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Effects of the heterogeneous landscape on a predator–prey system

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ABSTRACT

In order to understand how a heterogeneous landscape affects a predator–prey system, a spatially explicit lattice model consisting of predators, prey, grass, and landscape was constructed. The predators and preys randomly move on the lattice space and the grass grows in its neighboring site according to its growth probability. When predators and preys meet at the same site at the same time, a number of prey, equal to the number of predators are eaten. This rule was also applied to the relationship between the prey and grass. The predator (prey) could give birth to an offspring when it ate prey (grass), with a birth probability. When a predator or prey animal was initially introduced, or newly born, its health state was set at a given high value. This health state decreased by one with every time step. When the state of an animal decreased to less than zero, the animal died and was removed from the system. The heterogeneous landscape was characterized by parameter H, which controlled the heterogeneity according to the neutral model. The simulation results showed that H positively or negatively affected a predator's survival, while its effect on prey and grass was less pronounced. The results can be understood by the disturbance of the balance between the prey and predator densities in the areas where the animals aggregated.

1. Introduction

The landscape structure produces environmental or spatial heterogeneity [1], which may act as a template in generating complexity at other levels of ecological organization [2]. Heterogeneity in the landscape with regard to such features as the spatial arrangement and connectivity of habitats can influence biological diversity, including species diversity, and ecosystem function [3–7]. For this reason, many researchers have studied how the heterogeneity of a landscape influences species [8–11]. Heterogeneous landscapes have been characterized as isolated islands (patches) of semi-natural habitat within a matrix of diverse land cover types. Hansson [12] and Kareive and Anderson [13] showed that landscape heterogeneity produces barriers between these islands, which restricts the directions of movement of dispersing individuals. Kareiva [14] and Hanski and Gyllenborg [15] revealed that the barriers control the rate of dispersal and recolonization of populations, which in turn may determine the long-term persistence and stability of the populations. Other studies [16,17] have shown that the persistence probability of a population increases with an increase in the colonization rate, a decrease in the extinction probability, and an increase in the variance in the patch sizes and inter-patch distances. These studies were helpful in understanding the relationship between species and a heterogeneous landscape. However, most of them did not explicitly consider the population processes of births, deaths, emigration, and immigration. In addition, they did not take into account how the spatial arrangement of the land cover between habitat patches affects the behavioral movement of

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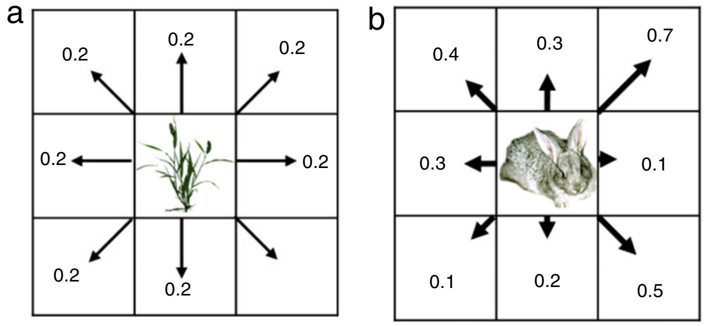


Fig. 1. (a) Growth process of grass with growth probability of 0.2, (b) example of a rabbit (or a wolf) surrounded by eight neighbor sites. Each neighboring site is labeled with its associated *h* value, reflecting the landscape property. The length of an arrow indicates the probability that the rabbit will move into a surrounding site.

dispersers among the patches [18,19], because it is difficult to measure the degree of hostility (or amenability) to movement according to species [20].

In order to overcome these problems, I constructed an ecosystem model consisting of a heterogeneous landscape along with three populations in a predator–prey situation; then, I used this model to explore how landscape heterogeneity influences the ecosystem in relation to species survival and extinction. In my model, the heterogeneous landscape was generated by using the neutral model [21–23].

2. Model description

I considered a square lattice $L \times L$ (=100), with periodic boundary conditions. There could be predators (later called wolves), prey (later called rabbits), or grass at each site of the lattice, or the site could be empty. Wolves (and rabbits) could occupy the same site at the same time. Double occupancy of grass at the same site was forbidden.

The initial distributions ($t = 0$) of the wolves, rabbits, and grasses were expressed by the field $n_w(i, j)$, $n_r(i, j)$, and $n_g(i, j)$, respectively, which denote the number of individuals at lattice site (i, j). I allowed at most one individual of each species to be present any lattice site, so $n_w(i, j)$, $n_r(i, j)$, and $n_g(i, j)$ were a binary field.

The occupancy of the individual for each species in each lattice was given by thresholding based on the probabilities W, R, and G:

$$n_w(i, j),\ n_r(i, j),\ n_g(i, j) = \begin{cases} 1, & \text{when rand } (i, j) < W \text{ (for wolf)}, R \text{ (for rabbit)}, G \text{ (for grass)} \\ 0, & \text{otherwise} \end{cases}$$

where $rand(i, j)$ represents a randomly generated number at site (i, j). Thus, the probabilities represented the initially assigned species densities. In the present study, each combination of W, R, and G was run for 2000 iterations, and the simulation results were statistically averaged over 300 independent runs.

2.1. Heterogeneous landscape

I created a spatially heterogeneous landscape in the lattice space by using a neutral landscape model [22,23]. Each lattice site had a value representing the spatially distributed property of the landscape. As the details of the complex effects of the properties on the species were unknown, the environmental properties were, for simplicity, represented as a value, h, ranging from 0.0 to 1.0. A high value of h represented favorable environmental conditions. Here, an internal parameter, H, controlling the aggregation of lattice sites with higher values of h, was assigned a value of 0.0–1.0. Higher H values corresponded to higher aggregation levels.

2.2. Species

- When a grass site had neighboring sites that included at least one site not occupied by grass, the grass could grow in that site according to its growth probability, which was arbitrarily set to 0.2. Note that it was possible for a given grass to grow into multiple neighboring sites during one iteration time step (Fig. 1(a)). The growth of grass was not influenced by the landscape heterogeneity, and the grass could occupy only a single lattice site.
- When a wolf (or a rabbit) was surrounded by neighboring sites with h values, it was more likely to move into a site with a higher h value than a site with a lower h value (Fig. 1(b)). For example, in this figure, the rabbit has the highest probability to move into the top-right site. The value of probability is calculated as $0.7/\Sigma$ (h values of the neighbor sites).

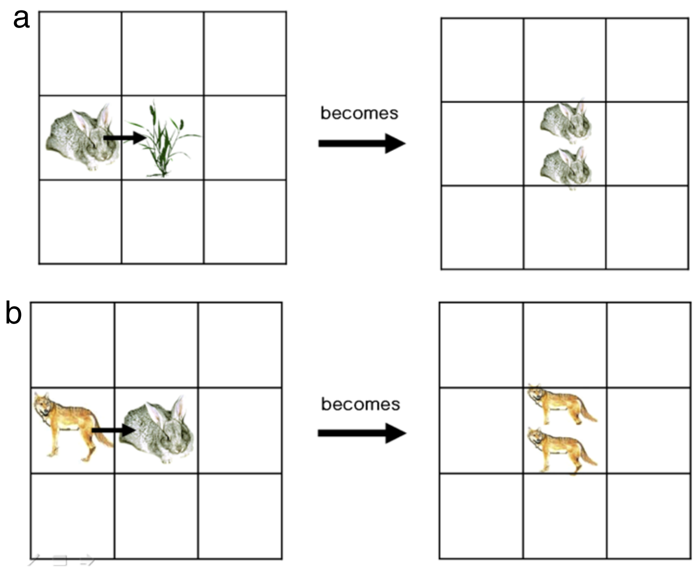


Fig. 2. Possible configurations encountered by a wolf and a rabbit at a site. When the rabbit eats the grass (or the wolf eats the rabbit), the rabbit (or wolf) gives birth to offspring.

- When wolves and rabbits met at the same site at the same time, a number of rabbits equal to the number of wolves were eaten by the wolves. The rabbits that were eaten were chosen randomly. This rule was also applied to the relationship between the rabbits and grass.
- The health state of a wolf or rabbit was represented by a value ranging from 0 to 20. When a wolf or rabbit was initially introduced, or newly born, its initial health state was assigned a value of 20.
- When a wolf (rabbit) moved a step, its health state decreased by one. When its health state decreased to below zero, the wolf (rabbit) died and was removed from the system.
- Before the wolf (rabbit) died, if it consumed food (grass for a rabbit; a rabbit for a wolf), its health state was recovered to the original value of 20.
- When a wolf ate a rabbit (or a rabbit ate grass), it gave birth to a single offspring with a birth probability of 0.2. The offspring was located at the same site as its parent (Fig. 2).

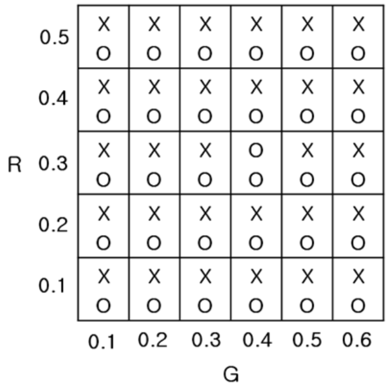
3. Simulation results

Fig. 3 shows the typical survival and extinction results for a wolf and rabbit for $W = 0.1$ and $H = 0.0, 0.3, 0.6$, and 0.9, where $G = 0.1, 0.2, \ldots, 0.6$ and $R = 0.1, 0.2, \ldots, 0.5$. The letters "*O*" and "*X*" in each site of the *R*–*G* space represent the survival and extinction results, respectively. The upper and the lower letters correspond to the wolf and rabbit results, respectively. At $H = 0.0$, the wolf became extinct in all areas of the $R - G$ space, while the rabbit survived (Fig. 3(a)). As H increased, the coexistence area for the wolf and rabbit increased (Fig. 3(b)–(d)). Here, the coexistence area, N, was defined as the number of sites where a wolf and rabbit coexisted in the $R - G$ space. At $W = 0.4$, N increased when $H = 0.0, 0.3$, and 0.6 and decreased when $H = 0.9$; in this case, the values of H, R, and G were the same as those of Fig. 3 (Fig. 4).

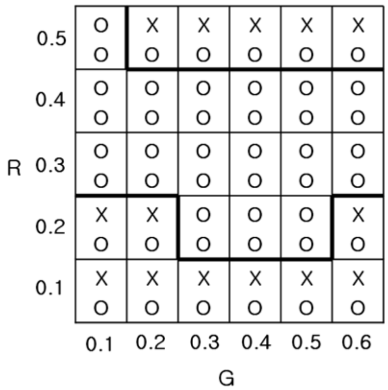
In order to further investigate the relationship between N and H, I plotted N against H for different values of W (Fig. 5). For $W < 0.4$, an increase in H caused N to increase and become saturated. N increased at $W \geq 0.4$ but decreased at $H = 0.6$. Saturation occurred when N became equal to the total number of sites of the $R - G$ space, and the decrease was caused by clusters with higher values of h. The clusters functioned not only as attractors to restrict the dispersal of wolves and rabbits but also as suppliers of rabbits to the wolves. These functions of the clusters can be understood by investigating the competition dynamics among the species.

Fig. 6 shows the typical pattern of the species dynamics, generated by a single simulation run, for $H = 0.0$ and 0.3 where $W = 0.1$, $R = 0.3$, and $G = 0.4$. In Fig. 6(a), the wolf population abruptly decreased at $t = 20$ because many wolves could not capture rabbits by that time, with the result that they starved and died. For $100 < t < 350$, the population of surviving wolves fluctuated slightly on account of the wolf's life cycle, comprising birth, reproduction, and death. The wolves became extinct at $t = 350$ because at $H = 0.0$, few clusters with high h values were formed (center of Fig. 6(a)). This lack of clusters led a long average distance between individual wolves and rabbits because of the absence of attractors (right side of Fig. 6(a)), which consequently decreased the chances for wolves to capture rabbits.

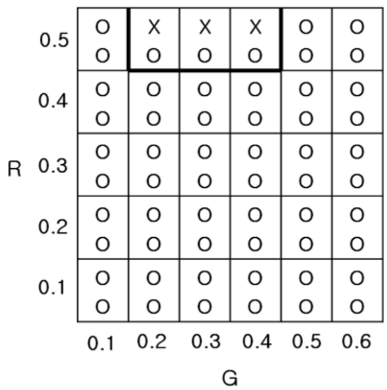
In Fig. 6(b), for $H = 0.3$, clusters higher h values were formed, as indicated by the dotted circles (center of Fig. 6(b)). The density of rabbits was higher inside these clusters than outside them because the clusters attracted wolves and rabbits (right side of Fig. 6(b)). Thus, wolves inside a cluster had a higher chance of catching rabbits. Although the wolves located



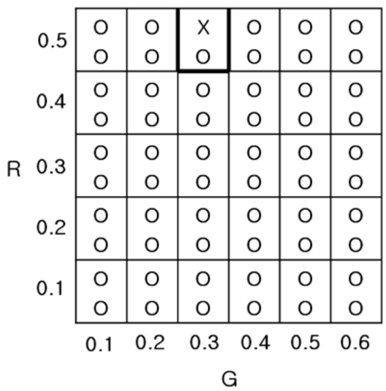
(a) $H = 0.0$.



(b) $H = 0.3$.



(c) $H = 0.6$.



(d) $H = 0.9$.

Fig. 3. The results for the wolf and rabbit in the $R - G$ space for $W = 0.1$ and $H = 0.0$, 0.3, 0.6, and 0.9 where $R = 0.1$–0.5 and $G = 0.1$–0.6. The upper and lower letters in each site represent the wolf and rabbit results, respectively.

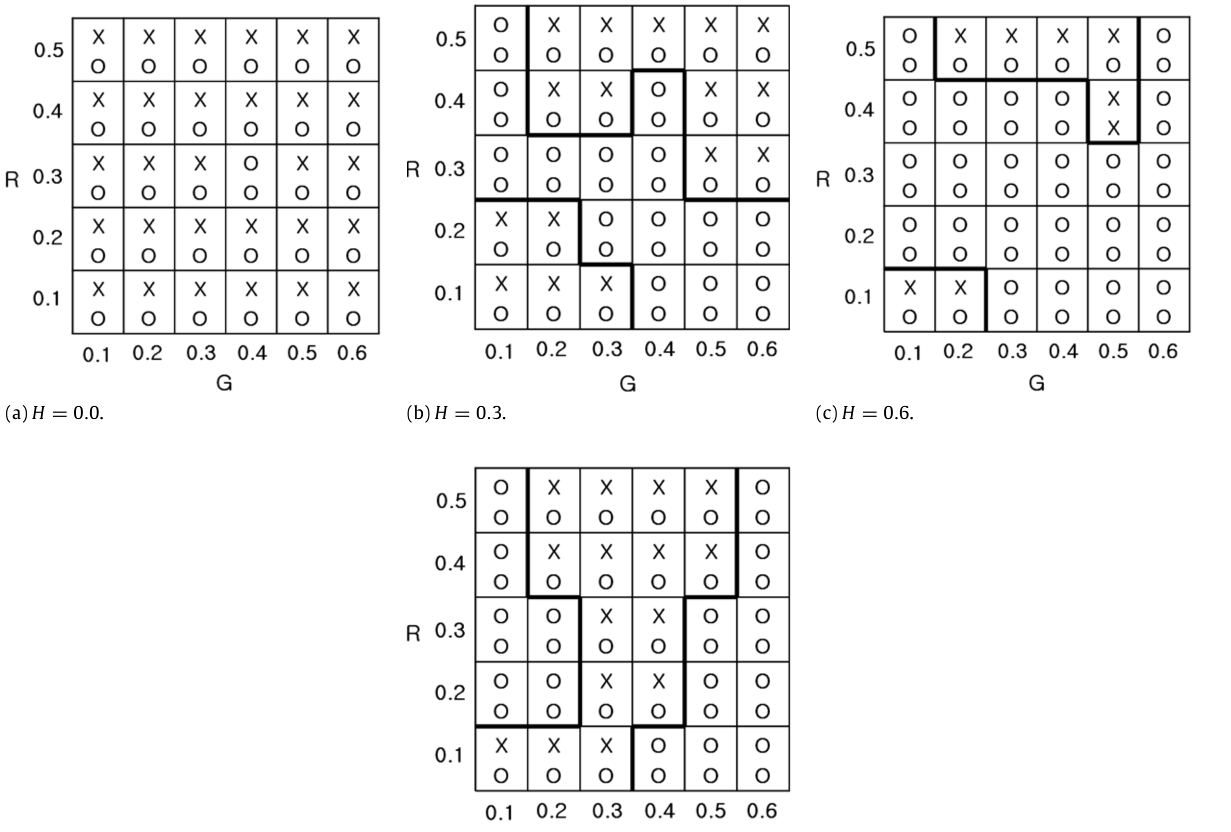
outside of a cluster would probably die, species extinction could be avoided due to the wolves inside the clusters. However, when the number of wolves in the clusters became too high as H increased, the number of rabbits in the clusters rapidly decreased, which in turn caused a decrease in N at $H > 0.6$ for $W = 0.4$ and 0.5.

4. Conclusions and discussion

In this study, I constructed a lattice model that simulated an ecosystem consisting of wolves, rabbits, grass, and a heterogeneous landscape in order to explore the effect of a heterogeneous landscape on an ecosystem. The wolf, rabbit, and grass densities were initially set at $W = 0.1$–0.5, $R = 0.1$–0.5, and $G = 0.1$–0.6. For all the combinations of W, R, and G, the rabbits and grass survived while the wolves were strongly dependant on the values of R and G (Figs. 3 and 4). Thus, I focused my attention on the wolf's extinction or survival for combinations of R and G ($R - G$ space) and measured the coexistence area, N, defined as the number of states where the wolves and rabbits coexisted in the $R - G$ space. Each lattice site had a value h, representing the spatially distributed property of the landscape. The landscape heterogeneity was characterized by a parameter, H, which controlled the clustering of lattice sites with higher values of h. Higher H values corresponded to higher clustering levels.

For $W = 0.1$, 0.2, and 0.3, an increase in H caused N to increase and become saturated, while N increased and then decreased for $W = 0.4$ and 0.5. As H increased, clusters with higher values of h formed and increased in size, and these clusters acted as attractors for wolves and rabbits. Unless the balance between the rabbit and wolf densities in the clusters was disturbed, the landscape heterogeneity positively affected the survival of the wolves. On the other hand, when the wolf density became too high in the clusters as H was increased, the number of rabbits in the clusters rapidly decreased. Thus, the wolves in the clusters starved and consequently died. This balance disturbance caused a decrease in N (Figs. 5 and 6).

To simplify the model, I assumed that the wolves and rabbits had the same health state and moving speed characteristics. In addition, both species were assumed to be equally influenced by the landscape heterogeneity. Although these assumptions are likely to be untrue for real animals in the field, the simulation results provided a possible explanation for the mechanism of how landscape heterogeneity influences a predator–prey system in relation to a predator's extinction. In the present study, the simulation experiments were carried out on the square-type lattice space. For different lattice types, N in the $R - G$ space



(a) $H = 0.0$.

(b) $H = 0.3$.

(c) $H = 0.6$.

(d) $H = 0.9$.

Fig. 4. The wolf and rabbit results in the $R - G$ space for $W = 0.4$ and $H = 0.0, 0.3, 0.6$, and 0.9 where $R = 0.1$–0.5 and $G = 0.1$–0.6. The upper and lower letters in each site represent the wolf and rabbit results, respectively.

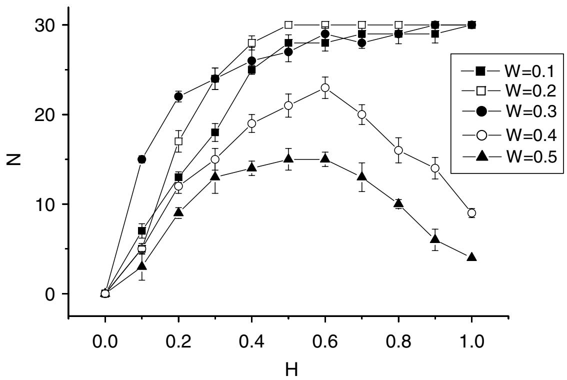


Fig. 5. Plots of the coexistence area, N, defined as the number of sites where a wolf and rabbit coexisted in the $R - G$ space against landscape heterogeneity, H, for $G = 0.1, 0.2, \ldots, 0.6$ and $R = 0.1, 0.2, \ldots, 0.5$, where the initial wolf density, $W = 0.1, 0.2, \ldots, 0.5$.

may be changed because the different lattice type provides different movement ways. For example, in the square type, each individual can move into eight neighboring sites, while in the honeycomb type, the number of movement direction of an individual is limited to six. However, I believe that the main mechanism showing that the balance between the rabbit and wolf densities in the clusters with higher h values plays an important role in the extinction and coexistence of the species would be adaptive for the different type systems.

In addition, the simulation results provided a basis for future work on the dynamics of a predator–prey system with regard to the innate abilities of individuals, e.g., the ability to search for food in an intelligent manner or the ability to communicate with other members of the same species.

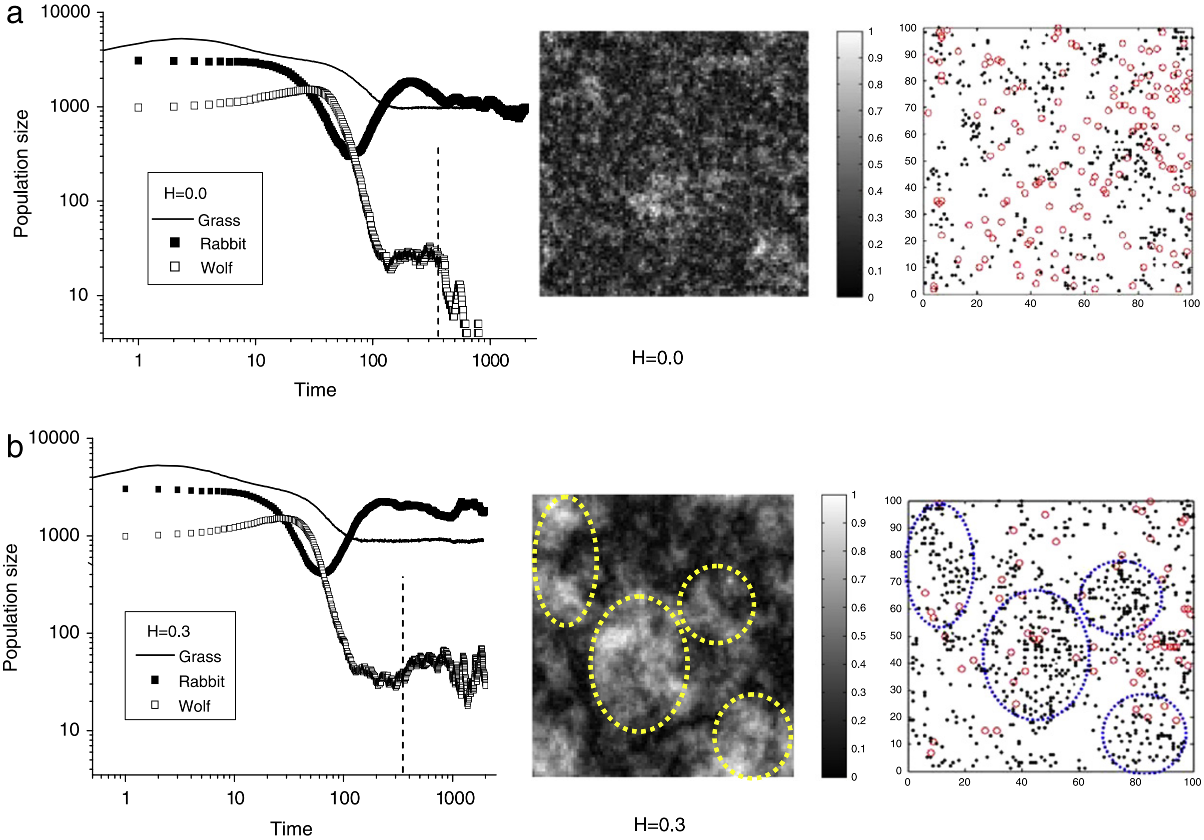


Fig. 6. (a) Heterogeneous landscapes with $H = 0.0$ (center), distribution pattern for wolves and rabbits (right), and population dynamics of species (left). (b) Heterogeneous landscapes with $H = 0.3$ (center), distribution pattern of wolves and rabbits (right), and population dynamics of species (left). Here in the right figures, black dots and red circles indicate rabbits and wolves, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

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