Causal relationship between leaf litter beetle communities and regeneration patterns of vegetation in the Atlantic rainforest of Southern Brazil (Mata Atlântica)

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A B S T R A C T

Old growth forests in the Atlantic rainforest of Southern Brazil are increasingly replaced by secondary forests. Effects on arthropods are assumed to be particularly important as they provide the bulk of biodiversity and play an integral role for ecosystem processes and services. During forest regeneration vegetation structure, leaf litter composition and microclimatic conditions were found to strongly affect leaf litter beetle communities. This study aimed at highlighting the question whether there is evidence that restoration actions to support the regeneration of old-growth forest vegetation structure can enhance the re-establishment of old-growth forest leaf litter beetle communities in secondary forests in the Mata Atlântica. A conceptual model structure representing a causal effect chain was built and checked against observational data for vegetation and leaf litter beetles from different regeneration stages using structural and microclimatic variables. By the results in this study the hypothesis of an ecological causal effect chain was clearly supported. There was reasonable evidence that during the regeneration process varying vegetation composition results in varying structural characteristics inside the vegetation stand and the associated leaf litter. The changed structural parameters proved to alter the microclimatic conditions within the leaf-litter and subsequently the differences in microclimatic conditions showed a significant influence on the leaf litter beetle community within the forest regeneration sites. These results have important implications for arthropod species conservation as they show that the probability of conserving or re-establishing old growth leaf litter beetle communities can be increased by maintaining and restoring suitable vegetation, structure and microclimatic conditions.

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1. Introduction

Old growth forests in the tropics are threatened and reduced, especially in the Atlantic rainforest of Southern Brazil, known as the Mata Atlântica. Only 10–15% of this biodiversity hotspot is left today (Myers et al., 2000; Ribeiro et al., 2009) of which a large part are secondary forests of different age and condition. With the reduction of old-growth forests the likelihood of extinction of old-growth forest arthropod populations increases, due to increasing fragmentation (edge effects), subsequent disturbance of meta-population structure and increasing relevance of stochastic events (Henle et al., 2004; Ribon et al., 2003; Tabarelli et al., 1999). In this context, fragmentation and habitat loss are termed key processes, which threaten the sustainability of biodiversity (e.g. Kupfer et al., 2006; Solé et al., 2004; Zuidema et al., 1996). Effects on arthropods are assumed to be particularly important as they provide the bulk

of biodiversity (Groombridge and Jenkins, 2000) and play an integral role for many ecosystem processes and services (Kremen and Chaplin-Kramer, 2007; Losey and Vaughan, 2006; Miller, 1993).

The remaining forests in the Mata Atlântica are mainly secondarily built from natural regeneration of abandoned farm-land (Ribeiro et al., 2009). In a recent study, Hopp et al. (2010) showed that older secondary forest can be a suitable habitat for old-growth leaf litter beetle species and a source for recolonization of younger regeneration stages; but, to establish stable populations of old-growth arthropods, habitat conditions must meet the requirements of these species. In particular, vegetation structure and corresponding microclimatic conditions as well as quality and quantity of leaf litter were found to strongly affect populations and communities (Antvogel and Bonn, 2001; Grimbacher et al., 2006; Jonsson and Jonsell, 1999; Magura et al., 2004; Migge-Kleian et al., 2007; Vanderwel et al., 2006; Warriner et al., 2004). Hence, natural forest regeneration or reforestation actions, which support the conversion of disturbed areas into forest ecosystems featuring old-growth forest like abiotic and biotic conditions, are postulated as

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efficient tools to stabilize and accelerate the recovery of arthropod communities, such as beetles (Grimbacher and Catterall, 2007; Nakamura et al., 2009).

Much restoration efforts have been made in the Mata Atlântica in younger times, e.g. active vegetation restoration of abandoned farmland by planting native tree seedlings or natural regeneration (Ferretti and Britez, 2006; Rodrigues et al., 2009). However, although Nakamura et al. (2009) confirmed the positive effect of shading of the litter layer on the recolonization for many arthropods in an experimental approach and showed positive effect of mulching on the recolonization of ants in an Australian rainforest, efficiency of such actions for the conservation of arthropod communities has seldom been reviewed (see Barlow et al., 2007a; Dunn, 2004) and is difficult to be assessed. Results which arise from studies examining species response to natural forest regeneration (e.g. focussing on ants: Bihn et al., 2008; Silva et al., 2007; butterflies: Barlow et al., 2007b; birds: Barlow et al., 2007c; beetles: Hopp et al., 2010) mostly lack the analysis of meaningful relationships to environmental factors or do not provide a clear definition of the statistical process of causal inference.

This study aims at highlighting the question whether there is evidence that restoration actions to support the regeneration of old-growth forest vegetation structure can enhance the re-establishment of old-growth forest leaf litter beetle communities in secondary forests in the Mata Atlântica. Successional long-term as well as seasonal processes are known to change microclimatic conditions in tropical forests (Fetcher et al., 1985; Pinker, 1980; Schulz, 1960) and affect the recovery pattern of leaf litter beetle species richness due to structural variables like litter quantity (Hopp et al., 2010). Based on these facts, our hypothesis was that by supporting vegetation regeneration towards old-growth conditions, favourable structural and microclimatic conditions for the regeneration of old-growth leaf litter beetle communities can be forced. To explore this hypothesis we built a conceptual model structure representing an assumed causal effect chain: (1) Changes in vegetation composition change structural variables (canopy closure, litter volume and composition, etc.) (Finegan, 1996; Kennard, 2002; Saldarriaga et al., 1988; Toky and Ramakrishnan, 1983). (2) Changes in structural variables change microclimatic conditions (temperature, humidity, light availability, etc.) (Leme-nih et al., 2004; Martius et al., 2004; Smith et al., 1992). (3) Changes in microclimatic conditions change leaf litter beetle communities (Antvogel and Bonn, 2001; Migge-Kleian et al., 2007). This model structure is checked against observational data for vegetation and leaf litter beetles from regeneration stages in the Mata Atlântica using structural and microclimatic variables in a series of multivariate analyses.

The objectives of this study were (1) to test the hypothesis that differences in vegetation patterns observed in regeneration stages of submontane forests in the Mata Atlântica are significantly correlated to the leaf litter beetle communities via altered structural parameters and subsequent changes in microclimatic conditions, (2) thereby verifying the conceptual model structure of the effect chain and (3) come towards a causal interpretation of the relationship between the leaf litter beetle communities and the vegetation pattern by ecological verification of the statistical correlation.

2. Methods

2.1. Study area and sites

The regeneration study was carried out in the coastal mountain range (Serra do Mar) of Paraná state, Southern Brazil, within the municipality of Guaraqueçaba (25°17′54″ S, 48°19′33″ W). The regional climate is classified as Köppens Cfa (humid subtropical, Peel et al., 2007). This climate zone is characterized by hot, humid summers and chilly to mild winters. Significant amounts of precipitation occur in all seasons showing an annual rainfall of 2545 mm (Ferretti and Britez, 2006). Data collections for 19 years conducted by the meteorological agency of Paraná state (SIMEPAR) indicate that approximately 40% of the annual rainfall occur in the summer (January through March) and only 15% in the driest months (June through August). The average annual temperature of Guaraqueçaba, about 12 km east of the study sites, is 20–22 °C (Ferretti and Britez, 2006). The study sites were located in the Serra do Itaqui Nature Reserve (Reserva Natural Serra do Itaqui) owned and administered by the NGO 'Society for Wildlife Research and Environmental Education' (SPVS). Intense disturbance of the original vegetation, due to timber exploitation, charcoal produc-tion and cattle grazing resulted in a mosaic of secondary forests with varied floristic, structural and physiognomic characteristics. All study sites were situated in the submontane forest zone, and were formerly covered with humid submontane forest (Floresta ombrophila densa submontana) (IBGE, 1992).

A chronosequence approach was used to investigate pattern of vegetation and leaf litter beetles during forest regeneration. The chronosequence comprises four a priori forest age classes: very young secondary forests (~5 years, stage H), young secondary forests (12–15 years, stage A) and old secondary forests (35–50 years, stage M) as well as old-growth forests (>100 years, stage F) as a reference. Three replicate sites per successional stage were established (e.g. H1, H2, and H3) scattered over the reserve. The soil type could be addressed as cambisol.

2.2. Community composition data, microclimatic data and structural data

Beetles were sampled by sifting forest leaf litter and extracting the samples using the Winkler technique from 20 subplots in each investigation site (for details of sampling see Hopp et al., 2010). Tree species composition and according structural variables were surveyed on 10 subplots within each study site.

Air temperature was continuously recorded within the leaf litter layer from mid-October 2007 to mid-August 2008 by hourly measurements using Watchdog data logger (Spectrum Inc., USA). To ensure consequent measurement, two parallel loggers were placed at each site. Data were available from 16.10.2007 0:00 until 22.01.2008 17:00 and from 20.02.08 4:00 until 20.07.08 11:00 including the sites H-1, H-2, H-3, A-1, M-1, M-2, M-3, F-1, F-2 and F-3. These data characterize all-season whole-time gradients, by covering the largest part of the hot rainy season from December to March and the much dryer season from May to August as well as measurements at daytime and nights.

Structural variables included in this analysis (mean values per site) were (abbreviations in parentheses): canopy closure in % (canopy) (calculated from hemispherical photos with GAP LIGHT ANALYZER (GLA), Version 2.0 (Frazer et al., 1999)), tree height in m (treeheig), canopy height in m (canheigh) (both estimated by eye by an experienced park ranger), tree vitality in a 4 stage ordinal scale from 0 (low vitality) to 5 (high vitality) (treevita), litter stock volume in L/m^2 (lsvol) (measurement of coarse litter in a graduated bucket, slightly compressing the foliage using a standard weight), basal respiration of litter in $\mu L\ CO_2\ h^{-1}\ g^{-1}$ (BR_litter), substrate induced respiration of litter in $\mu L\ CO_2\ h^{-1}\ g^{-1}$ (SIR_litter) (both according to Anderson and Domsch, 1978), C/N-ratio of litter (CN_litter) (determined by elemental analysis of total nitrogen content according to DIN ISO 13 878 (1998) and total organic carbon content), occurrence of liana in a 4 stage ordinal scale (0 (no lianas) – 5 (high quantity of lianas) (liana)), occurrence of epiphytes in a 4 stage ordinal scale (0 (no epiphytes) – 2 (high

Table 1
Structural variables used in this study (data quality (dq.): a = mean value from 10 repeated measurements per site, b = mean value from 40 repeated measurements per site, c = single value per site, d = mean value from 5 repeated measurements per site) (for variable abbreviations see text).

	Unit	H-1	H-2	H-3	A-1	A-2	A-3	M-1	M-2	M-3	F-1	F-2	F-3	dq.
canopy	%	26.52	22.18	44.89	9.59	12.42	8.92	12.42	6.01	8.38	8.19	3.94	4.84	a
treeheig	m	5.46	6.15	6.82	8.66	7.48	8.96	9.92	10.80	12.53	10.79	8.78	10.37	a
canheigh	m	3.02	3.23	3.81	5.77	5.05	5.35	5.93	6.21	7.53	6.77	5.22	6.39	a
treevita	0–5	3.40	3.75	3.37	3.62	3.34	3.19	3.45	3.54	3.56	3.62	3.30	3.80	a
lsvol	L/m^2	9.08	10.32	10.46	11.86	10.62	9.17	13.18	12.27	15.66	11.06	16.59	14.40	b
BR_litter	μL h^{-1} g^{-1}	77.2	89.2	171.6	105.5	119.0	117.6	130.1	109.1	192.6	171.4	174.4	153.4	c
SIR_litter	μL h^{-1} g^{-1}	195.9	197.3	321.5	243.9	222.1	259.0	335.9	276.1	492.5	339.2	382.9	367.3	c
CN_litter	–	30.4	40.0	28.4	24.0	28.8	28.6	22.9	25.5	23.6	21.7	23.2	23.7	d
liana	0–5	0.000	0.000	0.019	0.068	0.275	0.182	0.187	0.072	0.158	0.124	0.243	0.209	a
epiphyte	0–5	0.000	0.000	0.000	0.007	0.021	0.005	0.009	0.044	0.082	0.262	0.125	0.266	a
dbh	cm	1.88	2.51	3.95	5.73	4.68	3.91	5.43	8.10	7.66	8.27	8.81	10.94	a
treedens	1/100^2	272.0	158.0	104.0	628.0	430.0	482.0	456.0	390.0	396.0	470.0	318.0	330.0	a

quantity of epiphytes)) (epiphyte), diameter at breast height in cm (dbh) (measured at 1.3 m height for all specimen with diameter ≥10 cm), tree density in trees per 100 m^2 (treedens) (Table 1).

2.3. Classification of temperature data

Monthly mean temperature data were calculated from the sum of monthly temperatures divided by the number of measurements per month. Temperature time series were classified to state distinct classes of annual temperature dynamics (called 'T-Types') which characterized the microclimatic conditions within the leaf litter habitat of the investigation sites. Classification of the reduced data was performed by means of hierarchical classification (cluster analysis, Euclidean distance and Ward's amalgamation algorithm) (Anderberg, 1973; Lance and Williams, 1967; Sokal and Sneath, 1963) (TimeClust, Magni et al., 2008) and fuzzy c-means classification (procedure fcm from the Fuzzy Logic Toolbox (Ver. 2.2.7) in MATLAB (Ver. 7.6.0, MathWorks, 1999) (Bezdek, 1981). To test whether the T-Type temperature dynamic classes could be significantly separated, a repeated measurement ANOVA on the mean monthly temperature values from the classes was performed. The overall effect of T-Type was assessed by a standard repeated measurement ANOVA approach using the T-Types as fixed variables. Subsequently a linear mixed-effect model was fitted to the mean monthly temperature values with T-Type classes as fixed variable and time as random variable. To perform a pairwise test for the linear hypotheses a multiple comparison on the class means was performed by the use of Tukey contrasts. Repeated measurement ANOVA, linear mixed-effect model and pairwise test of T-Type temperature dynamics were calculated by means of the R environment for statistical computing, Ver. 2.8.1 (R Development Core Team, 2009) using the routine aov() from the package stats, routine lme() from the package nlme, Ver. 3.1-92 (Pinheiro et al., 2009) and routine glht() from the package multcomp, Ver. 2.9.2 (Hothorn et al., 2008), respectively.

2.4. Data modelling outline

To achieve the aim of analyzing the relationship between the leaf litter beetle communities and the vegetation pattern a causal effect chain model was conceptually set up. Changes in vegetation composition were assumed to change structural variables like canopy closure, litter volume and composition. Resulting changes in structural variables were assumed to change microclimatic conditions like temperature, humidity and light availability. Subsequently, changes in microclimatic conditions were assumed to change the leaf litter beetle communities. After a check for plausibility (theoretical model verification) the structural and microclimatic variables were used in statistical modelling to explain species composition for vegetation and beetles in the regeneration stages. From these results the causal effect chain represented by the model structure was ecologically verified.

2.5. Multivariate statistics for effect analysis

The variability in vegetation and beetle community composition was analyzed by means of non-metric multidimensional scaling (NMDS) (Kruskal, 1964; Shepard, 1962) based on the Bray–Curtis distance. Raw data were used for analysis. To find the optimal number of ordination axes a step-down procedure (6 to 1 axes) was used. 199 random permutations of the initial configuration were performed to find the best solution. The convergence ratio for the stress measure was set to 0.9999. A stress value of 0.1 was assumed to be adequate (Anderson, 2003; Kruskal and Carmone, 1973). To avoid the numeric optimization algorithm to get stuck in a local minimum before converging to the global minimum, NMDS analyses were performed in a large number of reruns (100), finally choosing the run with the lowest stress value. To visualize the results from classification within the ordination space, the clusters were displayed in an overlay using convex hulls.

2.6. Building the effect chain

An effect chain was build up from vegetation community composition to structural data, to the temperature dynamic types derived from the operationalization process, and further to the beetle communities by canonical correspondence analyses (CCA) (ter Braak, 1986). Monte-Carlo permutation tests were used to test the significances of the ordination axes (499 permutations under reduced model). A p-value ≤0.05 for the first ordination axis was accepted as an indicator for a significant relationship between the items. By use of manual forward selection it was tested in a preliminary CCA, which constraining variables explained a significant part of the overall variability in the data ($p \leq 0.05$). Because of the noisy character of multivariate field data a significance level slightly higher than 0.05 was assumed to be adequate. Subsequently only the significant variables were used to quantify the relationships in a final CCA run. The amount of variability explained by the analyses was calculated as the ratio of the sum of all canonical eigenvalues divided by the sum of all eigenvalues.

All multivariate analyses were performed with CANOCO for Windows 4.53 (ter Braak and Šmilauer, 2002). In the case of NMDS the Winkyst Addon Ver. 1.0 was used (Šmilauer, 2003). Regeneration stage A was excluded from the effect analyses, because only for one site from this class reliable temperature dynamics data were available. Nevertheless, the sites from stage A were integrated in NMDS to display the ecological distance to the other regeneration stages.
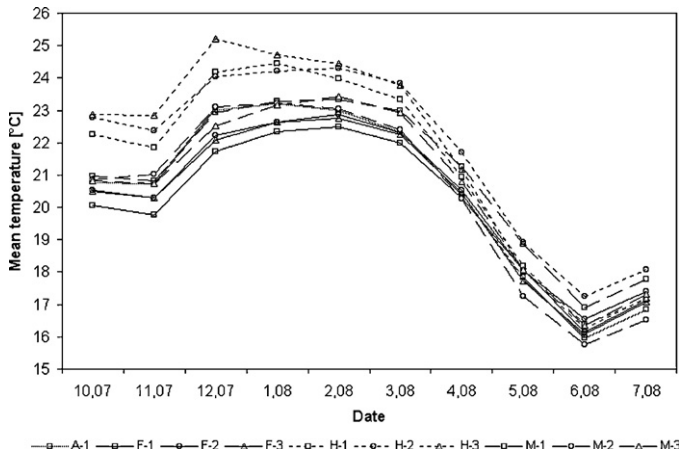
Fig. 1. Monthly mean temperatures from October 2007 to July 2008. Sites A-2 and A-3 were omitted due to incomplete logger data.

3. Results

All sites showed comparable temperature dynamics; but, with increasing age the mean monthly temperature decreased all over the year (Fig. 1). The stage replicates showed a small variation only. In summer (10.2007–03.2008) the differences between the stages were larger than in winter (04.2008–07.2008). The lowest measured temperature values occurred in June for all investigation sites.

From the classification of the time series data three clusters could be justified with respect to a Euclidean distance of about 3 in the hierarchical cluster analysis. Cluster 1 combined all initial H-sites (H-2, H-3, and H-1), cluster 2 combined the intermediate sites (M-3, M-1, M-2, and A-1) and cluster 3 contained only old-growth forest sites (F-1, F-3, and F-2). The heatmap displayed the influence of data sectors on the cluster results (Fig. 2). The temperature differences in winter (≥07.2008) only had a small influence. A larger influence was visible for the data from 03.2007 to 07.2008 (dark shading). The crisp classification revealed the following types of temperature dynamics:

Table 2a

Repeated measurement ANOVA of mean monthly temperatures with T-Type classes as fixed factor (cluster) by the use of R-routine aov().

	Df	Sum square	Mean square	F value	Pr(>F)
Error: time					
Residuals	9	625.11	69.46		
Error: time: cluster					
Cluster	2	30.8075	15.4037	27.336	3.509e−06
Residuals	18	10.1429	0.5635		
Error: within					
Residuals	70	9.0574	0.1294		

T-Type 1: "summer warm sites" (H-1, H-2, and H-3) (initial H-stages).

T-Type 2: "moderately warm sites" (A-1, M-1, M-2, and M-3) (intermediate stages A + M).

T-Type 3: "summer cool sites" (F-1, F-2, and F-3) (old-growth F-stages).

During the vegetation sampling site A-1 proved to be an inhomogeneous area which was half an A-stage and half a late M-stage. As the vegetation composition in the M-stage part was very dense it was not surprising, that site A-1 was clustered together with the M-replicates. Due to this inhomogeneity site A-1 was excluded from the further analyses later on.

The repeated measurement ANOVA for the T-Type temperature dynamics showed that the T-Type class has a highly significant influence on the mean monthly temperature dynamic (Table 2a: $p < 0.001$). The fitted linear mixed-effect model revealed highly significant effects of the cluster levels on the mean monthly temperature (fixed effects clusters 2 and 3 in Table 2b); but, a clear correlation between cluster 2 and 3 ($p = 0.508$). The pairwise test of temperature dynamics for the T-Types showed that T-Type 1 could clearly be distinguished from T-Types 2 and 3 ($p < 0.001$) but T-Type 2 was insufficiently separated ($p = 0.088$) from T-Type 3 (Table 2c).
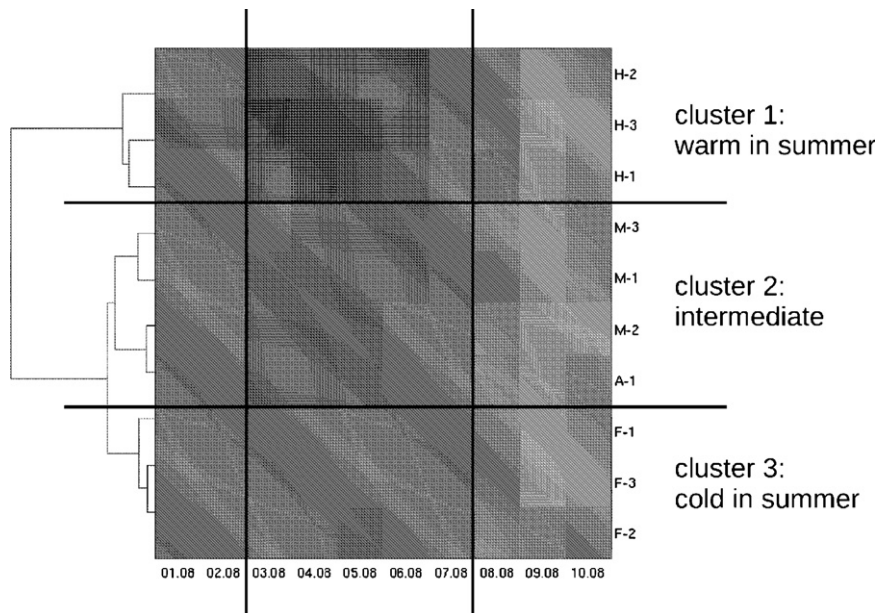

Fig. 2. Heatmap from hierarchical cluster analysis based on mean monthly temperatures. Clusters are mainly defined by temperature differences from December 2007 (time point 3 on x-axis) to April 2008 (time point 7 on x-axis). Sites A-2 and A-3 were omitted due to incomplete logger data. The darker the shading the higher the mean monthly temperature.

Table 2b

Linear mixed-effects model fitted by REML for mean monthly temperature (mmt) using T-type classes as fixed variable (cluster) and time as random variable (time) by the use of R-routine lme() (Number of observations: 100).

AIC	BIC	logLiK
183.6608	199.1091	−85.83041

Random effects:
Formula: ~1 | time

	(Intercept)
Std. dev.	2.62661

Formula: ~1 | cluster %in% time

	(Intercept)	Residuals
Std. dev.	0.37402	0.36060

Fixed effects: mmt ~ cluster

	Values	Std. error	DF	t-Value	p-Value
(Intercept)	21.55933	0.84156	70	25.61813	0.0000
Cluster 2	−0.98608	0.18858	18	−5.22884	0.0001
Cluster 3	−1.38400	0.19143	18	−7.22953	0.0000

Correlation

	(Intr)	Cluster 2
Cluster 2	−0.115	
Cluster 3	−0.114	0.508

Standardized within-group residuals:

Min	Q1	Med	Q3	Max
−2.09367	−0.66930	0.08559	0.45785	2.42652

Number of observations: 100
Number of Groups:

Time	Cluster %in% time
10	30

Table 2c

Simultaneous tests for the linear hypothesis from Table 2b: multiple comparisons of cluster means with Tukey contrasts by the use of R-routine glht() (Fit: lme.formula (fixed = mmt ~ cluster. data = mydata. random = ~1 | time/cluster)).

	Estimate	Std. error	z-Value	Pr(>|z|)
Linear hypotheses:				
Cluster 2 to Cluster 1 == 0	−0.9861	0.1886	−5.229	<1e−04
Cluster 3 to Cluster 1 == 0	−1.3840	0.1914	−7.230	<1e−04
Cluster 3 to Cluster 2 == 0	−0.3979	0.1886	−2.110	0.0877

The crisp hierarchical classification was not unambiguous for the intermediate stages in T-Type 2. Therefore, the assignment of the sites to the T-Types was improved by the use of fuzzy logic, so there was no need for a final decision to which T-Type the sites belonged. In all cases the assignment from crisp classification was in accordance with the highest membership from fuzzy classification (marked with an asterisk in Table 3). For the intermediated sites (A-1, M-1, M-2, M-3) the memberships for T-Type 2 were low in some cases and there were non-negligible memberships for T-

Table 3

Membership of sites for operationalized annual temperature dynamics classes from fuzzy classification. Fuzzy memberships were calculated by means of the fcm algorithm with $k = 3$. The memberships from hierarchical classification are marked by an asterisk.

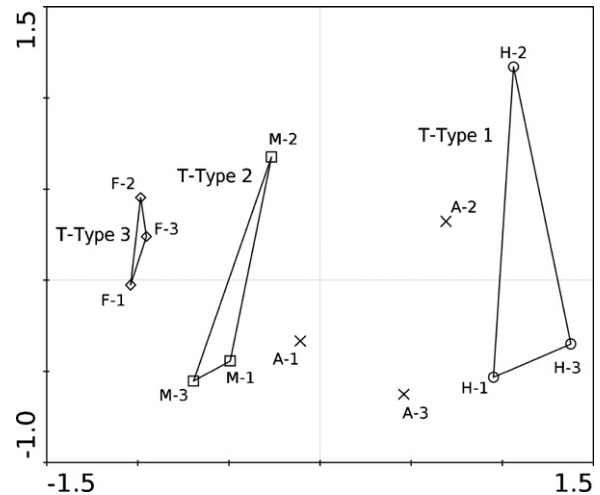|	T-Type 1	T-Type 2	T-Type 3
H-1	0.844*	0.108	0.048
H-2	0.863*	0.086	0.051
H-3	0.906*	0.060	0.034
A-1	0.016	0.864*	0.120
M-1	0.136	0.578*	0.287
M-2	0.056	0.712*	0.232
M-3	0.027	0.805*	0.169
F-1	0.018	0.122	0.860*
F-2	0.008	0.105	0.887*
F-3	0.005	0.067	0.928*

Fig. 3. Non-metric multidimensional scaling showing vegetation composition. Sites belonging to the same class of annual temperature dynamics are connected by convex hulls. As no temperature dynamics classes could be attributed to A-2 and A-3 the A-sites are missing a convex hull. The final stress of this NMDS solution was 0.07.

Types 1 and 3. These memberships were further used in the multivariate effect analysis.

In NMDS, based on vegetation data, the T-Types could be clearly separated on axis 1. T-Type 3 was located far from T-Type 1 and T-Type 2 could be assessed as an intermediate class (Fig. 3).

To elucidate the relationship between vegetation and structural variables, structural variables were explained by vegetation composition by means of canonical correspondence analyses. Five variables proved to be significant in manual forward selection: *Psychotria nuda* (psycnuda), *Cecropia pachystachya* (cecrpach), *Symplocos tetranda* (symptetr), *Trichilla* spec. (tric), *Tibouchina pulchra* (tibopulc). These species explained 95.3% variability in the structural variable data set. Axis 1 proved to be highly significant ($p = 0.032$) (Fig. 4).

Subsequently the T-Types were explained by the structural variables. Five variables (diameter at breast height (dbh), tree height (treeheig), height of the canopy (canheigh), canopy closure (canopy), litter C/N ratio (CN_litter)) explained almost all of the variability within the T-Types (98.3%). The first axis showed to be highly significant ($p = 0.006$) (Fig. 5).
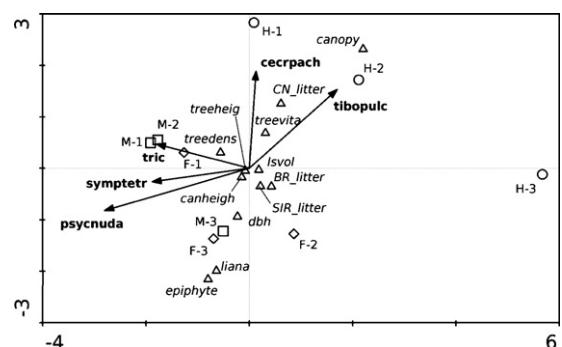

Fig. 4. Canonical correspondence analysis to explain structural variables (canopy: canopy closure, treeheig: tree height, canheigh: canopy height, treevita: tree vitality, lsvol: litter stock volume, BR_litter: basal respiration of litter, SIR_litter: substrate induced respiration of litter, CN_litter: C/N-ratio of litter, liana: occurrence of liana, epiphyte: occurrence of epiphytes, dbh: diameter at breast height, treedens: tree density) by vegetation composition (psycnuda: *Psychotria nuda*, cecrpach: *Cecropia pachystachya*, symptetr: *Symplocos tetranda*, tric: *Trichilla* spec., tibopulc: *Tibouchina pulchra*) (eigenvalue of first axis: 0.042, sum of all eigenvalues: 0.064, sum of all canonical eigenvalues: 0.061, p-value of first canonical axis: 0.032).
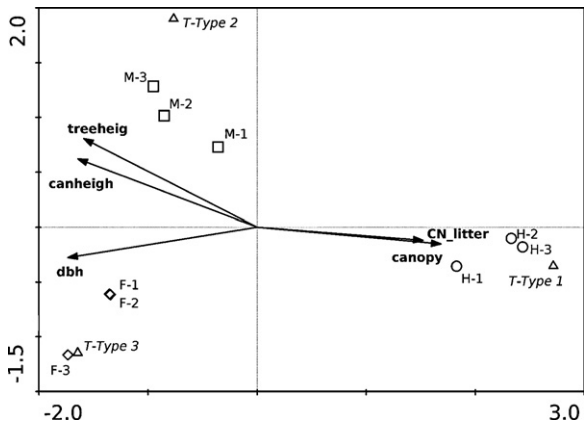
Fig. 5. Canonical correspondence analysis to explain T-Types (T-Types 1–3) by structural variables (canopy: canopy closure, treeheig: tree height, canheigh: canopy height, CN_litter: C/N-ratio of litter, dbh: diameter at breast height) (eigenvalue of first axis: 0.720, sum of all eigenvalues: 1.118, sum of all canonical eigenvalues: 1.099, p-value of first canonical axis: 0.006).

Canopy openness decreased significantly along the chronosequence ($p < 0.005$, except for comparison stage A to stage M: $p = 0.01$, pairwise Mann–Whitney U-test with Bonferroni correction) (Fig. 6).

In NMDS analysis for beetle species composition, T-Types 2 and 3 were clearly separated from T-Type 1; but, there was only an insufficient separation of T-Types 2 and 3 (Fig. 7).
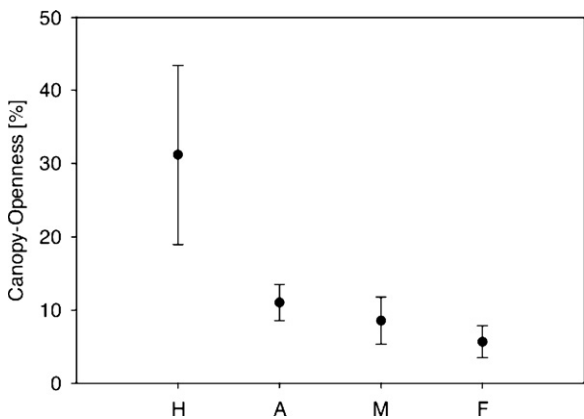

Fig. 6. Canopy openness of the regeneration stages (H, A, and M) and the old-growth forest (F) including mean values and standard deviations.
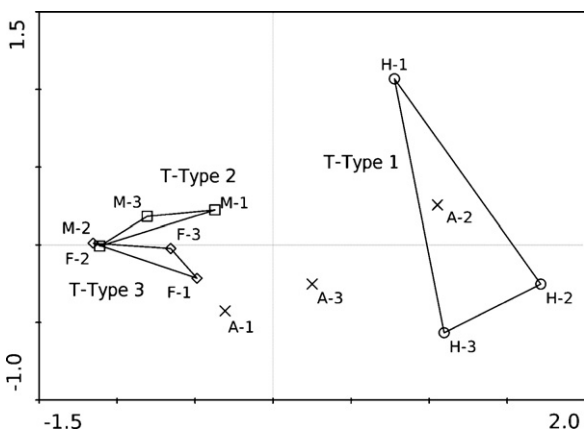

Fig. 7. Non-metric multidimensional scaling showing beetle species composition. Sites belonging to the same class of annual temperature dynamics are connected by convex hulls. As no temperature dynamics classes could be attributed to A-2 and A-3 the A-sites are missing a convex hull. The final stress of this NMDS solution was 0.05.

The first CCA ordination axis showed a highly significant relationship between the T-Types and the beetle community composition. As with the vegetation, there was a very significant relationship for T-Type 1 between the high temperatures in summer and the beetle community composition in the "summer warm" sites of T-Type 1 (H-1, H-2, and H-3) ($p = 0.006$). This ordination result explained 28.5% of the beetle community variation.

Explaining the beetle community composition via a short-cut path from structural variables to beetle pattern, 25.3% of the overall variability in the beetle community were covered, showing a highly significant first ordination axis ($p = 0.010$). From the structural variables only canopy closure showed a significant relationship to the beetle composition.

In the canonical correspondence analysis of T-Type data with vegetation species as explaining variables, five species proved to be significant: *Sloanea guianensis* (sloaguia), *Matayba cristae* (matacris), *Garcinia gardneriana* (garcgard), *Trichilla* spec. (tric) and *Vochysia bifalcata* (vochbifa). These five species explained 99.8% of the variability in T-Type data on a highly significant ordination axis ($p = 0.006$).

By manual forward selection it could be shown that there was a highly significant relationship between the increased temperatures in summer (T-Type 1) and the vegetation species composition in the "summer warm" T-Type 1 sites (H-1, H-2, and H-3) ($p = 0.002$). This correlation explained 25.4% of the overall vegetation variability.

4. Discussion

4.1. Classification

The fact that the mean monthly temperature decreased with forest age (see Fig. 1) could be attributed to the increasing canopy closure during the regeneration process (see Fig. 6). Due to the low vegetation cover the early regeneration stages could warm up in early summer much faster than the closed later regeneration stages.

A high canopy closure is known to even out temperature conditions in closed forest stands, including the investigated old-growth F-stages. It results in decreasing variance in temperature as well as decreasing maximum temperature (Pearson et al., 2002), which in turn leads to reduced soil temperature and its variance with increasing leaf area (Guarituaga and Ostertag, 2001). Decreasing canopy openness along the chronosequence, even between stages M and F resulted in a significant increase of the mean portion of shade tolerant species (Meyer, 2009).

The three clusters, which were built as a result of hierarchical classification (see Fig. 2), showed to be consistent over different methods of agglomeration (Ward's method, complete linkage, single linkage, centroid linkage, and average linkage). Cluster 1 combined all the initial stages (H-1, H-2, and H-3) with high temperatures in the leaf litter especially in the summer months. Old-growth forest sites with decreased mean monthly temperature, especially in summer, were joined in cluster 3 (F-1, F-2, and F-3). Finally, all intermediate stages (A-1, M-1, M-2, and M-3) could be found in cluster 2 for which the temperature dynamic curves were situated somewhat between the initial H- and the old-growth F-stages (see Fig. 1).

Thus, with respect to the mean monthly temperature dynamics, the clusters from hierarchical classification were in perfect concordance with the a priori classification, which reflected the age of the regeneration stages. Canopy openness, which showed significant differences between all regeneration stages, confirmed the clusters.

The heatmap in Fig. 2 showed that the temperature values in summer (03.2007–07.2008) had a large influence on the result of the cluster analysis. So cluster 1 could be addressed as a group of sites which exhibited very high temperatures in the summer

months and thus were called "summer warm" sites. Accordingly cluster 3 could be addressed as the "summer cold" sites whereas cluster 2 joined sites with a moderate annual temperature dynamics within the leaf litter. As the accumulated temperature sum has an important effect on arthropod larval development (Ratte, 1984) it was obvious that the type of temperature dynamic may show a strong correlation to the beetle community composition depending on the species specific phenology (e.g. Jensen, 1990; Lapointe, 2001; Walker, 1981).

It was remarkable that all the replicates from the regeneration stages could be found within a small range of dissimilarity in the dendrogram resulting from the cluster analysis. This suggested that the intra group variance within the clusters was smaller than the inter group variance between the clusters of temperature dynamics. The results of the according repeated measures ANOVA on the mean monthly temperatures with clusters as fixed factors demonstrated that the temperature dynamics could significantly be distinguished for the T-Type classes except for T-Types 2 and 3. Thus the mean monthly temperature decreased significantly with regeneration, a fact already observed by Fetcher et al. (1985).

The highest membership for the three temperature dynamic classes was in agreement with the results from hierarchical classification (see Table 3). The overall classification result reflected the a priori class assignment of the investigation sites to the regeneration stages and could be interpreted in an ecologically plausible way. Thus, the memberships from fuzzy classification could be assessed as a statistically robust result which could reasonably be integrated in an ecological effect analysis.

4.2. Effect analysis

The steps of the effect analysis process are discussed below with respect to the statistical properties. Additionally an ecological interpretation of the results is given. This allows for the verification of the statistically modelled effect chain and a development of an ecologically causal interpretation. Fig. 8 compiles the results from the effect analysis according to the conceptual model structure of ecological causality.

In the NMDS analysis the results of the vegetation data species composition showed a strong correlation to the temperature dynamic classes and the related a priori classification, representing the age of the investigation sites (see Fig. 7). The solution showed a small final stress (0.07) which could be considered as a good value according to Anderson (2003) and Kruskal and Carmone (1973). This confirmed that there was a strong relationship between the vegetation communities and the microclimatic conditions, especially in summer. Although the causal direction of this relationship could not be inferred from this result, according to the initial model structure it was assumed that vegetation had a stronger influence on microclimatic conditions than vice versa. It is known that microclimatic conditions, especially light availability in later successional stages, have an important influence on vegetation dynamics also (Whitmore, 1989). There was already evidence for this fact within the data, as a significant increased portion of shade tolerant species in the F-stages was found by use of a functional type analysis, which also showed a high correlation to the decreasing canopy openness (Meyer, 2009).

Due to the model structure it was assumed that the influence of vegetation on microclimatic conditions is mediated through structural variables determined by the vegetation itself. Although the eigenvalue of the first ordination axis was rather low ($\lambda = 0.042$) the ordinations axis was highly significant and the vegetation composition could explain almost all of the variability in the structural data (see Fig. 8). This result revealed that there was a strong and significant relationship between vegetation species composition and the structural variables. By the use of
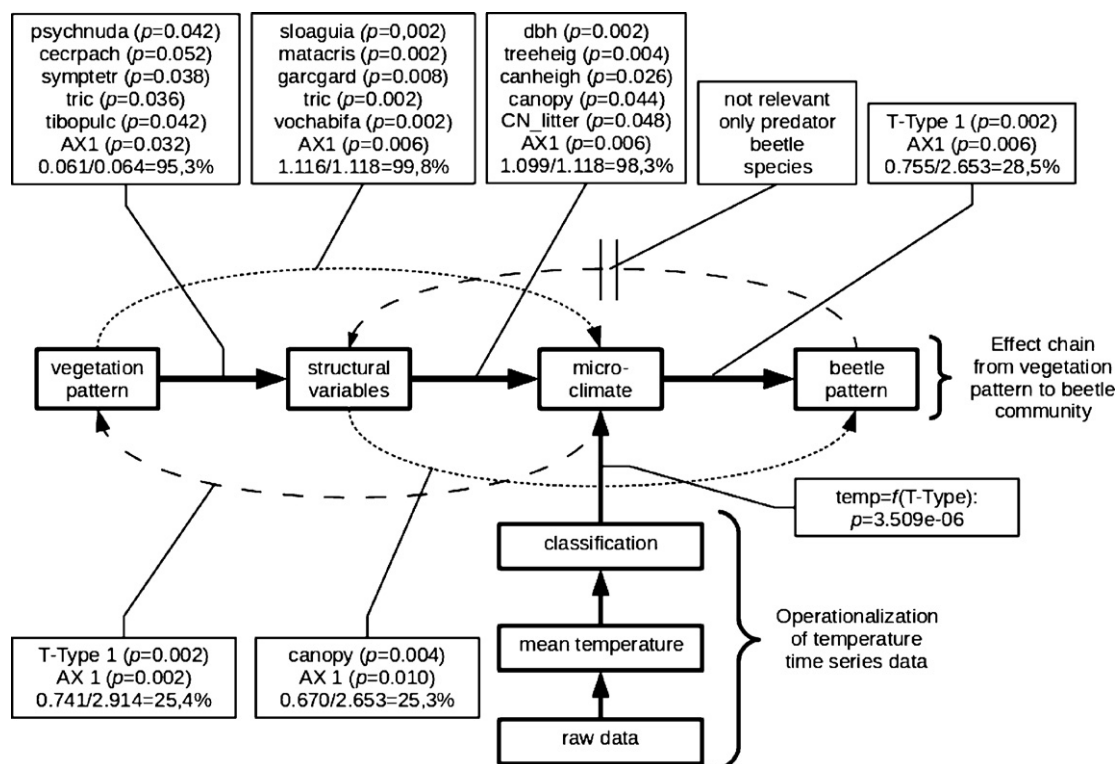

Fig. 8. Empirical effect chain from vegetation pattern to beetle community including the structural concept of operationalization of temperature time series data. *p*-Values are given for the first ordination axis (AX 1) as well as for the significant variables from manual forward selection (Monte-Carlo permutation tests with 499 permutations under reduced model). For the selected variables conditional effects from forward selection are given. The percentage of variability explained was derived from the ratio of the sum of all canonical eigenvalues divided by the sum of all unconstrained eigenvalues. Direct effects are indicated by bold arrows, short-cut effects indicated by dotted arrows, feedback effects indicated by dashed arrows (temp = mean monthly temperature, for species abbreviations see text).

forward selection five tree species could be identified to be significant predictors for the structural data: *P. nuda* (psycnuda), *C. pachystachya* (cecrpach), *S. tetranda* (symptetr), *Trichilla* spec. (tric), *T. pulchra* (tibopulc). These species are representing pioneer species, producing high amounts of leaf litter, like *T. pulchra*, as well as late secondary species, like *P. nuda* which is described as a shade-tolerant species (Reitz, 1974).

There is evidence that a changed vegetation composition changes the structure of the leaf litter in tropical forests. We think this is obvious as different tree species have leafs that are different in chemical characteristics as lignin and nutrients, leading to different decomposition rates (Schmidt et al., 2008; Xuluc-Tolosa et al., 2003). Zou et al. (1995) found no differences in leaf litter rate and annual leaf-fall rate between 50 year old secondary forest and mature forest, which showed that there were no differences in above ground net primary productivity. Nevertheless they found higher ground litter biomass in the mature forest during the wet season and thus concluded that the decomposition is faster in the secondary forest. Although there are clearly differences in the abiotic environmental conditions between secondary and mature forests influencing the decay rates, it could be shown that the litter structure (leaf chemistry) has a significant influence on the decay rates also. La Caro and Rudd (1985) found that differences in leaf decay rates between pioneer species and climax species was correlated with lignin and fiber content of leaf litter (Zou et al., 1995).

A very large amount of variability in the T-Type data could be explained by the available structural data (see Fig. 8). Diameter at breast height (dbh), tree height (treeheig), height of the canopy (canheigh), canopy closure (canopy) and the litter C/N ratio (CN_litter) proved to be significant predictors for the T-Types. The first ordination axis was highly significant, so it could be assumed that there was a significant relationship between the structural variables and the resulting microclimatic conditions, represented by the T-Types. This assumption is supported by several studies, which showed that litter composition has a significant influence on the microclimatic conditions within the litter. Altered CN-ratio corresponds with altered litter decomposition (Enriquez et al., 1993; Perez-Harguindeguy et al., 2000) and altered litter decomposition corresponds with changed micro-climate (Fierer et al., 2005; Moore, 1986). La Caro and Rudd (1985) found that leaf litter decay rates change during regeneration. We assume that this leads to differences in litter architecture which, in turn, affects microclimate within the litter layer (Kaneko and Salamanca, 1999; Klemmedson, 1992).

As with the vegetation analysis the final stress of this NMDS solution (0.05) can be considered as good. The intermediate T-Type 2 seemed to be a subclass of a united T-Types 2 + 3. This insufficient separation of T-Types 2 and 3 was already shown on the basis of species density and composition (Hopp et al., 2010). It reveals that secondary forests of 35–50 years are already very similar to old-growth forests concerning the most important variables affecting the microclimate in the litter layer, such as canopy openness.

In comparison to the preceding steps of analysis only a small amount of variability in the beetle species variability could be explained by the T-Type variables, but the high significance of the first ordination axis demonstrated the ecological relevance of the relationship between the T-Types and the beetle community pattern (see Fig. 8).

The small amount of variability in the beetle community composition explained by the T-Type variables suggested that the relationship between structural variables, microclimatic conditions and beetle community pattern maybe different from the conceptual model structure. Structural variables could have a direct impact on the beetle species bypassing the dependence via a microclimatic parameter. There is already evidence for this hypothesis as Hopp et al. (2010) showed that beetle species

community is correlated to litter volume. They assumed that the increment of litter allows the coexistence of a larger amount of beetle species mediated by an increase of habitable niches and food resources. This hypothesis was tested by explaining the variability in beetle community composition by the structural variables via a short-cut path (see Fig. 8). The analysis revealed that again only 25% of the overall variability in beetle pattern could be explained and only canopy closure showed a significant relationship to the beetle composition. From this result it was concluded that the short-cut relationship exhibits no better explanation then the mediated path via the microclimatic conditions, particularly as the short-cut path is difficult to interpret in an ecological way and canopy closure is included in the direct path anyway. So the mediated path is favoured here. Whether the amount of explained variance in the beetle species data could be increased by explaining beetle variability with T-Types and structural variables in a parallel way, thus altering the model structure from single-chain to a multi-path model, was not tested in this study.

Explaining the T-Types with the vegetation pattern via a short-cut relationship showed that a highly significant ordination axis with a reasonable eigenvalue ($\lambda = 0.726$) could be obtained and that a very large amount of the variability in T-Types could be explained by the vegetation pattern (see Fig. 8). Five significant tree species as predictors (*Sloanea guianensis* (sloaguia), *Matayba cristae* (matacris), *Garcinia gardneriana* (garcgard), *Trichilla* spec. (tric) and *Vochysia bifalcata* (vochbifa)) were sufficient to obtain this result. So, using this short-cut the variability in T-Type data was slightly better explained than via the structural parameters ($95\% \times 98\% = 93\%$).

This result brings up the question, whether the microclimatic conditions in the litter were more directly related to the vegetation than via structural variables. If we had measured air moisture and temperature outside the litter this could have been reasonably assumed for litter, as litter has no influence on the outside conditions. But instead the canopy closure, which is a structural variable again, would have a strong influence on the conditions inside the vegetation stand. As with the short-cut relationship between structural variables and the beetle community pattern, we think, that from an ecological point of view, it is not reasonable to relate the microclimatic conditions to the vegetation without a path via a structural variable. Statistically this can be done, but ecologically this bare correlation makes little sense as the relationship cannot be interpreted in an ecological way. Over-fitting as a reason for the very high amount of explained variance could be excluded because we used manual forward selection and subsequent reduction of dimensionality.

In the analyses it could be shown that not only T-Types could be explained by vegetation pattern but vice versa vegetation composition could also be explained by the microclimatic condition T-Types. The highly significant first ordination axis (see Fig. 8) suggested that the relationship was a feedback loop, already described in literature. Pearson et al. (2002) and Foster and Janson (1985) found that germination rates of pioneer and climax species seeds depend on light and temperature conditions. The germination of small-seeded plants is fostered by a high far red ratio within the light spectrum, found in open sites or forests with high canopy openness. Instead temperature fluctuation has a significant impact on large-seeded species. Also soil depth of buried seeds or litter quantity, which seems to be correlated with reduced canopy openness and forest age, may reduce far red ratio and therefore reduce germination of small-seeded plants (Tester and Morris, 1987). Still the amount of explained variation (see Fig. 8) in this direction of the relationship was small compared to the variation explained by the other direction. Accordingly, the feed-forward process via the structural variables can be assumed to be far more important in this modelling context.

5. Conclusions, implications and outlook

5.1. Conclusions

By the results in this study the initial hypothesis of an ecological causal effect chain from vegetation patterns via structural parameters and microclimatic conditions to beetle species composition was clearly supported. There was reasonable evidence that varying vegetation composition (resulting from variable historical events, nutrient conditions, etc.) results in varying structural characteristics inside the vegetation stand and the associated leaf litter (like canopy closure, leaf litter composition, leaf litter amount, etc.) (Denslow and Guzman, 2000). The changed structural parameters can alter the microclimatic conditions within the leaf litter (mainly temperature dynamics) and subsequently the differences in microclimatic conditions have a strong influence on the leaf litter beetle community within the forest regeneration sites. These results are particularly important regarding the increasing interest and suitability of using beetles for conservation purposes also in tropical regions (Anderson and Ashe, 2000; Didham et al., 1998; Grimbacher and Catterall, 2007).

The fact that microclimatic conditions can be extremely limiting factors for small animals like most arthropods has been shown in a number of studies (Didham et al., 1998; Kaspari, 1993; Nadkarni and Longino, 1990; Nicolai, 1986; Rodgers and Kitching, 1998). Thus, from our results we conclude that the leaf litter beetle communities in the investigated forest regeneration stages in the Atlantic rainforest of the Mata Atlântica are structured by vegetation patterns via structural characteristics and microclimatic parameters.

Nevertheless, the authors are aware that additional factors have a strong influence on leaf litter composition, as e.g. prey density or substrate quantity (Hopp et al., 2010). Analysis of further factors and their importance for the local leaf beetle community is still in progress and the results will be published elsewhere.

5.2. Implications

We think that these results have important implications for arthropod species conservation as they show that the probability of conserving or re-establishing old growth leaf litter beetle populations and communities in regeneration sites in the Mata Atlântica can be increased by maintaining and restoring suitable vegetation, structure and microclimatic conditions. Due to the strong susceptibility of leaf litter beetles to these parameters, this becomes an increasingly important task in the light of climate change and its influence on local rainfall patterns and temperature regimes.

Furthermore, the findings confirm the usefulness of management actions to support the restoration process like tree planting to accelerate vegetation succession (mainly native pioneer species and species from mid age stages) (Aide et al., 2000; Holl et al., 2000; Vieira et al., 1998), improving structural properties (e.g. bringing out litter) (Koivula et al., 1999; Magura et al., 2005; Sayer et al., 2010) or direct manipulation of microclimatic conditions (e.g. "artificial" shading by seeding of woody shrub species) (Engel and Parrotta, 2001; Holl et al., 2000; Ramos and del Amo, 1992).

However, it is important to note that these assumptions are based on results of leaf litter beetles, which showed to recolonize rapidly under suitable conditions. Taxa differing in mode of life and reproduction cycles may exhibit different regeneration pattern as shown for ants sampled on the same study sites (Bihn et al., 2008) and accordingly different dependencies upon environmental parameters.

5.3. Correlation and causality

It has long been debated whether statistical correlation can tell anything about causality (Holland, 1986) and a number of techniques have been developed to illuminate this relationship, like covariance structure analysis or structural equations (Jöreskog, 1970, 1973; Keesling, 1972). Nevertheless, with those techniques it is not straightforward to analyse the relationship between a number of multivariate data sets like the vegetation composition and the leaf litter beetle communities in this study. Although there are multivariate techniques to achieve this goal, e.g. canonical correspondence analysis (ter Braak, 1986), co-correspondence analysis (ter Braak and Schaffers, 2004) or co-inertia analysis (Dolédec and Chessel, 1994; Dray et al., 2003), these methods are not optimal to test an effect model with mediator variables between these representations.

Usually details about causal links are not available when studying a complex interaction system for which only little background knowledge can be provided, like in this study. But dependencies generated from associational information alone which are not supported by causal links are considered as odd or spurious (Granger, 1969). To overcome this dilemma, in the presented study a simple model was built around generally accepted causal information which gives an interpretation that is consistent with actual observations as well as prior information about the processes (Pearl, 2000). Additionally, by ecological validation it was assured that each step in the causal inference process included in this study meant more than a bare correlation.

Although we reduced the number of possible feedback loops within the model structure (e.g. by assuming that there is no herbivory effect on the vegetation and no decomposer activity by the beetle species analyzed) there are some possible short-cut effects left (e.g. litter as feeding habitat for beetle prey organisms). Up to now these dependencies prevent the model from having strict Markovian properties and to convert it to a directed acyclic graph (DAG). To come towards the necessary Markovian compatibility between the DAG and the empirical probability distributions (Pearl, 1988), further work on this aspect will be conducted in the future.

Acknowledgements

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