). If fragmentation results in increased production of mast or increased availability of food due to accessibility of agricultural crops, woodlots should support an increased biomass per unit area of granivores relative to continuous forest sites. In our study, however, neither production of mast nor overall biomass of granivorous mammals differed between woodlots and forest sites. Nonetheless, interspecific differences in use of agricultural crops could elevate resource availability for populations of certain species in woodlots. In west-central Indiana, forest-dwelling granivores most likely to use agricultural crops such as corn and soybeans are white-footed mice and fox squirrels (Baumgartner, 1943; Nixon and Hansen, 1987; Yeager, 1959). Although we captured only 95 fox squirrels during the study, their biomass (kg/ha) in woodlots and forest sites did not differ ($F = 0.13$; $d.f. = 1, 28$; $P = 0.72$). Moreover, captures of white-footed mice were no more frequent along the edge of woodlots than would be expected by chance (Nupp and Swihart, 1996), which suggests that they were not concentrating their activity in fields surrounding woodlots. Our results do not support increased production of resources (mast or row crops) as a likely explanation for the patterns we observed, but the low power of some of our tests should encourage further study of the role of food resources.

The amount of resources available to granivorous rodents could be influenced indirectly through changes in the density of competing species of granivores. Although woodlots and forest sites apparently produce comparable amounts of mast per unit area, a greater proportion of mast is available to white-footed mice in woodlots because woodlots support a lower overall biomass of potentially competing species. Species richness also was lower in woodlots; southern flying squirrels and gray squirrels were absent. These patterns are consistent with data from a larger sample of woodlot sites and with data derived from nested subsamples of continuous forest (Nupp, 1997). White-footed mice seem to have responded to changes in species composition by attaining heavier adult body mass and higher population densities in woodlots. Williamson (1981) used the term “density compensation” to describe the condition whereby island and mainland communities may be equally dense in terms of total numbers of individuals, but because island communities have fewer species, each island species attains a greater population density on islands than on the mainland. In our study, total biomass of granivorous rodents was similar in woodlots and forests, but biomass of potential competitors of white-footed mice was reduced in woodlots. Thus, our data most strongly support the notion that competitive release or density compensation produced the results that we observed for white-footed mice.

In contrast to the patterns observed for white-footed mice, the greater rate of loss of eastern chipmunks in woodlots is con-
sistent with increased predation as a possible causal factor. However, population density was not reduced and may even have increased as patch area declined (Nupp, 1997). It is unclear if elevated levels of predation would function in an additive or compensatory fashion (Anderson and Burnham, 1976; Bartmann et al., 1992; Johnnensen and Ims, 1996). If predation has a significant compensatory component, changes in levels of predation may fail to significantly alter population density. As previously noted, the full complement of terrestrial predators visited woodlots in our region, and woodlots represent a high concentration of prey relative to the surrounding agricultural matrix. Other studies have documented an inverse relation between area of forest patches and levels of predation on seeds (Telleria et al., 1991) and bird nests (Telleria and Santos, 1992) and elevated levels of predation in forest fragments compared with surrounding agricultural fields (Santos and Telleria, 1992). Thus, an increased rate of predation in woodlots provides a plausible explanation for patterns we observed with eastern chipmunks. It is possible that increased densities of white-footed mice in woodlots may attract more predators without changing the proportion of white-footed mice preyed upon relative to forest sites. Because population densities of eastern chipmunks are similar in woodlots and forests, an increase in the number of predators in woodlots could result in elevated predation rates. Unfortunately, we have no data on cause-specific losses of chipmunks from woodlots, and other explanations warrant consideration in future studies. For example, increased rates of emigration from woodlots also could produce patterns we observed. Detailed studies of radiomarked individuals are needed to permit an assessment of relative contributions of these factors to observed rates of loss.

Reduced survival of eastern chipmunks in woodlots could lead to local extinctions, which seem to be common with chipmunks in agricultural landscapes (Henderson et al., 1985). Frequency of recolonization of woodlots likely would depend on distance to other wooded areas, types of crops surrounding the woodlot, and presence of fencerow connections (Bennett et al., 1994; Henderson et al., 1985; Kozakiewicz and Jurasinska, 1989), with the most severe consequences in highly fragmented landscapes containing small, isolated forest patches.

Our study, like others (Dunstan and Fox, 1996; Laurence, 1991; Laurance and Yensen, 1991; Marsh and Pearman, 1997), documents that responses to habitat fragmentation can be species-specific. We examined three causative mechanisms separately (dispersal, predation, resource availability), but observed patterns may be the consequence of multiple causative factors. The entire spectrum of possible effects of fragmentation, including changes in numbers of competitors and predators, should be considered if we are to better understand responses of individuals, populations, and communities to anthropogenic changes in landscapes.

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