Habitat Loss and Changes in the Species-Area Relationship

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Abstract: *The species-area relationship (SAR) has been used successfully to predict extinction from extent of habitat reduction. These extinction estimates assume that species have uniformly distributed range requirements and a minimum abundance level required for persistence; how many species are lost depends solely on how much habitat is removed, not on where it is removed. We consider another limiting case in which range requirements, rather than abundances, determine extinctions. We used a new method for constructing SARs based on assumptions about geographic ranges of species. Our results show that habitat destruction can change the SAR and consequently the number of species predicted to be lost due to habitat destruction. Our method generates SARs that vary in shape according to the specific distributions of geographic range and occupancy but that have the common feature of being described by a power law with an exponent of* <1*. When the geographic range of species was included in the SAR, the way habitat was lost became important. Although the SAR before habitat destruction is often used to predict species loss after habitat destruction, assumptions must be clearly stated. To predict the damage caused by habitat loss with our model, it is necessary to know the fraction of aggregated species, the distribution of geographic ranges, the form of habitat destruction, and the sampling protocol. The remaining theoretical challenge is to develop a full theory that links abundance and range.*

Pérdida del Hábitat y Cambios en la Relación Especie-Area

Resumen: *La relación especie-área (REA) ha sido utilizada exitosamente para predecir la extinción a partir de la extensión de la reducción del hábitat. Estas estimaciones de extinción asumen que las especies tienen requerimientos de rango uniformemente distribuidos y un nivel mínimo de abundancia requerido para persistir; cuantas especies sean perdidas depende únicamente de cuanto hábitat es removido, y no en base a donde el hábitat es removido. Consideramos otro caso limitante en el cual los requerimientos de rango, en lugar de la abundancia, determinan las extinciones. Usamos un método nuevo para construir REAs basadas en conjeturas sobre los rangos geográficos de las especies. Nuestros resultados muestran que la destrucción del hábitat puede cambiar la REA y consecuentemente el número de especies predecidas a ser perdidas debido a la destrucción del hábitat. Nuestro método genera REAs que varían en forma de acuerdo con las especificidades de las distribuciones del rango geográfico y la ocupación, pero tienen la característica común de estar descritos por una ley de poder con un exponente* <1*. Cuando los rangos geográficos de la especie fueron incluidos en la REA, la pérdida del hábitat se volvió importante. A pesar de que el valor de REA antes de la destrucción del hábitat es utilizado como un predictor de la pérdida de especies después de la destrucción, uno debe ser claro con las conjeturas. Para predecir el daño ocasionado por la pérdida del hábitat usando nuestro modelo, uno necesita conocer la fracción agregada de especies, la distribución de los rangos geográficos, la forma de destrucción del hábitat y el protocolo de muestreo. El reto teórico remanente es el desarrollar una teoría completa que vincule la abundancia con el rango.*

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Introduction

The species-area relationship (SAR) is one of the cornerstones of modern ecological science (Rosenzweig 1995) and conservation biology. In general, the relationship between the number of species S and the area A of a habitat is $S = CA^z$, where the parameter z is generally <1, typically around 0.1–0.4 (McGuinness 1984; Rosenzweig 1995; He & Legendre 1996). Although they are usually treated as constants, it is recognized that the intercept C and exponent z may change as area changes (Preston 1962; MacArthur & Wilson 1963, 1967; Brown 1984; reviewed in Rosenzweig 1995). Because $z < 1$, the number of species increases with area, but it does so at a decreasing rate: larger areas hold proportionately fewer species than smaller areas.

The standard species-area relationship has been used successfully in a number of cases to predict extinction based on habitat reduction (e.g., Pimm & Askins 1995; Pimm et al. 1995; Brooks et al. 1997; Pimm 1998). These extinction estimates assume that species have uniformly distributed range requirements and a minimum abundance level required for persistence. Thus, as the total number of all species is reduced during habitat destruction, an increasing fraction of species falls below the minimum number needed to persist. In this case, how many species are lost depends solely on how much habitat is removed, not on where the habitat is removed. Species abundances determine which species are lost and thus as area decreases the SAR can be used to predict species loss (Fig. 1).

Assuming that species have essentially uniform ranges is a good approximation to the applications in which the SAR has been used to predict extinctions. It is a limiting case, however, in which abundance determines extinction. We considered another limiting case in which range requirements rather than abundances determine extinctions. We used a new method (Ney-Nifle & Mangel 1999) for constructing SARs from assumptions about the geographic ranges of species. Our results show that habitat destruction can change the SAR and consequently the number of species predicted to be lost due to habitat destruction.

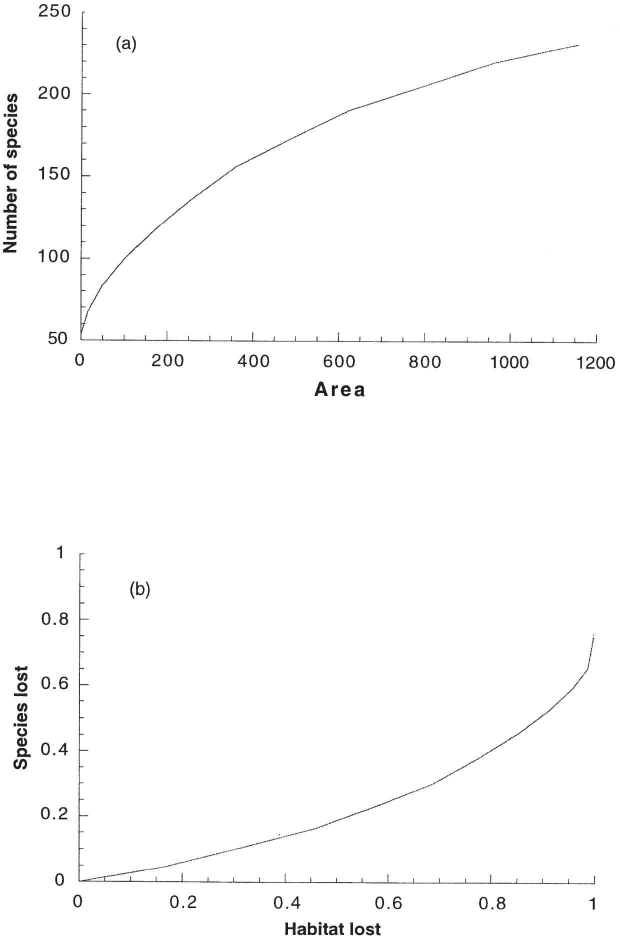


Figure 1. How the species-area relationship (SAR) ($S = CA^z$*:*S*, number of species;* A*, habitat area;* C*, intercept;* z*, exponent) can be used to predict species loss when species are widely distributed and extinction is determined by an abundance criterion: (a) SAR with* $z = 0.23$ *determined by our method with an exponential distribution of ranges, and (b) predicted fraction of species lost as a function of the fraction of habitat lost (obtained by following along the SAR from (a) as area decreases).*

Methods

Geographic Ranges of Species and an SAR Model

Common explanations for the SAR (MacArthur & Wilson 1967; Coleman 1981; Rosenzweig 1995; Gotelli & Graves 1996) or species loss (Koopovitz et al, 1994; Tilman et al. 1994) assume that species are uniformly distributed in space. In general, however, different species have different geographic range requirements and different densities. Geographic range requirements in particular can become crucial in understanding how many species will be lost as habitat is destroyed.

We superimposed a grid of cells over a map of a physical region and created a hypothetical community by assigning species to cells of the grid. We used grids of size 64 × 64 and up to 250 species. Instead of assuming that species were uniformly distributed over the grid, we assumed that each species could be characterized by the number of cells it occupied (occupancy) and the spatial extent required for it to persist (geographic range requirement). For example, some species could be geographically restricted and occupy one small patch (a set of connected cells), whereas others could be widespread and uniformly distributed (Fig. 2a). In the latter

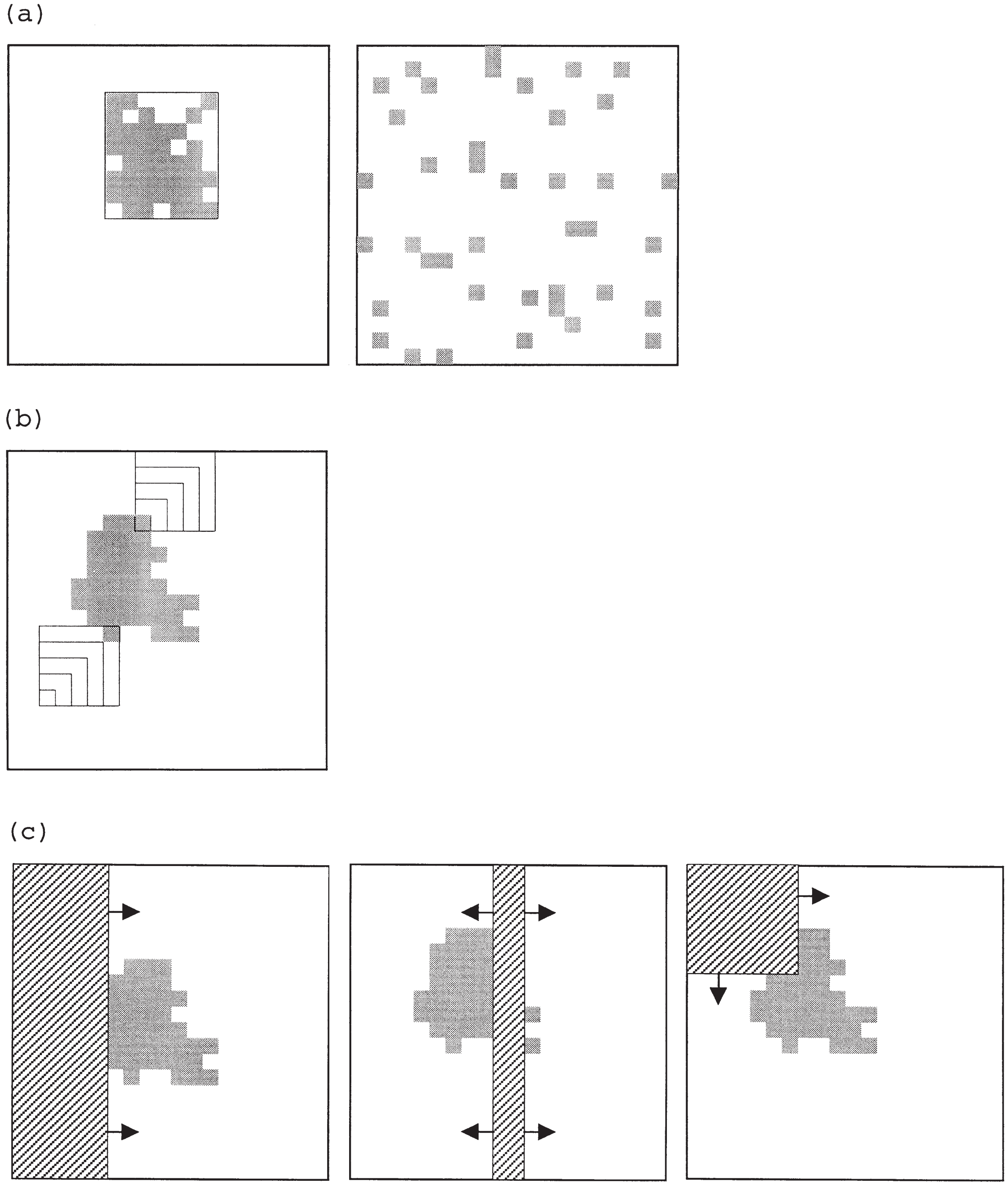


Figure 2. (a) Examples of species distributions on a grid. Both species have the same occupancy (10% of the area), but one is geographically restricted and the other is uniformly distributed inside the area. (b) Species-area relationship created by randomly picking a starting point and surveying areas of increasing size. (c) Three ways in which the same amount of habitat may be lost from a system: rectangular cut, rectangular cut plus habitat fragmentation, or square cut.

case, our model was equivalent to the random placement model (Coleman 1981; Gotelli & Graves 1996) except that we used occupancy instead of abundance. An empirical reason for doing so is that occupancy requires presence-absence data, whereas abundance requires actual numbers of individuals. Each community of species was characterized by appropriate distributions for geographic range and occupancy.

Previously, (Ney-Nifle & Mangel 1999), we have demonstrated how to construct SARs for communities characterized by different assumptions about the distribution of geographic range and occupancy. Here, we made the simplifying assumption that all grid cells within the geographic range were occupied so that there were no fragmented ranges. We used a generalized distribution of geographic ranges (Gaston 1994) in which ranges varied between 0.05% and 0.65% of the total area and the distribution decayed rapidly, so there were few species with large ranges and many species with small ranges (cf. Leitner & Rosenzweig 1997). If species with restricted ranges are randomly distributed on the grid, there will be fewer species near the edges (Colwell & Hurtt 1994). For example, specialized species might aggregate in the center of the area, which would reduce the number of species near the edges (e.g., forest boundaries or coastlines).

We computed the SAR by randomly picking a starting location on the grid, counting species in that square, and then expanding the census area, thus accumulating species as the census area increased (Fig. 2b). This procedure generated both an SAR and variance about the averaged SAR associated with different starting points. For computations we used as many starting points as there were cells to reduce the error estimate for the number of species. In one case, described below, we used only the interior 30% of cells as starting points. This avoided an "edge effect" in sampling (Colwell & Hurtt 1994).

For ease of presentation, we present only the average SAR (for variation around the average SAR, see Ney-Nifle & Mangel 1999). This approach can generate SARs that vary in shape according to the specific distributions of geographic range and occupancy (Ney-Nifle & Mangel 1999), but that have the common feature of being described by a power law with an exponent of <1. For example, the SAR used to generate the results in Fig. 1 has $z = 0.23$ and was based on an exponential distribution for the geographic range.

Simulating Habitat Loss and Species Number Declines

When the geographic range of a species was included in the SAR, the cause of habitat loss became important. Thus, we simulated the destruction of part of the habitat in one of three ways (Fig. 2c): (1) we removed a rectangle from the boundary, (2) we removed a rectangle from the interior of the habitat, thus fragmenting it into two pieces, or (3) we removed a square, leaving an oddly shaped patch. In the second case of habitat fragmentation, we introduced the probability (p) that if the range of a species crossed the new border of the fragmented area, then the species was able to survive. In the third case, to avoid edge effect we used only the interior cells as starting points.

We assumed that all species present in the destroyed area were locally extirpated, and we determined, in the same manner as before, the number of species remaining after a new equilibrium had been reached, because it takes time for some species to become extinct after habitat destruction. We thus generated a "new" SAR based on habitat destruction.

Results

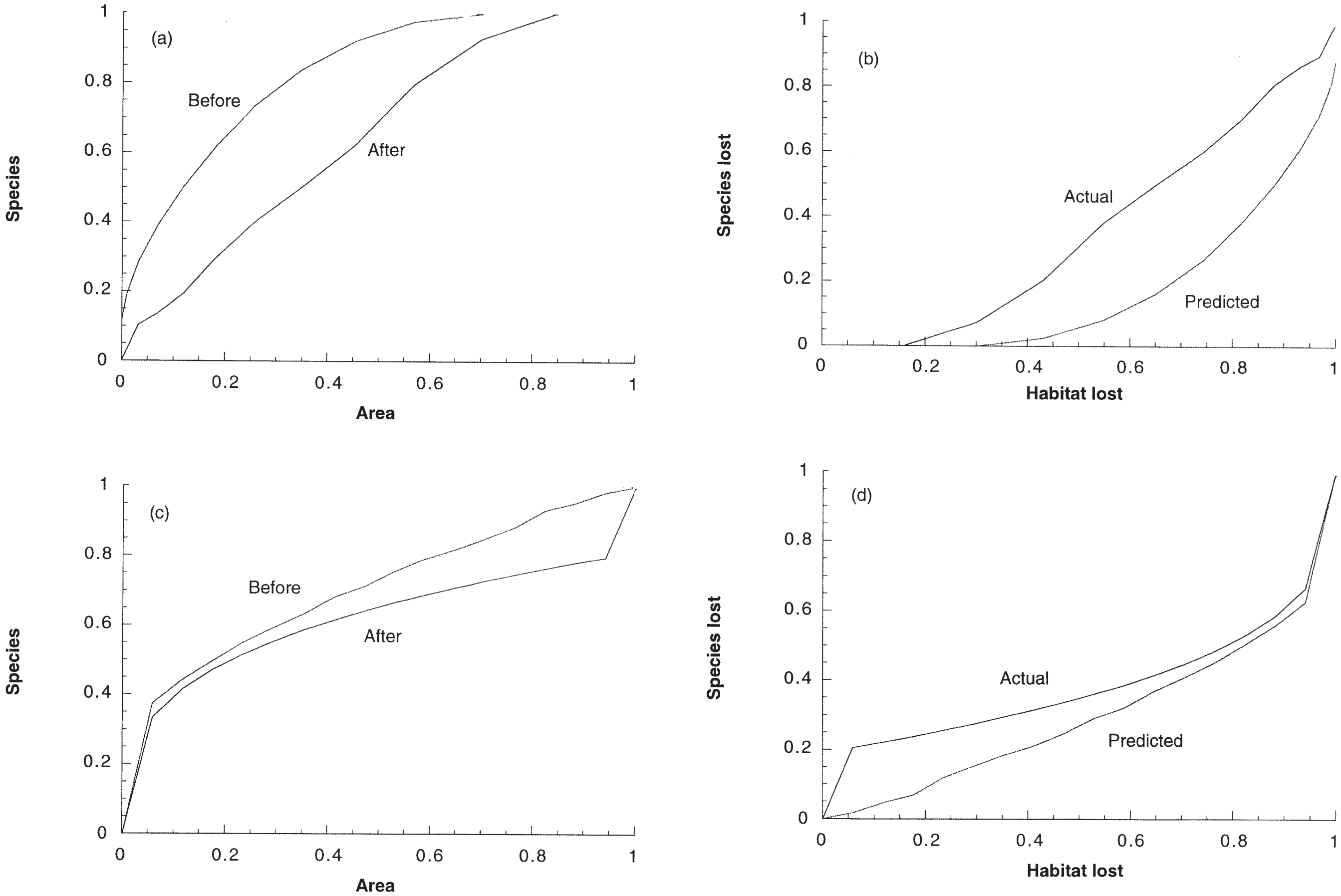
In the case of a rectangular cut with or without habitat fragmentation, using the original SAR led to a vast underestimation of species loss (Fig. 3). For example, for the rectangular cut without habitat fragmentation, the original SAR predicted that only 10% of the species would be lost with 50% habitat loss. The actual loss, based on the SAR after habitat destruction, was more than 30%. With a square cut and only interior points used to start the survey of species, the number of species was higher after habitat loss.

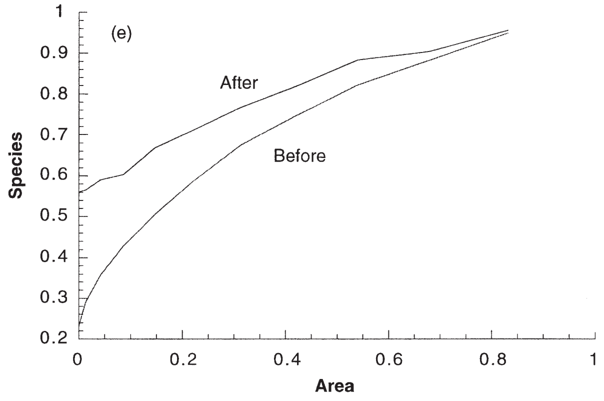
Discussion

Although the SAR before habitat destruction is often used to predict species loss after habitat destruction, assumptions must be stated clearly. We demonstrated that spatial effects such as geographic range distribution and minimum viable ranges, edges, and fragmentation can change the SAR. In particular, the larger the fraction of aggregated species (those having a restricted range), the more likely a change in the SAR with habitat destruction. This may be especially applicable to tropical forests because their species ranges tend to be more aggregated than those of temporal forests, or to birds across a suite of oceanic islands where the islands are typically either mostly deforested or altered only lightly.

It was surprising that the square cut led to a prediction of more species after habitat loss. This occurred because the square cut minimized the perimeter to a fixed amount of lost area. Thus, the likelihood of losing species because of range effects was smallest with a square cut; and, if sampling did not take one near the boundary, the SAR after habitat destruction could be greater than that before habitat destruction. In essence, roughly the same number of species occurs in a smaller area because fewer species are removed with a square cut than with a rectangular cut of the same area. In part, this effect is caused by our intentional avoidance of edge effects by considering only the central cells as starting points for creating the SAR (Pimm et al. 1995; Harte & Kinzig 1997).

To predict the damage caused by habitat loss using our model, it is necessary to know the fraction of aggregated species, some information about the distribution of geographic ranges (e.g., mean and variance or at least presence-absence data), the form of habitat destruction,





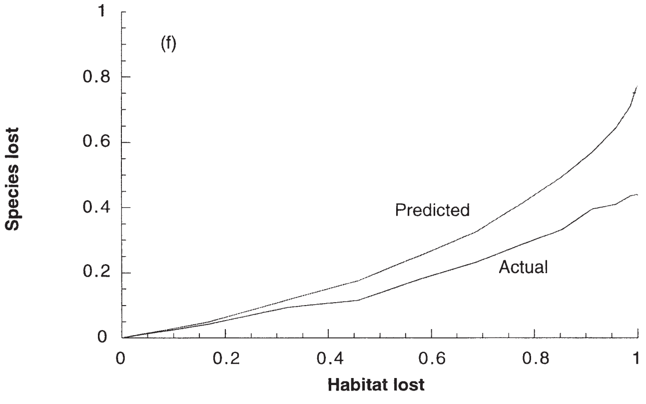


Figure 3. Predictions of species lost with habitat loss: (a, c, e) SAR before and after habitat destruction, and (b, d, f) the fraction of species predicted to be lost (based on the original SAR) as a function of habitat loss and the actual fraction (based on the new SAR) of species lost. For simplicity, we have normalized areas and number of species; hence area has no units. (a) Species-area relationships with a rectangular cut; (b) species lost with a rectangular cut; (c) species-area relationships with a rectangular cut with habitat fragmentation and $p = 0.5$; (d) species lost with a rectangular cut with habitat fragmentation and $p = 0.5$; (e) species-area relationship with a square cut with only the interior region used to assess the number of species; and (f) species lost after a square cut with only the interior region used to assess the number of species.

and the sampling protocol. With this information, how many species are lost depends on where the habitat is removed because species' ranges rather than abundances determine which species are lost.

Finally, real-world situations occur between the two limiting cases of abundance and range requirements. Species with small ranges are also usually rare within them. In practice, this means that, in addition to the species lost from the destruction of habitat, a group of species will survive outside the destroyed area and will, in time, go extinct because they are not sufficiently numerous. To fully address this case requires a theory of the covariation of abundance and range.

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