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High resilience of galling insect communities to selective and clear-cut logging in a tropical rainforest

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Abstract. Increasing anthropogenic disturbance in tropical rainforests is a major challenge to biodiversity conservation. The responses of herbivorous insect communities to habitat changes are not well understood. In this study, we investigated the resilience of galling insect communities associated with *Neoboutonia macrocalyx* (Euphorbiaceae) trees to logging in Kibale National Park, Uganda. Resilience was measured by comparing the species density, abundance and community structure of gallers in nine differently aged successional forests with those in adjacent primary forests. Insect galls were sampled from the canopy of 10 randomly selected trees in each successional stage, five times in a 10-month period. A total of 7219 individuals representing five galler species were recorded. No significant differences were found in the species density and overall density of gallers between the regenerating and primary forests. The mean tree height was positively correlated with the overall density of gallers. The community structure of gallers differed significantly among the successional stages, but exhibited no clear directional recovery trend. In addition, remarkable seasonal variations were observed in galler communities, with peak abundance being found in the wettest months. The results of the preset study indicate that specialist galling insects whose hosts are pioneer trees can recolonize successional sites rapidly and are resilient to the effects of selective and clear-cut logging in case primary or secondary forests with an established population of *Neoboutonia* host trees (source populations) are close by. Thus, recovering tropical forests can provide important habitats for galling insect biodiversity, highlighting the need to include them in management and conservation priority plans.

Key words: Afrotropical gallers, deforestation, Kibale National Park, recovery, regeneration, secondary forests, seasonality, succession, Uganda

Introduction

Given the widespread anthropogenic alteration of tropical biota, e.g., through fragmentation, selective logging, clear-cutting, wildfires and clearing for agriculture (Harris and Johnson, 2004; FAO, 2007; Morris, 2010), understanding whether communities in human-modified sites can withstand habitat changes, i.e., remain unchanged (resistance) or recover to an approximation of a primary forest status (resilience), is a critical issue (Holling, 1973; Isaac *et al.*, 2009; Kohv *et al.*, 2013). Understanding resilience and resistance of biotic communities to habitat alteration is important for sustainable forest ecosystem management (Summerville, 2013), and these factors have been widely studied in arthropods from boreal and temperate systems (e.g., Dynesius *et al.*, 2009;

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Summerville, 2013). Empirical data from tropical forests are scarce, especially for endophytic herbivorous insects.

Endophytic herbivores, e.g., gall-forming and leaf-mining insects, constitute important links in terrestrial food webs (Nyman *et al.*, 2007; Paniagua *et al.*, 2009), and thus their recovery is an indicator of ecosystem stability and function (Fernandes *et al.*, 2010). Information on the responses of tropical galling insects to habitat modification is very limited (but see Oyama *et al.* (2003); Julião *et al.* (2004); de Araújo *et al.* (2011); de Araújo and do Espírito-Santo Filho (2012)). Because of their extreme specificity to their host plants (Cuevas-Reyes *et al.*, 2007), galling insects are highly sensitive to forest fragmentation (Oyama *et al.*, 2003; Malinga *et al.*, in press). The responses of different species to the same or different kinds and scales of habitat modification can vary widely depending on dispersal ability and degree of habitat specialization (Watt, 1998; Ewers and Didham, 2006). Tropical galling insects may exhibit resilience to moderate modification of their habitats by rapidly colonizing regenerating sites (Oyama *et al.*, 2003), especially when the recolonization source populations are close by. For example, in the Brazilian tropical savannah, galling insects have been found to rapidly colonize newly sprouted host plants in burned areas adjacent to unburned areas (Vieira *et al.*, 1996).

Two approaches to measure resistance or resilience include the following: (i) evaluating the changes in species density and abundance, community structure or guild diversity of the same habitats over different time periods (Rydgren *et al.*, 2004; Summerville, 2013) and (ii) comparing different aged habitats (successional forests) with nearby primary forest sites (Dynesius *et al.*, 2009). The latter approach assumes that the ecological conditions in the modified habitats are similar to those in the reference primary forests prior to the modification. Herein, we address the resilience of specialist galling insect communities associated with *Neoboutonia macrocalyx* trees to selective and clear-cut logging in Kibale National Park (KNP), Uganda. We use the term resilience (and not resistance) because most of the *Neoboutonia* trees were removed during harvesting. To test for evidence of resilience in communities of galling insects to habitat modification, we compared the species density, abundance and community structure (i.e., the relative proportion of gallers (Magurran, 2004)) of nine aged compartments with those in nearby primary forests as a reference state. We also examined whether the possible patterns in galler density were associated with plant vigour, measured as the mean leaf size (Santos *et al.*, 2011; Malinga *et al.*, 2014*a*,*b*), resource availability, measured as the mean tree height (Neves *et al.*, 2014), or density of host plant at the landscape level, measured as the distance to the nearest neighbouring host tree. We chose these factors because changes in resource quality have been used to explain ontogenic succession of galls (Fonseca *et al.*, 2006). To our knowledge, this is the first study on the resilience of galling insect communities to logging in a tropical rainforest.

Specifically, we addressed the following questions: (i) Do species density, overall density and community structure of galling insects vary among forest successional stages and are there seasonal variations? (ii) Is there a directional successional trend for communities of gallers along the recovery gradient? (iii) Do the possible patterns in overall density of gallers correlate with the mean leaf size (vigour), mean tree height (resource availability) or density of host plants across the landscape? We considered resilience as a recovery in terms of species richness, abundance and community structure to primary forest status (Dynesius *et al.*, 2009; Montúfar *et al.*, 2011).

Methods

Study area

The study was carried out in a medium-altitude moist evergreen tropical forest of KNP, western Uganda (0°13′ to 0°41′N and 30°19′ to 30°32′E). KNP covers approximately 795 km^2 and receives an average annual rainfall of 1698 mm (Chapman *et al.*, 2010), which predominantly falls during March–May and September–December (Chapman *et al.*, 2005). Dry season months are from June to August. The study sites were located in nine aged compartments (Fig. 1 and Table 1), representing a gradient of forest recovery as different successional stages, namely four regenerating aged forests of a former clear-cut of coniferous plantations (hereafter referred to as ‘regenerating age classes’, RAC9, RAC11, RAC14 and RAC19, name indicating the approximate years since clear-cut (Nyafwono *et al.*, 2014); three natural forest compartments selectively logged at different intensities between 1967 and 1969 (K13, K14 and K15); and two primary forest compartments (K30 and K31).

Study system

Neoboutonia macrocalyx Pax (Euphorbiaceae) is a pioneer deciduous indigenous tree species growing in light gaps of swamps and valley bottoms in forest edges, regrowths, and partially logged, primary and secondary forests (Chapman *et al.*, 1999) from 600 to 2500 m above sea level (Lovett, 1991; Fischer and Killmann, 2008). Trees are 10–25-m tall (Lovett *et al.*, 2006) with an open crown and a canopy

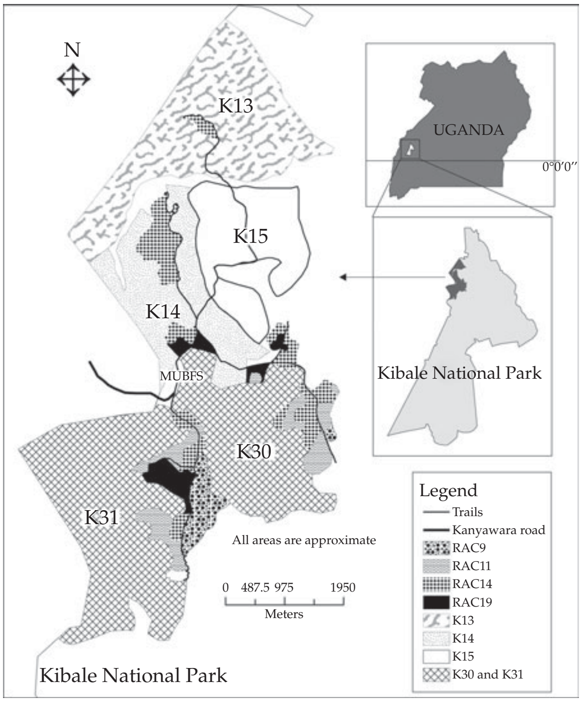

Fig. 1. Location of study sites in Kibale National Park, Uganda. K30 and K31, natural intact primary forests; K14, natural forest lightly logged in 1969; K15, natural forest heavily logged between 1968 and 1969; K13, natural forest heavily logged and treated with arboricide between 1968 and 1969; and RAC9, RAC11, RAC14 and RAC19, regenerating former clear-cuts of coniferous plantation named following the approximate years since clear-cut (Nyafwono *et al.*, 2014). MUBFS (Makerere University Biological Field Station).

width of 7–12 m (Hamilton, 1991). Leaves are continuously produced year round (Kasenene and Roininen, 1999). Based on DNA barcoding identification, *N. macrocalyx* trees are attacked by five undescribed multivoltine galling insect species (four gall midges, Diptera: Cecidomyiidae; and one galling psyllid, Homoptera), which we named cecidomyiid leaf galler, cecidomyiid hairy stone galler, cecidomyiid shoot galler, cecidomyiid flower stalk galler and psyllid leaf galler (Skippari *et al.*, 2009; Heimonen *et al.*, 2013; Malinga *et al.*, 2014*a*,*b*,*c*). To our knowledge, these galler species are highly specialized and have been recorded only from *N. macrocalyx* trees (Skippari *et al.*, 2009; Heimonen *et al.*, 2013; Malinga *et al.*, 2014*a*,*b*).

Sampling

A total of 10 *Neoboutonia* trees were randomly sampled in each successional stage. Six apical branches were randomly cut from each tree using a tree pruner. The branches were cut from the middle canopy, 6–14 m high. The total number of leaves, mid-rib lengths and number of different galler species per leaf were recorded in the branch samples. In the laboratory, all galls were dissected under a stereomicroscope to justify the species morphological identifications. All the *N. macrocalyx* trees in each compartment were also mapped, and using the latitude and longitude of each tree, the Euclidean distance between trees for each sampled tree was calculated, as an approximate indication of host density (or tree isolation) at a landscape scale.

In addition, the stem diameter at breast height (DBH) and the height (m) of each sampled tree, using a 1-m marked pole, were estimated (Table 2). Estimates of mean tree height and host tree density were used as indicators of resource availability (Neves *et al.*, 2014). Sampling was done twice during the wet season (December 2011 and March 2012) and thrice during the dry season (June, July and August 2012). The same trees were studied in all samplings, and each sampling lasted 2–3 weeks with successional stages visited in random order.

Statistical analysis

The effects of successional stage, month (seasonality), and their interactions on the species density (Gotelli and Colwell, 2011) and overall density of gallers in each sampled tree were determined using generalized linear model (GLM) with a negative binomial error distribution and a log link function (in IBM SPSS 19; IBM, Armonk, NY, USA). To take into account the variation due to host tree size, DBH was included as a covariate in each model (Cuevas-Reyes *et al.*, 2006), but the effect of covariate was not significant in either model ($P > 0.05$ in both cases). In case of significant GLM results, multiple pairwise contrasts were performed with sequential Bonferroni adjustments. Species density was measured as the number of species per tree (six branches pooled to tree level) and density of gallers as the total number of individuals per leaf area. *Neoboutonia macrocalyx* leaf area (Y) is dependent on the mid-rib length (x), and it was calculated with a regression model, $Y = 5.03x + 0.83x^2$, $R^2 = 0.99$, $N = 159$, $P < 0.01$ (according to Savilaakso *et al.*, 2009).

To test for a directional pattern in the species density and overall density of gallers along the successional gradient, Spearman's rank correlations between the average values of either variable and the 'order' of the successional gradient were calculated (in IBM SPSS statistics, version 19). The following order of succession was used in the correlation analysis: RAC9 = 1, RAC11 = 2, RAC14 = 3, RAC19 = 4, K13 = 5, K15 = 6, K14 = 7, K30 and K31 = 8. The successional order was based on time since disturbance and also the seriousness of disturbance (Nyafwono *et al.*, 2014).

Table 1. Characteristics of the nine forest successional stages studied at Kibale National Park

Successional stages	Area (ha)	Approximate years since logging[1]	Disturbance history
Early successional stage			
RAC9	60	9	Coniferous plantation clear-cut between 2002 and 2004 and left to regenerate naturally[1]
RAC11	104	11	Coniferous plantation clear-cut from 2000 to 2001 and left to regenerate naturally[1]
Intermediate successional stage			
RAC14	171	14	Coniferous plantation clear-cut between 1995 and 1999 and left to regenerate naturally[1]
RAC19	61	19	Coniferous plantation clear-cut between 1987 and 1994 and left to regenerate naturally[1]
Later successional stage			
K13	622	43	Heavily logged (50% basal area reduction) during 1968–1969, treated with an arboricide, Finopal (2:1 mixture of 2, 4-D and 2, 4, 5-T), and left to regenerate naturally[2]
K15	347	43	Intensively logged (40% basal area reduction) from 1968 to 1969 and left to regenerate naturally[2]
K14	405	42	Lightly logged in 1969 (25% basal area reduction) and left to regenerate naturally[2]
Primary forests			
K30	282		Primary forest. Two to three trees per km^2 were removed prior to 1970 with little effect on forest structure[2]
K31	754		Primary forest[2]. Unlogged part of K31, also called K32 by Olupot (2000)

[1] Data from Nyafwono *et al.* (2014).
[2] Adapted from Kasenene (1987), Struhsaker (1997) and Kasenene (2007).

To assess differences in the community structure of galling insects among the successional stages, months or their interactions, permutational multivariate analysis of variance (PERMANOVA) run by PERMANOVA + package for PRIMER-E, version 6 (Plymouth, UK) (Anderson *et al.*, 2008), based on Bray–Curtis similarity, was used. *P* values were calculated from 999 permutations of residuals under a reduced model and type III sums of squares.

Similarities in the community structure of galling insects among the successional stages and months were illustrated using a non-metric

Table 2. Mean tree height (as a measure of resource availability), mean leaf area (as a measure of resource quality) and the distance to the nearest host tree (as a measure of the density of host trees) in successional stages studied at Kibale National Park, Uganda+

Successional stages	Mean tree height (m)	Mean leaf area (cm^2)	Distance to the nearest host tree (m)
Early successional stage			
RAC9	10.5 ± 0.5	289.9 ± 12.9	89.6 ± 28.3
RAC11	14.0 ± 1.0	301.6 ± 8.7	21.7 ± 5.1
Intermediate successional stage			
RAC14	14.4 ± 1.0	288.8 ± 9.1	23.4 ± 3.4
RAC19	14.8 ± 1.2	269.2 ± 6.5	17.8 ± 3.6
Later successional stage			
K13	13.9 ± 1.0	241.1 ± 6.6	31.3 ± 4.5
K15	16.0 ± 1.4	263.8 ± 8.1	33.6 ± 11.0
K14	14.9 ± 1.0	275.0 ± 10.1	90.8 ± 24.7
Primary forests			
K30	16.2 ± 0.8	275.4 ± 9.3	54.8 ± 17.4
K31	13.3 ± 0.9	256.5 ± 9.3	54.9 ± 13.2

+ Values are means ± SE.

multi-dimensional scaling (NMDS). NMDS was generated with the program PRIMER-E, version 6 (Clarke and Gorley, 2006), from square-root transformed abundance data and a zero-adjusted Bray–Curtis similarity matrix between samples. For clarity, distances among the centroids of successional stages and months are shown. The full NMDS graph showing all the samples is shown in Supplementary material 1 (available online).

To test for a directional pattern in the community structure of galling insects along the successional gradient, a distance-based linear model (DISTLM, conducted with PRIMER-E, version 6) was fitted, where Bray–Curtis similarity matrix (response variable) was modelled with the 'order' of successional stages (RAC9 = 1, RAC11 = 2, RAC14 = 3, RAC19 = 4, K13 = 5, K15 = 6, K14 = 7, K30 and K31 = 8) as the predictor variable.

Finally, the associations between the mean leaf area (plant vigour), mean tree height and host tree density (resource availability) and the overall density of gallers of each successional stage were tested using Spearman's correlation tests.

Results

A total of 7219 individuals belonging to five galler species were recorded (see online Supplementary material 2). The most dominant species was the cecidomyiid leaf galler (58.4% of total counts), followed by the psyllid leaf galler (26.5%), and the least dominant species was the cecidomyiid shoot galler (0.2%).

Species density and abundance of gallers

The species density of gallers did not differ significantly among the successional stages (GLM: $\chi^2 = 3.3$, $P = 0.91$, degrees of freedom (df) = 8, $n = 450$), but differed significantly among the months ($\chi^2 = 26.3$, $P < 0.001$, df = 4, $n = 450$). The species density of gallers was significantly higher in December than in all other months (sequential Bonferroni tests: $P < 0.05$ for all months, except March, $P = 0.11$). The successional stage × month interaction had no significant effect on the species density of gallers ($\chi^2 = 10.3$, $P = 1.00$, df = 32, $n = 450$).

The overall density of gallers differed significantly among the successional stages (GLM: $\chi^2 = 71.1$, $P < 0.001$, df = 8, $n = 450$). All regenerating forests had galler density similar to that in the primary forests (sequential Bonferroni tests: $P > 0.05$; Fig. 2A). The oldest clear-cut forest (RAC19) had a significantly higher overall density of gallers than the two selectively logged forests (K13 and K15) and the younger clear-cut forests (RAC9, RAC11 and RAC14) (sequential Bonferroni tests: $P < 0.05$ for all tests; Fig. 2A). The overall density of gallers also differed significantly among the months ($\chi^2 = 482.8$, $P < 0.001$, df = 4, $n = 450$), and all months differed significantly from each other with regard to the overall density of gallers (sequential Bonferroni tests: $P < 0.05$, for all multiple pairs for months), except July and August ($P = 0.41$; Fig. 2B). The successional stage × month interaction was not significant ($\chi^2 = 37.6$, $P = 0.23$, df = 32, $n = 450$). There were no significant directional patterns in either species density or overall density of gallers along the successional gradient (Spearman's correlations: species density: $r = -0.49$, $P = 0.18$; overall density: $r = 0.56$, $P = 0.12$).

Community structure of gallers

The community structure of gallers differed significantly among the nine forest successional

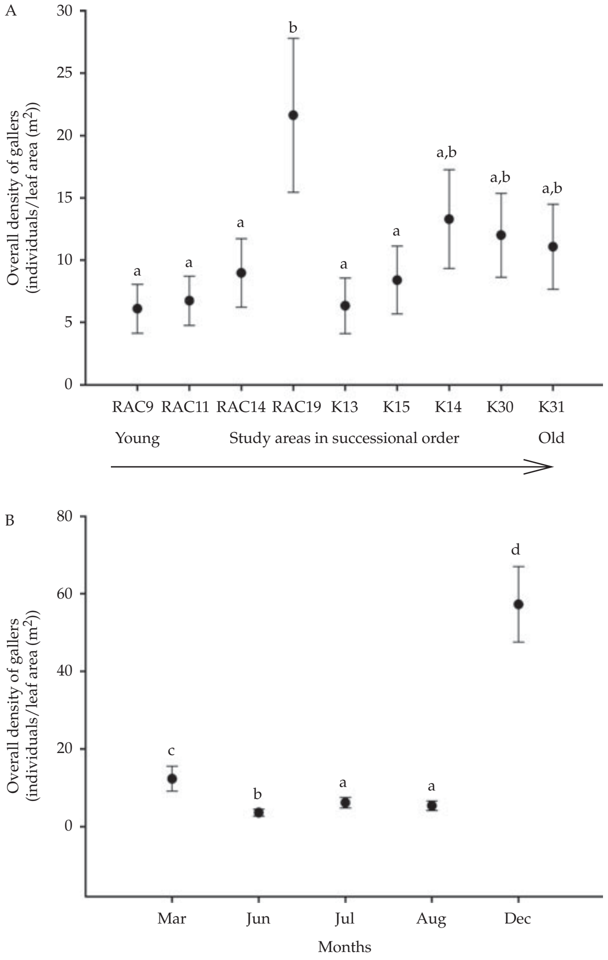

Fig. 2. Marginal means (±95% confidence limits) of overall density (individuals/leaf area (m^2)) of gallers per tree on *Neoboutonia* trees sampled from the nine forest successional stages (A) and the five study months (B). Different letters denote significant differences in means among the successional stages or months.

Table 3. Results of PERMANOVA for the effects of forest successional stage, month and their interactions on the community structure of gallers

Sources of variation	df	MS	*F*	*P*	UP	Sq. Var (%)
Successional stage (SS)	8	3487	4.1	0.001	999	7.3 (11%)
Month (M)	4	35,091	41.0	0.001	999	19.5 (30%)
SS × M	32	1697	2.0	0.001	998	9.2 (14%)
Residual	405	857				
Total	449					

df, degrees of freedom; MS, mean-squares; *F*, pseudo-*F* value; *P*, permutational *P* value; UP, unique permutations of the test statistic obtained under 999 permutations; Sq. Var, square-root of the component of variation (percentage of the total variation explained).

stages and months (PERMANOVA; Table 3). In addition, there was a significant successional stage × month interaction, indicating that the patterns of differences in the successional stages differed in different months. Successional stage explained 11%, month 30% and their interaction 14% of the variations in the community structure of gallers (Table 3). There was no significant directional pattern in galler community structure along the successional gradient (DISTLM: pseudo-$F = 2.64$, $P = 0.08$). The NMDS ordination for successional stages revealed no clear directional trend of recovery in the community structure of gallers (Fig. 3). The variations in the proportions of galler species in different successional stages are shown in Fig. 4. The NMDS ordination on centroids for months (Fig. 5) showed a distinct seasonal grouping of months. All dry season months (June, July and August) grouped together, whereas the two wettest months were clearly separated from all dry season months and from each other.

Influence of leaf size, mean tree height and host density on gallers

There was a significant positive correlation between the mean tree height and overall density of gallers (Spearman's correlation: $r = 0.82$, $n = 9$, $P = 0.007$). Neither the mean leaf area ($r = -0.18$, $n = 9$, $P = 0.64$) nor the host tree density ($r = -0.05$, $n = 9$, $P = 0.90$) correlated significantly with the overall density of gallers.

Discussion

Our results show that the species density and abundance of galling insects were highly resilient to habitat modification. No significant differences were found in the species density and overall density of gallers between the regenerating and primary forests 9–19 and 42–43 years after clear-cutting and selective logging, respectively. These findings corroborate those of a previous study carried out by Oyama *et al.* (2003) indicating that pioneer host plants recolonizing disturbed tropical forest habitats are rapidly colonized by galling insect species. There might be several reasons for the high resilience of galling insects to forest harvesting in KNP. First, the presence of primary forests (source populations) at a comparatively short distance from the regenerating forests allowed for dispersion and recolonization to take place as soon as the host trees re-established (Bengtsson, 2002). Second, *N. macrocalyx* is an early successional tree that has a patchy spatial distribution (G.M. Malinga, personal observation). This ephemeral and unpredictable existence of the host tree may have caused efficient colonization of host-specific gallers on *Neoboutonia* trees. The good colonization ability of tropical insects during tropical forest regeneration has also been indicated in other groups (e.g., Quintero and Roslin, 2005). Quintero and Roslin (2005) found that the abundance of Amazonian dung beetle assemblages recovered to a near original state following clear-cut, fragmentation and regrowth of secondary vegetation within 15 years. In contrast, a study on the same host plant system in Kibale forest found that the abundance of lepidopteran species in selectively logged areas was still significantly different from that in primary forests (Savilaakso *et al.*, 2009). Thus, different insect taxa exhibit different resilience to habitat disturbances, indicating that they can have different colonization abilities, preference or performance on their host plants in different habitats.

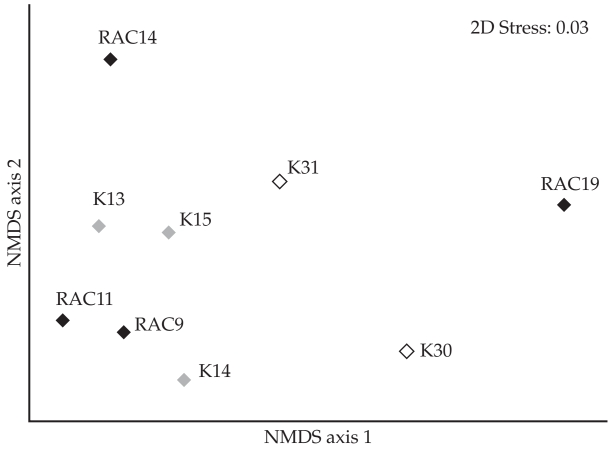

Fig. 3. Non-metric multi-dimensional scaling (NMDS) ordination on centroids for similarities in the community structure of gallers among the successional stages: primary forests (◇), selectively logged forests (◆) and regenerating former clear-cuts of coniferous forests (◆).

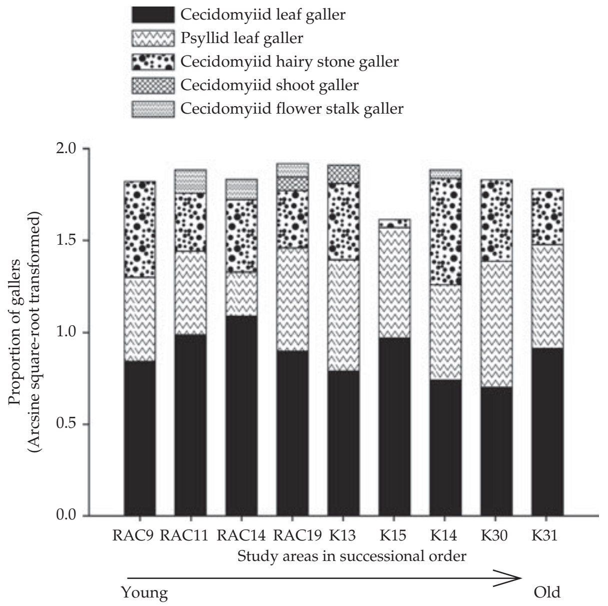

Fig. 4. Proportion of each galler species (arcsine square-root transformed) for each successional stage.

Despite the high resilience of galler species to habitat modification, there was no predictable directional trend of recovery in the patterns of galler community structure along the successional gradient or no existence of 'climax' galler community (Fig. 3). These patterns might be explained by the following: (i) the stochastic processes of recolonization and extinction of successional stages (see Wool (2012)) due to the patchiness of *Neoboutonia* trees, (ii) differences in the species-specific traits, e.g., recolonization efficiency of individual species, which is strongly affected by dispersal abilities and the matrix vegetation, and (iii) differences in the degree of past disturbances among the successional stages. We confirm earlier results reported by Dunn (2004) suggesting that whereas species richness of tropical fauna recovers relatively faster, a substantially longer period is required for the complete recovery of community composition.

Resource availability (mean tree height) was positively associated with the density of gallers. Many previous studies have found a significant relationship between host plant height and galling insect abundance (Caballero and Lorini, 2000; de Araújo and Dos Santos, 2009; Neves *et al.*, 2014). Taller host plants provide abundant resources (e.g., apical meristems) and are more evident in space to herbivorous insects (Neves *et al.*, 2014). The lack of a positive correlation between mean leaf size and density of galling insects suggests that galling insects may be less responsive to the quality (vigour) of host plants at the landscape level. In our earlier study (Malinga *et al.*, 2014*b*), we found that within colonized host trees, cecidomyiid leaf gallers select vigorously growing modules (larger sized leaves) as predicted by the plant vigour hypothesis (Price, 1991). Also, the lack of correlation between galler density and host tree density is surprising. Previous studies (Caballero and Lorini, 2000; Cuevas-Reyes *et al.*, 2004) and our earlier study (Malinga *et al.*, 2014*b*) have revealed that increasing host plant density increases the abundance or frequency of galling insects as predicted by the resource concentration hypothesis (*sensu* Root, 1973). The contrasting result of this study might be attributed to the presence of many non-host trees in the matrix vegetation that interfere either physically or chemically with how insect herbivores locate their host plants (associational resistance; Sholes (2008)). Associational resistance has been shown to confound the effects of host density on insect herbivore abundance in previous studies (reviewed in Barbosa *et al.* (2009)).

Lastly, remarkable seasonal variation was found in the species density, overall density and community structure of galling insects in all successional stages, with peak abundance being found in the wettest months. Our findings are consistent with those of several previous studies conducted in tropical forests on galling insects (Cuevas-Reyes *et al.*, 2006; de Araújo and Dos Santos, 2009) and other tropical insect groups, e.g., butterflies and moths (Kasenene and Roininen, 1999; Skippari *et al.*, 2009), butterflies (Valtonen *et al.*, 2013; Nyafwono *et al.*, 2014) and dung beetles (Nyeko, 2009). The peak in galler abundance during the wet season might be related to synchronization with the period of host tree production of young leaves, which are less toxic, softer and highly nutritious (Coley, 1983; Neves *et al.*, 2014) and onto which females lay eggs. However,

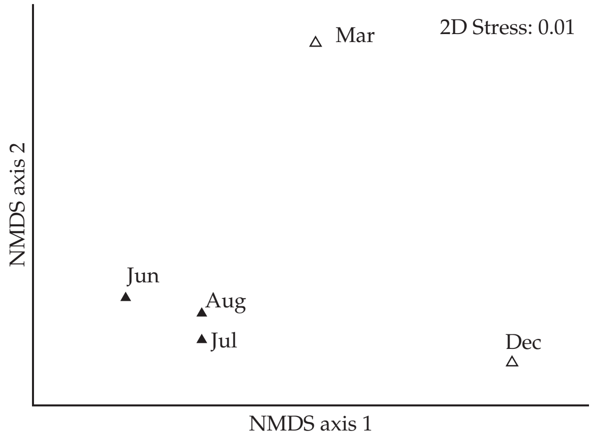

Fig. 5. Non-metric multi-dimensional scaling (NMDS) ordination on centroids for similarities in the community structure of gallers among the months: dry season (▲) and wet season (△).

this is less likely given that *N. macrocalyx* trees produce leaves continuously throughout the year (Kasenene and Roininen, 1999). Another possible reason might be related to the seasonality of rainfall as found for other herbivores (Wolda, 1988; Kasenene and Roininen, 1999; Valtonen *et al.*, 2013), which influences the nutritional quality and quantity of resources (de Araújo and Dos Santos, 2009).

The results of the present study indicate that specialist galling insects on pioneer host plants are resilient to habitat disturbance due to logging, provided that primary or secondary forests with an established *Neoboutonia* population (source populations) are sufficiently close by. The results also indicate that seasonal variations strongly affect galler communities, with peak abundance in the wettest months. These findings highlight the need to include recovering tropical forests into galling insect biodiversity management and conservation priority plans.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S1742758414000460

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References

Anderson M. J., Gorley R. N. and Clarke K. R. (2008) *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. PRIMER-E, Plymouth.

Barbosa P., Hines J., Kaplan I., Martinson H., Szczepaniec A. and Szendrei Z. (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annual Review of Ecology, Evolution, and Systematics* 40, 1–20.

Bengtsson J. (2002) Disturbance and resilience in soil animal communities. *European Journal of Soil Biology* 38, 119–125.

Caballero P. P. and Lorini H. (2000) Does resource concentration affect attack by galling and folivorous insects on *Schinus polygamus* (Cav.) Cabr. (Anacardiaceae)? *Revista Chilena de Entomología* 26, 89–92.

Chapman C. A., Chapman L. J., Jacob A. L., Rothman J. M., Omeja P., Reyna-Hurtado R., Hartter J. and Lawes M. J. (2010) Tropical tree community shifts: implications for wildlife conservation. *Biological Conservation* 143, 366–374.

Chapman C. A., Chapman L. J., Kaufman L. and Zanne A. E. (1999) Potential causes of arrested succession in Kibale National Park, Uganda: growth and mortality of seedlings. *African Journal of Ecology* 37, 81–92.

Chapman C. A., Chapman L. J., Struhsaker T. T., Zanne A. E., Clark C. J. and Poulsen J. R. (2005) A long-term evaluation of fruiting phenology: importance of climate change. *Journal of Tropical Ecology* 21, 31–45.

Clarke K. R. and Gorley R. N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.

Coley P. D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53, 209–234.

Cuevas-Reyes P., Quesada M., Hanson P., Dirzo R. and Oyama K. (2004) Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. *Journal of Ecology* 92, 707–716.

Cuevas-Reyes P., Quesada M., Hanson P. and Oyama K. (2007) Interactions among three trophic levels and diversity of parasitoids: a case of top-down processes in Mexican tropical dry forest. *Environmental Entomology* 36, 792–800.

Cuevas-Reyes P., Quesada M. and Oyama K. (2006) Abundance and leaf damage caused by gall-inducing insects in a Mexican tropical dry forest. *Biotropica* 38, 107–115.

de Araújo W. S. and do Espírito-Santo Filho K. (2012) Edge effect benefits galling insects in the Brazilian Amazon. *Biodiversity and Conservation* 21, 2991–2997.

de Araújo W. S. and Dos Santos B. B. (2009) Effects of seasonality and the size of host plants on abundance of Cecidomyiidae (Diptera) galls on *Piper arboreum* (Piperaceae). *Revista Brasileira de Entomologia* 53, 300–303.

de Araújo W. S., Julião G. R., Ribeiro B. A., Abraham Silva I. P and Dos Santos B. B. (2011) Diversity of galling insects in *Styrax pohlii* (Styracaceae): edge effect and use as bioindicators. *Revista de Biología Tropical* 59, 1589–1597.

Dunn R. R. (2004) Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18, 302–309.

Dynesius M., Hylander K. and Nilsson C. (2009) High resilience of bryophyte assemblages in streamside compared to upland forests. *Ecology* 90, 1042–1054.

Ewers R. M. and Didham R. K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81, 117–142.

FAO (Food and Agriculture Organisation of the United Nations) (2007) *State of the World's Forests 2007*. FAO, Rome. ISBN 978-92-5-105586-1.

Fernandes G. W., Almada E. D. and Carneiro M. A. A. (2010) Gall-inducing insect species richness as indicators of forest age and health. *Environmental Entomology* 39, 1134–1140.

Fischer E. and Killmann D. (2008) Illustrated field guide to the plants of Nyungwe National Park, Rwanda.

In *Volume 1 of Koblenz Geographical Colloquia: Series Biogeographical Monographs*. University of Koblenz-Landau, Koblenz. 771 pp.

Fonseca C. R., Fleck T. and Fernandes G. W. (2006) Processes driving ontogenetic succession of galls in a canopy tree. *Biotropica* 38, 514–521.

Gotelli N. J. and Colwell R. K. (2011) Estimating species richness, pp. 39–54. In *Biological Diversity: Frontiers in Measurement and Assessment* (edited by A. E. Magurran and B. J. McGill). Oxford University Press, Oxford.

Hamilton A. (1991) *A Field Guide to Ugandan Forest Trees*. Makerere University Press, Kampala. 111 pp.

Harris L. F. and Johnson S. D. (2004) The consequences of habitat fragmentation for plant–pollinator mutualisms. *International Journal of Tropical Insect Science* 24, 29–43.

Heimonen K., Lwanga J. S., Mutanen M., Nyman T. and Roininen H. (2013) Spatial and temporal variation in community composition of herbivorous insects on *Neoboutonia macrocalyx* in a primary tropical rain forest. *Journal of Tropical Ecology* 29, 229–241.

Holling C. S. (1973) Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4, 1–23.

Isaac J. L., Vanderwal J., Johnson C. N. and Williams S. E. (2009) Resistance and resilience: quantifying relative extinction risk in a diverse assemblage of Australian tropical rainforest vertebrates. *Diversity and Distributions* 15, 280–288.

Julião G. R., Amaral M. E. C., Fernandes G. W. and Oliveira E. G. (2004) Edge effect and species-area relationships in the gall-forming insect fauna of natural forest patches in the Brazilian Pantanal. *Biodiversity and Conservation* 13, 2055–2066.

Kasenene J. M. (1987) The influence of mechanized selective logging, felling intensity and gap size on the regeneration of a tropical moist forest in Kibale Forest Reserve, Uganda. PhD dissertation, Michigan State University, East Lansing, MI.

Kasenene J. M. (2007) Impact of exotic plantations and harvesting methods on the regeneration of indigenous tree species in Kibale forest, Uganda. *African Journal of Ecology* 45, 41–47.

Kasenene J. M. and Roininen H. (1999) Seasonality of insect herbivory on the leaves of *Neoboutonia macrocalyx* in the Kibale National Park, Uganda. *African Journal of Ecology* 37, 61–68.

Kohv K., Zobel M. and Liira J. (2013) The resilience of the forest field layer to anthropogenic disturbances depends on site productivity. *Canadian Journal of Forest Research* 43, 1040–1049.

Lovett J. C. (1991) Notes on the forests at Ambangulu and Kunga in the West Usambara mountains, Tanzania. *East African Natural History Society Bulletin* 21, 29–30.

Lovett J. C., Ruffo C. K., Gereau R. E. and Taplin J. R. D. (2006) *Field Guide to the Moist Forest Trees of Tanzania*. The Society for Environmental Exploration, UK and the University of Dar es Salaam, Tanzania. 303 pp.

Magurran A. E. (2004) *Measuring Biological Diversity*, 2nd edn. Blackwell, Oxford. 264 pp.

Malinga G. M., Valtonen A., Nyeko P. and Roininen H. (2014*a*) Bottom-up manipulations alter the community structures of galling insects and gall morphs on *Neoboutonia macrocalyx* trees in a moist tropical rainforest. *Agricultural and Forest Entomology* 16, 314–320.

Malinga G. M., Valtonen A., Nyeko P., Vesterinen E. J. and Roininen H. (2014*b*) Bottom-up impact on the cecidomyiid leaf galler and its parasitism in a tropical rainforest. *Oecologia* 176, 511–520.

Malinga G. M., Valtonen V., Vesterinen E. J., Nyeko P. and Roininen H. (2014*c*) Communities of galling insects on *Neoboutonia macrocalyx* trees in continuous forests and remnants of forest fragments in Kibale, Uganda. *African Entomology* (in press).

Montúfar R., Anthelme F., Pintaud J.-C. and Balslev H. (2011) Disturbance and resilience in tropical American palm populations and communities. *The Botanical Review* 77, 426–461.

Morris R. J. (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. *Philosophical Transactions of the Royal Society of London B* 365, 3709–3718.

Neves F. S., Silva J. O., Espírito-Santo M. M. and Fernandes G. W. (2014) Insect herbivores and leaf damage along successional and vertical gradients in a tropical dry forest. *Biotropica* 46, 14–24.

Nyafwono M., Valtonen A., Nyeko P. and Roininen H. (2014) Butterfly community composition across a successional gradient in a human-disturbed Afro-tropical rain forest. *Biotropica* 46, 210–218.

Nyeko P. (2009) Dung beetle assemblages and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. *Biotropica* 41, 476–484.

Nyman T., Bokma F. and Kopelke J.-P. (2007) Reciprocal diversification in a complex plant–herbivore–parasitoid food web. *BMC Biology* 5, 49. doi:10.1186/1741-7007-5-49.

Olupot W. (2000) Mass differences among male mangabey monkeys inhabiting logged and unlogged forest compartments. *Conservation Biology* 14, 833–843.

Oyama K., Pérez-Pérez M. A., Cuevas-Reyes P. and Luna-Reyes R. (2003) Regional and local species richness of gall-inducing insects in two tropical rain forests in Mexico. *Journal of Tropical Ecology* 19, 595–598.

Paniagua M. R., Medianero E. and Lewis O. T. (2009) Structure and vertical stratification of plant galler–parasitoid food webs in two tropical forests. *Ecological Entomology* 34, 310–320.

Price P. W. (1991) The plant vigor hypothesis and herbivore attack. *Oikos* 62, 244–251.

Quintero T. and Roslin T. (2005) Rapid recovery of dung beetle communities following habitat fragmentation in Central Amazonia. *Ecology* 86, 3303–3311.

Root R. B. (1973) Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs* 43, 95–124.

Rydgren K., Økland R. H. and Hestmark G. (2004) Disturbance severity and community resilience in a boreal forest. *Ecology* 85, 1906–1915.

Santos J. C., Tavares C. B. and Almeida-Cortez J. S. (2011) Plant vigour hypothesis refuted: preference–performance linkage of a gall-inducing weevil on small-sized host plant resources. *Brazilian Journal of Biology* 71, 65–69.

Savilaakso S., Koivisto J., Veteli T. O. and Roininen H. (2009) Microclimate and tree community linked to differences in lepidopteran larval communities between forest fragments and continuous forest. *Diversity and Distributions* 15, 356–365.

Sholes O. D. V. (2008) Effects of associational resistance and host density on woodland insect herbivores. *Journal of Animal Ecology* 77, 16–23.

Skippari S., Veteli T. O., Kasenene J., Niemelä P. and Roininen H. (2009) High temporal variation in the assemblage of Lepidopteran larvae on a constant resource. *African Journal of Ecology* 47, 537–545.

Struhsaker T. T. (1997) *Ecology of an African Rain Forest: Logging in Kibale and the Conflict between Conservation and Exploitation*. University Press of Florida, Gainesville, FL. 456 pp. ISBN 0-8130-1490-5.

Summerville K. S. (2013) Forest lepidopteran communities are more resilient to shelterwood harvests compared to more intensive logging regimes. *Ecological Applications* 23, 1101–1112.

Valtonen A., Molleman F., Chapman C. A., Carey J. R., Ayres M. P. and Roininen H. (2013) Tropical phenology: bi-annual rhythms and interannual variation in an Afrotropical butterfly assemblage. *Ecosphere* 4, 36. http://dx.doi.org/10.1890/ES12-00338.1.

Vieira E. M., Andrade I. and Price P. W. (1996) Fire effects on a *Palicourea rigida* (Rubiaceae) gall midge: a test of the plant vigor hypothesis. *Biotropica* 28, 210–217.

Watt A. D. (1998) Measuring disturbance in tropical forests: a critique of the use of species–abundance models and indicator measures in general. *Journal of Applied Ecology* 35, 467–469.

Wolda H. (1988) Insect seasonality: why? *Annual Review of Ecology and Systematics* 19, 1–18.

Wool D. (2012) Autecology of *Baizongia pistaciae* (L.): a monographical study of a galling aphid. *Israel Journal of Entomology* 41, 67–93.