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Matrix habitat restoration alters dung beetle species responses across tropical forest edges

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ABSTRACT

External threats from agricultural intensification, fire encroachment, species invasion and illegal harvesting present major conservation challenges in isolated tropical forest remnants. These processes can greatly exacerbate the magnitude of edge effects as the degree of patch to matrix contrast increases. Theory suggests that mitigation of these effects should be possible through conservation strategies that remove external threats and restore adjacent matrix structure, but this has not been tested experimentally. In the rapidly-dwindling Afromontane rainforests of Nigeria, where nature reserves have the least protection of all African conservation areas, we created an experimental matrix restoration treatment in which we excluded livestock by fencing, maintained a fire-exclusion break, and passively revegetated a 200 m buffer zone in the surrounding matrix at replicated edges. After three years, dung beetle communities in remnant forests showed a 53% increase in abundance at sites adjacent to the restored matrix. Over 90% of the common dung beetle species differed in the magnitude of their edge responses between forest-to-restored versus forest-to-degraded matrix sites. Moreover, a significant difference in species richness across the forest-to-degraded matrix edge became non-significant following matrix restoration, and there was also a significant decrease in community dissimilarity across the edge gradient in these regenerating sites. Just three years after excluding threatening processes from comparatively small areas of matrix habitat, we found that these efforts not only reduced edge effects, but also (1) enhanced dung beetle populations in the adjacent reserve, (2) led to an increase in dung beetle capture rates in the regenerating matrix, and (3) facilitated re-establishment of species that were absent due to matrix degradation. Therefore, regenerating buffers can substantially increase effective reserve size and restore invertebrate communities in landscape mosaics where remnant habitats are embedded within anthropogenic landscapes.

1. Introduction

Edge effects are trans-boundary phenomena that result from the biotic and abiotic contrast between two adjoining habitat types (Campbell et al., 2011; Ewers and Didham, 2006b; Fonseca and Joner, 2007). These effects may represent a modification or intensification of existing processes following the fragmentation of continuous habitat, or entirely novel and induced phenomena for species in habitat remnants (Ries and Sisk, 2004). As edge effects are strongly affected by the degree of patch versus matrix contrast, the degree to which edges act as a barrier vs a zone of interchange for organisms in remnant habitat patches cannot be quantified without explicit consideration of the adjacent matrix habitat characteristics (Campbell et al., 2011; Murphy and Lovett-Doust, 2004). Surprisingly, despite edge effects being widely recognized as the product of the flow of materials, energy, and organisms between adjoining habitats (Fagan et al., 1999), relatively few studies have quantified edge responses across both sides of edge gradients (Fonseca and Joner, 2007), and fewer still have determined the interacting effect of variation in adjacent matrix structure on continuous edge response functions (Campbell et al., 2011).

Edge effects are exacerbated by external anthropogenic processes that have direct and indirect impacts on remnant communities. For example, fire encroachment from land-clearing in the surrounding matrix can have a major impact on the vegetation structure at forest edges (Cochrane and Laurance, 2002), and on the associated animal communities within the forest remnants

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themselves (Prieto-Benítez and Méndez, 2011). Similarly, livestock encroachment from the pastoral matrix into adjacent forest remnants can have direct negative impacts on vegetation structure, soil compaction and nutrient inputs (Martinez and Zinck, 2004; Van Uytvanck and Hoffmann, 2009), as well as indirect flow-on effects on associated animal communities (Abensperg-Traun et al., 1996). Moreover, multiple threats from intensification of land-use practices in the surrounding agricultural matrix can interact synergistically to exacerbate impacts on biodiversity in small habitat remnants (Ewers and Didham, 2006a). For example, increased ease of human access and livestock use of forest remnants frequently leads to increases in hunting, poaching and illegal logging, bringing conservation and human welfare into ever greater conflict (Peres, 2001).

Nowhere are these effects more severe than in the rapidly dwindling Afromontane forests of Sub-Saharan Africa. In this region, nature reserves have the least protection of all African conservation areas and yet have among the highest incidence of threatened endemic taxa in Africa (Blom, 2001). Degradation of these montane forests is increasing dramatically with Africa's rapidly growing human population (Hurault, 1998). Of particular concern for forest conservation in this region is the intensification of cattle grazing (Hurault, 1998) and the associated ecological impacts through fire (Chapman et al., 2004) and illegal hunting (Maisels et al., 2001).

Effective strategies for the exclusion or minimization of anthropogenic edge effects into Afromontane forest remnants are urgently needed because of a combination of political instability and poverty, which present substantial conservation challenges in the region (Oates, 1999). Elsewhere in the world, fencing to exclude livestock has proven to be an easy and cost effective conservation measure for the protection and restoration of forest remnants (Brooks, 1995), but this does not limit all external anthropogenic influences, such as fire encroachment. Alteration of matrix land-use through the establishment of plantation forests has also been promoted as a means of reducing biotic and abiotic contrasts between patch and matrix (Campbell et al., 2011; Denyer et al., 2006). Alternatively, we suggest that a combination of fencing to exclude livestock and the restoration of matrix vegetation structure for conservation, rather than production gain, might well be an effective combined management strategy to ameliorate the proximate drivers of edge responses in ecological communities.

In this study, we experimentally tested the influence of matrix restoration on biotic responses to edge effects in remnant Afromontane forest. At three replicate forest edges we excluded livestock by fencing 200 m buffer zones in the surrounding matrix. These were permitted to passively re-vegetate behind fire-exclusion breaks. Across these three forest-to-regenerating matrix edges, we compared short-term differences in dung beetle species richness and composition with those observed at three forest-to-degraded matrix edges. We used dung beetles as a focal taxon as they exhibit high sensitivity to disturbance (Nichols et al., 2007), changes in vegetation structure and microclimate at forest edges (Davis et al., 2001), as well as fluctuation in dung resource availability due to shifting distributions of native mammals (Estrada and Coates-Estrada, 2002) and livestock encroachment (Hanski et al., 2008). Therefore, dung beetle responses across edge gradients effectively integrate many facets of habitat degradation, providing a generalized indication of the role of matrix restoration in the conservation of threatened Afromontane forest ecosystems.

2. Methods

2.1. Study area

The study was conducted at the Ngel Nyaki forest reserve, located on the Mambilla Plateau in Taraba State, Nigeria. The forest reserve is an outlying section of the West African montane forest network within the Cameroon Highlands ecoregion (Olson et al., 2001). This region comprises a network of sub-montane forest remnants at elevations up to 2300 m, with a mean annual rainfall of approximately 1800 mm and mean monthly temperatures of 13–26 °C and 16–23 °C for the wet and dry seasons, respectively (Chapman et al., 2004). Ngel Nyaki forest reserve covers approximately 4600 ha and comprises a mosaic of overgrazed montane grasslands, degraded streamside forest/shrubland strips, and 720 ha of dense sub-montane forest (Chapman et al., 2004; Chapman and Chapman, 2001). The forest has a unique floristic community composition with over 146 vascular plant species, many of which are endemic to Afromontane regions, including four IUCN Red Data Listed species (Chapman and Chapman, 2001).

2.2. Study design

As part of the Nigerian Montane Forest Project (NMFP) aimed at protecting Ngel Nyaki forest reserve from land clearing, burning, and cattle grazing, we established three fenced exclusion zones up to 200 m outside the dense sub-montane forest zone, 3 years prior to the sampling procedure. The length of fenced sections around the forest perimeter varied from 0.25 km to 1.6 km long. Within the 200 m fenced zone, cattle-grazing was eliminated and ~1 m wide fire breaks were established by removing all vegetation down to bare soil within 2 m of each fence-line as a passive restoration strategy (Benayas et al., 2009).

We compared dung beetle (Coleoptera: Scarabaeidae, Scarabaeinae) community responses across three replicate forest edge gradients within the 'regenerating' matrix zones versus three replicate forest edge gradients in the 'degraded' matrix zones exposed to anthropogenic threats that were typical of the area. The locations of the three regenerating edges and three degraded edges around the perimeter of Ngel Nyaki were interspersed to reduce potential spatial autocorrelation of treatment effects. Replicate sites were at least 100 m apart, which was at least twice the distance that was maintained among sampling points within sites (Appendix A).

At each of the three regenerating and three degraded edges, sampling points were established at 13 distances along a forest-to-matrix gradient spanning both sides of the forest edge on a doubling scale: −160, −80, −40, −20, −10, −5, 0, 5, 10, 20, 40, 80 and 160 m (negative values denote forest sites). The edge (0 m) was defined as the drip line of the outermost canopy trees at the forest perimeter. This doubling-scale design is one approach that allows for the fine-scale detection of ecological responses within close proximity of the forest edge where edge effects were expected to be most intense, while at the same time still allowing for the detection of edge effects over a potentially large spatial extent. Sampling was conducted on both sides of the forest edge to account for trans-boundary processes (the flow of energy, materials, and organisms between adjoining habitats) that drive edge effects (Ewers and Didham, 2006b; Fonseca and Joner, 2007).

To avoid trap interference (i.e. the capture interference of one trap on another due to spatial non-independence [Baker and Barmuta, 2006]), sampling points were staggered laterally (i.e., parallel to the forest edge) such that all sampling points were at least 50 m apart, just exceeding the distance over which dung beetles are thought to be able to detect dung (Larsen and Forsyth, 2005), whilst still maintaining their respective distance from the edge (Appendix B). As a further control against potential sampling bias, two 'dummy' edge gradients were established as reference sites (Baker and Barmuta, 2006) with one dummy gradient located in the forest interior and the other located in the grassland matrix interior, both at least 640 m from the nearest forest edge. These gradients were used to test for trap depletion effects and effects