

Problems with the application of cladistics to forest fragmentation studies

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Recently, Pellens et al. (2005) applied standard parsimony methods to the analysis of species communities in forest fragments. Their proposal consists of assembling a data matrix of species presence/absence for each fragment and submitting it to a parsimony tree search using an adjacent continuous forest as outgroup. As such, fragments become analogous to terminal taxa and species to characters, with character states being the recorded presence/absence of such species in each fragment.

The justification provided by Pellens et al. for such use of parsimony is that “the fragmentation effect is a matter of history: fragments are the remnants of previously continuous large forests...” so that “fragments can be merely characterized as descendants rather than remnants of an ancestrally continuous forest, since they have evolved after their isolation” (p. 9). Pellens et al. indicated that this evolution is due to “the *spatial* breakup of communities that become separate entities” (pp. 9–10, our italics), and assumed a strong direct link between community change and evolutionary change by stating that “...establishing relationships among communities and looking at their nestedness is not only a practical classificatory procedure but is also aimed at interpreting their evolution by descent with modification” (p. 10). Thus, parsimony would discover the pattern of nestedness among fragmented areas as well as the evolution of characters (i.e., presence/absence of species) “polarizing the changes in either extinctions or colonizations” (p. 10); i.e., species gains (0 → 1) and species losses (1 → 0).

The aim of this paper is to report problems with this application using both case studies provided by Pellens et al. The first example deals with the distribution of frog species sampled by Tocher et al. (1997) at the experimentally fragmented landscape of the Biological Dynamics of Forest Fragments Project (BDFFP) site in Central Amazonia. This example is thus specially important because in the BDFFP site the fragmentation history is accurately documented. The second example deals with birds sampled in fragments of the Atlantic forest, Eastern Brazil, by Anciães and Marini (2000).

In the first case study there is a lack of spatial consistency of the BDFFP fragments in the reconstructed tree using Pellens et al. approach. Fragments 3304 and 3209 originated from the clearing “Fazenda Porto Alegre”, whereas fragments 1104 and 1112 originated in a separate, independent clearing “Fazenda Esteio” (Fig. 1). Therefore, the *known* fragmentation history, evident in Fig. 1, is ((3304 3209)(1104 1112)). However, the cladogram presented by Pellens et al. (their fig. 1) recovers the groupings (3304 (3209 (1104 1112))). This creates a problem for the interpretation of clades within this system given that there is no way to reconstruct a meaningful ancestor (area or community) for fragments (3209 (1104 1112)). On the other hand, the resulting clades roughly reflect a grouping order by decreasing fragment size, with 1104 and 1112 being the smallest fragments.

It is of course possible that the data on the current distribution of these frogs are not able to reconstruct the history of terminals (fragments), a potential problem in phylogenetic inference for any character system. Nevertheless the problem is more fundamental and unique for the type of data from fragmentation studies. The process

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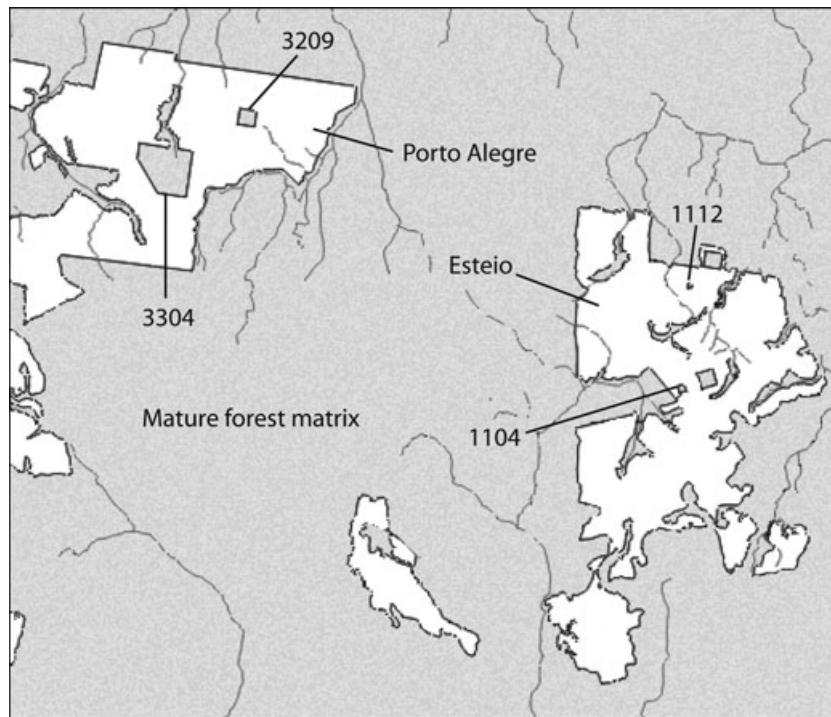


Fig. 1. Map of a fraction of the BDFFP fragmentation experiment near Manaus, Amazonia, Brazil. Indicated are the two main clearings discussed in the text (Fazendas Porto Alegre and Esteio), and the location of the four fragments used by Pellens et al. in their frog example (numbered 3209, 3304, 1104 and 1112).

of forest fragmentation is, initially, analogous to the exercise of drawing samples from a community; the samples have a definite position in space and time, and a given size. When a resulting fragment is very large, it would contain most of the species in the original community. However, as fragments become smaller the number of individuals that have been “sampled” during the process of fragmentation is increasingly limited, with the concomitant decrease in the chance of including many species. In addition, species richness in a fragment large or small is further restricted by the likely universal phenomenon of dominant species. In any forest, even tropical rainforests, a few species are very common, and many species are rare. For instance, in BDFFP, all fragments are dominated by one species of seedlings regardless of fragment size (Benítez-Malvido and Martínez-Ramos, 2003, fig. 5b), while rare species tend to appear randomly in few fragments. In a cladistic context, all shared absences are potential synapomorphies, so *any* two small fragments have a high chance to group together in a clade only because they lack many species—an artifact of the sampling that occurred during the fragmentation process—and not necessarily as a result of a common fragmentation history.

One way to expose this problem is to detect false species losses acting as apomorphies. One such instance is presented by the frog species *E. femoralis* (sp. 9 in Pellens et al., 2005), which is optimized as a species loss

in fragment 1104 (an autapomorphy in this case), but was nevertheless known to be absent from the original area in the survey made *before* the experimental fragmentation occurred (Tocher et al., 1997, table 9.2). Given this, the claim by Pellens et al. that with the application of cladistics “it is possible to determine whether some poor communities have actually been impoverished by a fragmentation effect or if they were originally poor” (p. 10) does not hold: the reconstructed tree shows that fragment 1104 is losing a species that was never present in the original corresponding unfragmented area. Therefore, prefragmentation conditions continue to affect the isolated community long after fragmentation took place (as in the case of sp. 9). Standard parsimony analysis was not designed to overcome this problem.

In contrast to species losses, species gains reveal the imperfect correspondence between standard characters and species as characters. The frog species 43 is lost in the branch that groups all fragments, and it is gained higher up in the tree in fragment 1104 (see fig. 1 in Pellens et al.). As species 43 is indeed present in the continuous adjacent forest, this colonization event can only be interpreted as horizontal transfer from the outgroup, because species are historically unique; i.e., species 43 could not have evolved *de novo* in fragment 1104. In standard parsimony analysis (a method that only explains vertical transfer, on the assumption of

descent with modification), homoplastic gains cannot be directly attributed to a specific cause (as independent originations or horizontal transfer, for example). However, when species are used as characters, gains must always be attributed to horizontal transfer—colonization. This apparent advantage (i.e., unambiguously identifying the cause of homoplasy) is nonetheless a departure from standard character analysis, simply because in the latter multiple independent originations can be interpreted as such.

Other problems with species gains are more of interpretation. Pellens et al. say on p. 11 that “The case studies re-analyzed with parsimony showed that communities have complex histories, not necessarily evolving by species loss in the smallest fragments”. Consider the small forest fragment F3 in the bird example, which has gained several species (see fig. 4 in Pellens et al.). Species 33, *Turdus amaurochalinus*, is a typical savanna and dry forest bird; the same is true for sp. 49, *Saltator caeruleus*, and other species. In fact, F3 lost several forest species and was invaded by numerous open-area species. Therefore, F3 actually behaves quite like predicted by forest fragmentation theory, exhibiting increased vulnerability to invasion (by generalist or exotic species of minimum conservation value), and loss of forest specialists (of high conservation value when the forest is the conservation target). That is, a face-value interpretation of optimization results, such as “fragmentation has not decreased but increased the species number” (p. 11) can be misleading for the conservation endeavor.

In conclusion, recovered clades of fragments are not necessarily descendants of a common ancestral larger fragment, nor are their species compositions due to common spatiotemporal causes. Failure to explicitly incorporate spatial information (e.g., fragment size, proximity to continuous forest, and prefragmentation heterogeneity) into a method that tries to reconstruct forest fragmentation history results in a lack of discrimination between postfragmentation ecological processes and purely spatial sampling processes. Adjacent fragments of different ecological properties may not group together while distant, historically unrelated fragments that are ecologically similar (e.g., isolated

swamp forests) may, specially if they are both small. Failure to account for real and well-documented ecological processes (e.g., known habitat requirements, generation time, known interspecific interactions, such as, active diaspore dispersals) makes several errors not preventable. Certain phenomena, such as horizontal transfer, false species losses, and invasions from newly formed habitats (neglected descendant areas such as savannas), seriously compromise the interpretation of species presences and absences as synapomorphies. Pellens et al. borrowed extensively from parsimony theory to favor its application over other methods to the history of forest fragments. However, given the questionable correspondence between fragments and taxa as well as between conventional characters and species as characters, the superiority of parsimony is in this context unwarranted. Standard parsimony analysis seems not directly applicable to the study of forest fragmentation.

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