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Unveiling a mechanism for species decline in fragmented habitats: fragmentation induced reduction in encounter rates

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Several studies have reported that fragmentation (e.g. of anthropogenic origin) of habitats often leads to a decrease in the number of species in the region. An important mechanism causing this adverse ecological impact is the change in the encounter rates (i.e. the rates at which individuals meet other organisms of the same or different species). Yet, how fragmentation can change encounter rates is poorly understood. To gain insight into the problem, here we ask how landscape fragmentation affects encounter rates when all other relevant variables remain fixed. We present strong numerical evidence that fragmentation decreases search efficiencies thus encounter rates. What is surprising is that it falls even when the global average densities of interacting organisms are held constant. In other words, fragmentation *per se* can reduce encounter rates. As encounter rates are fundamental for biological interactions, it can explain part of the observed diminishing in animal biodiversity. Neglecting this effect may underestimate the negative outcomes of fragmentation. Partial deforestation and roads that cut through forests, for instance, might be responsible for far greater damage than thought. Preservation policies should take into account this previously overlooked scientific fact.

1. Introduction

A problem of great concern is why animal species disappear from environments which suffer a fragmentation process. In fact, a major issue in conservation efforts around the world [1] is to determine to what degree protected lands and ecological reserves should stay physically connected.

From a purely spatial point of view, a fragmented landscape can be thought of as the extreme limit of a patchy or heterogeneous landscape, when the patches become completely disconnected. Patches represent local peaks or local maxima in the density of some resource, and fragments are patches outside of which the local density vanishes. Assuming animal species are adapted to the patchy nature of their habitat [2–4]—i.e. for the resources distributed not uniformly but heterogeneously, with clustering—the relative probability of visiting distinct patches underlies a variety of subjects in ecology. For instance, the number of species present on a given island seems to strongly depend on the probability of successful colonization [5]. Also, the rate at which migrants move among habitat patches is crucial for determining the degree of demographic coupling of populations [6], as well as the level of gene flow and genetic differentiation [7,8].

However, the picture is completely different if a previously contiguous environment becomes fragmented, for instance, owing to anthropogenic causes. A large body of accumulated empirical data [9–14] point to the decline of diversity in

fragmented landscapes. Many important processes—especially those studied in the context of tropical forests [15]—may be responsible for the above-mentioned decline. Among them, we can cite: (i) species that are overly sensitive to habitat size; (ii) a lower genetic variability associated with a smaller number of individuals living in fragments (thus decreasing the fitness of future generations); (iii) reduction of migration owing to hostile interfragment regions (known as the matrix [16]); (iv) edge effects induced by a larger border/interior ratio (see [17–19]), influencing the patch microclimate (light conditions, wind, humidity, etc.) and so exposing the species in the border to unfamiliar conditions and stress; (v) a chain effect, when one species is not immediately influenced by the fragmentation but depends (e.g. by predation) on another species which does and (vi) invasion of ‘exotic’ species from the matrix into the fragment. Furthermore, in some cases it may be possible that very particular features (perhaps not generalizable to other contexts) of a group of species in an ecosystem may trigger species reduction (or even the opposite, increase) in a fragmented region. Interesting examples are given for reef fishes in [20] and for tree species in fragmentation caused by floods in [21].

We emphasize that this phenomenon is not restricted to forests. Coral reefs and grassland, for instance, can likewise suffer from fragmentation and destruction—each environment presenting its own features. Consider reefs: fish species may profit from coral reef disjunction (owing to board increasing), whereas other species may not [20]. Similarly, fragmentation patterns can present a threat to grassland-nesting birds [22]. Also, a decreasing of available patches might cause a reduction of biodiversity, as reported for Fynbos ecoregions in South Africa [23]. Finally, fragmentation-induced decline of abundance is not limited to animals. Intricate ecological correlations might lead to local (within-fragments) plant extinctions as well [12].

Despite a slow and steady increase in our knowledge about the distinct mechanisms acting on fragmented environments, at present no single unifying theory seems to explain the general features of all the observations regarding biodiversity reduction associated to fragmentation [24]. Recent studies [10] suggest nonlinear and highly complex interactions, with considerable interspecific variability, possibly causing strong parallel decline in animal species [11]. For example, birds that disappear from fragments show a tendency to disperse considerably over large distances in connected forest, but not in fragmented forest. By contrast, species that persist in fragments are usually those that do not cross gaps as often, yet dispersing further after than before fragmentation [10]. Actually, tropical forest birds may disperse more than commonly believed [10].

It may happen that some consequences of fragmentation are still not well understood. Certainly, one of the important missing ingredients is knowledge of how fragmentation alters biological encounter rates, a key factor governing foraging [13] and mating [14]. In fact, the resulting changes in the locomotion dynamics (e.g. changes in the number of biological encounters) can have important consequences for diversity [4,9].

Encounter rates are often bottlenecks. There are different adverse consequences of decreasing the rates at which individuals find (and interact with) each other. Predator species can have difficulties to locate prey; lekking species may not be able to produce enough displaying males; mates may exhaust too many resources looking for partners; social species with smaller groups may become more vulnerable and so forth. Therefore, reductions in encounter rates

should have consequent effects leading to reduced populations, which in turn can cause further reductions in encounter rates—Allee effects [25,26]. So, a ripple feedbacks may cascade through the ecosystem.

With these queries in mind, here we shall study how landscape fragmentation affects biological encounter rates. We consider a widely studied model [27], which is able to capture the essential ingredients in foraging behaviour, moreover addressing sufficiently well the distinct biological aspects of animal movement [28,29] (for instance, beyond simple diffusion—e.g. [30]—often biologically unsatisfying). It is loosely based on a minimal Lévy walk model which is robust and quite general [31–33] and can reproduce all the scales of movement found in foraging patterns.

As reported below, our results show that fragmentation decreases the search efficiency. Most importantly, the encounter rate falls even when the global average densities of interacting organisms are held constant. In other words, encounter rates reduce with fragmentation even when there is no immediate change in the populations. This finding is quite unexpected and with important aftermaths: as any reduction in encounter rates will lower the associated reproductive rates, food intake rates, etc. this puts individuals and even whole species in more challenging conditions. We are thus led to a conjecture about one of the main causes of the empirically observed decline in diversity owing to fragmentation. We hypothesize that reduced encounter rates bear a causal relation to diversity decline in fragmented landscapes.

2. Material and methods

2.1. The model

To address this essential problem, here we investigate a widely studied random search model [27]. We consider that the full environment is a square region of side D and assume a perceptual range for the searcher, such that any target within a distance r_v from it (a ‘radius of vision’) is directly identified. Targets can include food, sexual partners or anything that an organism needs to encounter frequently for survival [27]. The model assumes that searchers are continually seeking to find targets.

The searcher moves as follows:

- (i) In each step (or ‘flight’) j , the direction is taken randomly (i.e. equal probability in any direction) and the step length ℓ_j from a probability density distribution $P(\ell_j)$, for $r_v < \ell_j < D$, and zero otherwise. There is no reason to take steps longer than the environment size D . Similarly, there is little incentive to take steps much shorter than the radius of vision r_v (see below).
- (ii) While covering the distance ℓ_j , the forager constantly looks for targets within r_v . If a target is detected, the forager moves straightforwardly to it and the step ℓ_j is truncated, returning to rule (i). If no targets are detected after transversing ℓ_j , the step is completed, returning to rule (i). The process is repeated until Q targets are found.

To introduce landscape fragmentation, we suppose a different number, N_p , of circular patches randomly distributed in the square environment of area D^2 . The total area of the patches is kept constant. We assume that the target density inside each patch remains the same. Thus, we can vary the local density of targets while keeping the global target density constant. This introduces heterogeneity in the system. We use periodic boundary conditions to avoid having to deal with boundary walls.

To make the analysis as broad as possible, for the probability density function of the step length ℓ_j we take

$$P(\ell_j) = \begin{cases} \frac{\mu-1}{(r_v^{1-\mu} - D^{1-\mu})} \frac{1}{\ell_j^\mu} & \text{if } r_v < \ell_j < D, \\ 0 & \text{otherwise.} \end{cases} \quad (2.1)$$

This choice of (family of) distribution is to allow not only normal diffusion (e.g. Brownian motion), but also superdiffusion (e.g. Lévy walks). Considering long enough D 's (the case we suppose here), during a long time—usually much longer than typical times in a foraging event [34,35]—equation (2.1) yields similar results to the long-range asymptotic limit of Lévy stable distributions with index $\alpha = \mu - 1$ (for a detailed mathematical discussion, see [10]). This process is generally characterized by allowing the existence of rare but extremely long steps, alternating between sequences of many short-length jumps (figures 2 and 3 in §3). Furthermore, by varying the parameter μ in the interval $1 < \mu < 3$, we have a superdiffusive dynamics for the searcher. The ballistic behaviour arises in the limit $\mu \rightarrow 1$, whereas the usual Brownian (diffusive) one emerges for $\mu > 3$. Ballistic motion is not a random walk, because there are no turning points.

We also remark that the power-law dependence on the ℓ 's implies in the approximate self-affine property $p(\gamma\ell) \approx \gamma^{-\mu}p(\ell)$, valid down to the scale of the lower cut-off, r_v . Self-affinity, like self-similarity, implies scale-free behaviour. It is known that [36] ecological phenomena (and complex phenomena in general) are often approximately fractal or scale-free. Finally, different types of short-range correlations—for example, in certain correlated random walks [14,34]—do not change the qualitative results obtained from the above model [31]. So, the findings below are valid in many different scenarios.

The results are obtained by numerically simulating the random walk described above in a fragmented environment. In each computer initialization, the searcher starts randomly outside the patches and the searching ends when a stop condition is achieved, namely, to find $Q = 10^4$ targets. The environment is constructed so that the total number of targets and their density inside the patches are kept constant. Regarding the nature of the targets, we consider two situations: non-destructible and destructible. For non-destructible targets, they are preserved after detection and the searcher, in possible future visits, can still profit from them. For destructible targets, they are eliminated after detection, becoming unavailable afterwards (but recreated in another location in order to keep the targets density constant). To intuitively picture a non-destructive (destructive) target, one could think about a large (small) fruit tree, far from being depleted (fully depleted) in a single visit by the forager. Moreover, to consider the intermediate case of targets that re-appear after a period of recovery [37] leads to qualitative similar findings. All the quantities presented below are obtained by averaging over $\bar{N} = 2.5 \times 10^3$ simulations run and for which we set $D = 10^4 r_v$ (along the work the distance units are such that $r_v = 1$).

Finally, the search efficiency η , defined as the ratio between the number of targets found Q and the total distance travelled L , is a relevant statistical measure to characterize the search performance of each strategy (parametrized by the exponent μ in equation (2.1)).

2.2. The model underlying biological assumptions

Prior to presenting the results, we should comment on the main biological aspects underlying our mathematical formulation for the problem.

We start by considering the way fragmentation is introduced. First, actual patterns of fragmentation can be rather complex. For instance, a worldwide survey of forests using satellite images

has identified six distinct categories of fragmentation [38], some more frequent than others depending on the spatial scale considered. Furthermore, the separation between patches and their typical shapes—two features that influence local abundance of species—strongly depends on the particular process leading to the fragmentation [39]. Second, for a large fraction of animal (and plant) species, the highest impact on diversity for a given ecosystem comes from the total area rather than the formats or shapes of the fragments [40]. Actually, the area is more important in large scales: the habitat loss dominates an eventual global decrease in species [41]. Finally, species will respond differently to a particular patch shape, depending on where they live, whether in the interior or at the boundary edge of the fragment region (the edge effect, see Introduction). For the majority of the species, circular patches cause the least damage [40,42].

Hence, our choice of circular patches is appropriate for analysing the adverse consequences of fragmentation in large territories once this is a common approximate pattern at large scales [38]. Also, by assuming randomly distributed and circular patches we are determining a minimum impact condition, given that other shapes, contours and clustering dispositions may amplify the negative effects of fragmentation [42]. In this sense, we are considering the 'best case scenario'.

Another point is that the landscape of the present model does not take into account geometric short-range asymmetries, as seen in fragments with curved corridors or in branched structures. In these cases, certain directions are cut-off, creating preferential channel paths, with consequences for the local rates of encounters (e.g. [43]). On the other hand, spatial anisotropy, induced by the search dynamics, is naturally incorporated into our description. In fact, owing to the searching rules, within a fragment most of the steps are truncated, reflecting thus the size of that fragment. But when venturing into the empty regions (the matrix), the steps reproduce the actual distribution of step lengths, equation (2.1) (because no truncation occurs until finding a new fragment). Therefore, our framework captures the average reduction in encounter rates owing to the geographical fragmentation. Nevertheless, it does not aim to pinpoint the specific variations at the ordinary dimensions of single fragments. Such details would certainly demand a more context-dedicated (contrary to our simplified but generalist) model.

The size of an actual region characterizes the resources it can hold in absolute terms, defining the carrying capacity. So, small fragments (structurally isolated from other patches) usually cannot sustain a metapopulation. This is particularly critical for small species, which in principle could live in a small area when embedded in a forest, but not at the same area if within a fragment [44]. An important parameter in our model is the number of patches, N_p , in the environment (with their total summed up area kept constant). As we are going to see, the encounter rates decrease as N_p increases. But from the above comments, it is clear that to assume fragment sizes below a certain threshold is not biologically reasonable. So, we will analyse our results by setting arbitrarily a minimum size for a fragment (in the following simulations, having a diameter of around 280 times its detection radius r_v). However, for quantitative estimations in a concrete situation, it would be important to have an idea of a minimum possible size for a fragment in that particular case.

All these assumptions reflect our goal with this study: we want to understand the 'macroscopic' or average effects of fragmentation, even without complete knowledge of the 'microscopic' details. It is well known that such a methodological approach led to advances in other sciences and is now being applied to biological and ecological phenomena (for example, see [27]). But certainly individual animals are usually all different, even within species, thus they may move distinctly from one another. This raises the relevant issue of how a statistical method like ours can be useful to describe the phenomenon of

encounter rates reduction. The scope and generality of the proposed model thus merit some discussion.

The random walk model we are considering clearly does not reproduce the movement of all organisms. For example, whereas our model assumes a limited radius of detection, in contrast some organisms have sophisticated capabilities to detect long-range pheromone, hence to locate mates. So, it should be seen as a first-order approximation of how real organisms move (and in fact, it could be modified to include many other complicated types of interactions). Our aim here is to obtain some intuition about what happens when all such effects are neglected. In other words, if we know absolutely nothing about how the animals move, what can we predict about the effects of fragmentation on encounter rates? This is the question we are actually addressing. Moreover, an associated question of great importance relates to the usefulness of our results. For what types of organisms and under what circumstances is the proposed model applicable? We give two different, but complementary, answers below.

On the one hand, we expect that this model will describe an idealized organism, therefore representative of a general situation, instead of a specific actual instance. If one wants a complete or near-perfect description of how specific animal species move in fragmented environments, then this is not a realistic choice. Our model does not take into consideration the known 'microscopic' details of how particular individuals move.

On the other hand, the model is well suited for gaining a deeper understanding of the relationship between 'macroscopic' variables and how fragmentation affects biodiversity. Indeed, the very neglect of the microscopic details allows the model to more faithfully encode all the other information regarding: (i) the fragmentation and (ii) diffusion and encounter rates. Once we are interested in a basic relationship between (i) and (ii), the proposed model is ideal for capturing the bare minimum 'microscopic' ingredients (those common to any species) that are necessary to tackle such a relationship [27].

3. Results

Figure 1*a–c* shows landscapes with three distinct numbers of patches N_p , from lower to higher fragmentation degree, but for which the density of targets inside each patch is kept constant and equal in all the cases (for a comparison with a real fragmented scenario, see the similarity with the first figure in [45]). Also, the total number of targets in any example is always the same. A fixed total number of targets and density, regardless N_p , is assumed in the analysis below.

To illustrate a typical path during a search, figure 2*a,b* shows trajectories stretches of the searcher for a non-destructive environment and for the $\mu = 2.0$ strategy.

In figure 2*a*, the landscape has only one patch (fragment) and we can identify the usual pattern associated with random walk strategies given by equation (2.1): clusters of many small steps connected by few long jumps. Also, the distance travelled outside the patch is larger than that inside. The same type of behaviour is observed in figure 2*b*, where the targets are distributed among 10 patches.

To quantify the two distinct instances involved in a fragmented environment search, namely, locomotion inside and outside the fragments, we compute the total distance travelled inside (L_{in}) and outside (L_{out}) the patches during a full search. They are shown in figure 3 for $N_p = 1$ and $N_p = 10$, in the non-destructive (a)–(b) and destructive (c)–(d) cases. For non-destructive targets, L_{in} for $N_p = 1$ is never higher than that for $N_p = 10$ (a), whereas L_{out} in most of the μ range is also smaller when $N_p = 1$ (b)—the exception being at the

Figure 1. A set of landscapes (square regions with $D = 10^4 r_v$) with an increasing fragmentation of resources: (a) one patch with a radius $R = 1389 r_v$; (b) 10 patches with $R = 439 r_v$ and (c) 100 patches with $R = 139 r_v$. In all cases, the patches have exactly the same density of targets, amounting in total to $N_t = 9697$. Also, within each patch two neighbours targets are in average $l_t = 25 r_v$ distant from each other.

Figure 2. (a) The initial part of searching trajectory along which the searcher (with $\mu = 2.0$) detects 10 targets. Here, the search space has one patch with $R = 1389 r_v$, with the average distance between the non-destructive targets $l_t = 25 r_v$. (b) The same as in (a), but in a more fragmented space with $N_p = 10$ patches of radius $R = 439 r_v$ each. The total area covered with targets is the same as in figure 1. Both are square regions with $D = 10^4 r_v$.

extremes $\mu \sim 1$ and $\mu > 2.8$. For destructive targets, L_{in} is smaller (greater) in the case of $N_p = 1$ when $\mu < 2.5$ ($\mu > 2.5$), case (c). On the other hand, L_{out} in (d) presents the similar trends of (b), only with the crossing between the cases $N_p = 1$ and $N_p = 10$ taking place at $\mu \approx 2.7$ (d).

From the previous definition, we have $\eta = Q/L = Q/(L_{in} + L_{out})$. As the order of magnitude of L_{out} is always higher than that of L_{in} (figure 3), it is the former that essentially sets the η values. For different values of N_p , we display in figure 4 the search efficiency η as function of the strategy parameter μ for the non-destructive and destructive cases, respectively, (a) and (b). For the former, in all curves the maximum is reached for $\mu \approx 2$, in accordance with the behaviour observed in figure 3 for (a) and (b). For the latter, the η 's also have a peaked shape. But now the optimization takes place about $\mu \approx 1.9$, reflecting the minimums of $L_{in}(\mu)$ and $L_{out}(\mu)$ in figure 3 for (c) and (d). For both situations, the search efficiency (for $\mu = 2$) was reduced by about 30% after the division of one patch in 100 patches. However, the exact value of this reduction depends on the parameters used in the simulations. For a quantitative comparison with real instances, the actual correct parameters should be known [44].

4. Discussion

From our previous results, a very important difference between searches in less or more fragmented environments is that for most of the μ values (i.e. searching diffusiveness)

Figure 3. For a full-search run ($Q = 10^4$), the total travelled inside, L_{in} , and outside, L_{out} , distances as function of the search strategy parameter μ for the situations as in figure 2a ($N_p = 1$) and figure 2b ($N_p = 10$). The non-destructive (destructive) cases are shown in (a) and (b) ((c) and (d)). For most μ values, the fragmentation will increase the travelled distance cases.

Figure 4. The searching efficiency for different degrees of environment fragmentation and forager diffusiveness. The statistical efficiency η is shown for four values of N_p , the other parameters as in figures 1 and 3, and for the (a) non-destructive and (b) destructive cases. Practically, for all μ 's the efficiency decreases as the landscape becomes more fragmented.

the greater the number of patches the greater the covered distance. In fact, for μ below the values of the Brownian regime (i.e. $\mu < 3$), larger L_{out} 's for increasing N_p can be understood as follows. Once at the patch border, and then leaving it by means of not-too-small steps ℓ_j —shorter ℓ_j 's result from μ around 3—the forager will have a lower probability to return to the initial patch or to find other patches if their areas are smaller. Hence, the searcher will spend more time wondering around in the 'open field' if N_p increases. Also note that even when there is an inversion in the L_{out} curves with respect to the N_p 's for $\mu \approx 3$ (figure 3 for (b) and (d)), the difference is not so important: the corresponding η 's are

practically the same in this case, figure 4. By the same token, for μ not too close to 3, the higher number of events of coming in and out the patches without finding targets if one has more fragments increases L_{in} .

Thus, the crucial finding is that often fragmentation can reduce search efficiencies even when the global average density of targets is held constant. Our finding points to the important mechanism of *fragmentation-induced reduction in encounter rates*, which should be taken into account when studying the effects of fragmentation on biodiversity [24]. Most importantly, this newly uncovered phenomenon does not depend on global or average target density at all, but rather only on local density.

Our results lead to a sharp theoretical prediction: fragmentation of habitats in the real world should lead to lower encounter rates, and hence should strongly and adversely affect foraging and reproductive rates. Actually, this prediction can explain different empirical findings [11,13,14], so it is not a surprise that populations (i.e. global density of species) should decrease over time in fragmented landscapes. Indeed, we hypothesize that species disappear from forest fragments (at least in part) because of the reduced encounter rates.

From the above discussion, the subsequent step should be to determine the specific mechanisms linking a final diminishing in species richness to a reduction in biological encounter rates. In this work, we have focused only on how fragmentation reduces the searching success, and have not tried to model possible implications of this fact (what certainly would demand a much more sophisticated and complex mathematical description for the problem). Nevertheless, a few considerations in this respect can be drawn.

First, we have not assumed any induced restriction in the searcher motility owing to the fragmentation process. Of course, it can happen for different species, as for the already mentioned case of tropical forest birds [10]. Then, the reduction in encounter rates would be just a natural (and even trivial) consequence of limitations in the available space

to explore. But in many instances, the fragmentation does not restrict the species diffusiveness [43], i.e. μ is not a function of N_p . In such cases, our analysis can help to explain the decreasing of population. In particular, we observe that fragmentation makes individuals remain for a considerably longer time outside their usual habitats (the fragments environment), figure 3 for (b) and (d). As a result, they may be exposed to dangerous conditions when in such an unfamiliar landscape (the matrix), thus increasing the death rates [46].

Second, fragmentation is not always negative for every species [47]. In fact, this can be concluded from our simulations as well. For those that usually forage using high values of μ (a Brownian-like behaviour), the search efficiency does not change significantly (figure 4). This is typical, for instance, of small animals with short home-ranges. Therefore, considering the prey–predator relationship, fragmentation may be an advantage for the former [48]. A patch can represent a good hiding region for the prey, once predators tend to be much more diffusive, with the lower encounter rates results applying to them. The species benefits by the patch confinement, on the other hand, may themselves be also threatened owing to biological invasion [49], having no possibility to migrate to other regions.

Third, in Lévy models for animal foraging [27], μ has a very important role [29,37]. It describes the diffusiveness presented by the dynamical motion of an individual [30]. In other words, larger (smaller) values of μ imply a tendency to take shorter (longer) travel steps during the foraging process. The general theory for non-destructive targets, supported by strong empirical evidence [27], shows that the best strategy is to take $\mu \sim 2$ (mid-way between the ballistic, $\mu \rightarrow 1$, and the Brownian, $\mu > 3$, behaviour) so to increase η . This being essential in adverse situations (e.g. scarcity of resources) [29,32]. Indeed, many different animal species, from microorganisms to big mammals and fishes [27], have

been reported to use $\mu \approx 2$ while searching. From figures 3 and 4, we see that the fragmentation affects much more the value of η when μ is around 2. So, it is a negative fact for biodiversity preservation which is exactly for the optimal value of μ (the one increasing the encounter rate efficiency η) that the action of fragmentation becomes more drastic.

All these examples illustrate the many interdependent ecological mechanisms possibly involved in the decreasing of the number of species because of fragmentation.

Finally, we believe that the present results (directly illustrated by a recent study on the decreasing of a species of owls in Alberta, Canada [50]) have immediate practical relevance to biodiversity and conservation efforts, specially considering the long period of time necessary for cleared forests to regenerate [51]. It also adds a new ingredient to the SLOSS debate [52] and highlights the necessity of more well-planned surveys [53] on fragmentation effects in the long run. For example, a new road that cuts through a forest may dramatically reduce encounter rates even if the construction of the road does not *ipso facto* immediately decrease populations (owing to forced truncations of the step lengths, as those in rule (ii), but artificially induced by the road). We give an even more drastic example relating to creation of reserves: some countries regulate only the percentage of the original area of vegetation which should be protected in a given location, but do not regulate the degree of aggregation or fragmentation. Such legal measures may not be effective if they allow unlimited fragmentation and the displacement pattern of the endemic animals is not previously known. Our findings suggest that, until fragmentation is better regulated, species may continue to disappear [54–56].

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