

SHORT COMMUNICATION

Consequences of a severe drought associated with an El Niño-Southern Oscillation on a light-attracted leaf-beetle (Coleoptera, Chrysomelidae) assemblage in Borneo

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The El Niño-Southern Oscillation (ENSO) phenomenon occurs irregularly and supra-annually at intervals of 2–7 y (Hughen *et al.* 1999, McPhaden *et al.* 2006), and is the strongest source of supra-annual climate fluctuation (Hughen *et al.* 1999, Philander 1990). During ENSO, the interior of the South-East Asian tropics, which is characterized by constant high temperature and no distinct dry season, experiences severe drought (Walsh 1996).

In recent decades, the impacts of ENSO-related events on terrestrial ecosystems have become global concerns (Holmgren *et al.* 2001, McPhaden *et al.* 2006). Several studies have demonstrated the effects of severe droughts associated with ENSO on the abundance and species composition of living organisms in the South-East Asian tropics (Bebber *et al.* 2004, Delissio & Primack 2003, Harrison 2001, Inoue *et al.* 1993, Itioka & Yamauti 2004, Nakagawa *et al.* 2000, Nakamura *et al.* 1990, 2001; Nishimura *et al.* 2007). A smaller number of studies have compared temporal changes in species composition during a period without drought to those during a period of the same length with drought, and analysed the similarities between them.

The purpose of this paper was to determine the relative significance of a 1998 ENSO-related drought compared with normal conditions before the drought in influencing species richness and species composition of Bornean chrysomelid assemblages across a 5-y period (1994–1999).

The study was conducted in a lowland dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia

(4°2'N, 113°50'E, 150–200 m asl). Mean annual temperature is *c.* 26°C (Nakagawa *et al.* 2000). Monthly rainfall is rarely less than 100 mm, and the average annual rainfall is 2751 mm y⁻¹ over 17 y (Ichie *et al.* 2004). A severe drought associated with the 1997–1998 ENSO occurred from January to March 1998 (Nakagawa *et al.* 2000). Cumulative monthly rainfalls during the first quarter of 1998 were consistently less than 60 mm, and the total rainfall in that period was approximately 24% of the mean rainfall from January to March in the last 14 y (Nakagawa *et al.* 2000).

At the study site, three light-traps were placed on a tree tower for four consecutive days during the new-moon period (Kato *et al.* 1995). All insects collected were kept at Forest Research Centre of Sarawak in Kuching. We sorted out almost all of the chrysomelid beetles (Coleoptera, Chrysomelidae) from the light-trap collections obtained from February 1994 to July 1999. Light-trapping was not performed during September 1997 to March 1998, during which there was a 3-mo-long drought. The total number of specimens collected in three light traps during the four consecutive days of each new-moon period was considered the 'monthly' catch.

We determined temporal variation in the number of species in the monthly catches, and that in the proportions of species loss in the monthly catches. We calculated the proportion of species loss (P_i) as follows:

$$P_i = L_{(i+t)}/N_i,$$

where N_i was the number of species in the monthly catch of the i th month and $L_{(i+t)}$ was the number of species that, of the N_i species, disappeared in the monthly catch of the $(i+t)$ th month. In order to evaluate the degree of

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change (decrease) in the number of species across the drought, we compared the species-loss proportion across the drought with the species-loss proportions during the periods not across the drought, i.e. pre- and post-drought periods. Here we assigned 8 to t , which was the minimum interval between the time of the last monthly catch before the drought, across the period when no trapping took place, to the time of the first monthly catch after the drought. By determining the position of the only species-loss proportion across the drought in the frequency distribution of the other 44 species-loss proportions during non-drought periods, we attempted to evaluate the deviation or extremity of the species loss across the drought. We also calculated the species-loss proportions by assigning 12 to t to check effects caused by different intervals and possible annual cycle inherent in chrysemelid population fluctuations.

We quantified the magnitude of changes in species composition in the non-drought period and that in the period during which the drought occurred, by using similarity indices (Sørensen and two types of NNESS). The Sørensen index is based on presence-absence data in the sample, and its value ranges from 0 (no common species) to 1 (identical species composition). The new normalized expected species shared (NNESS) index is a modified version of NESS (Trueblood *et al.* 1994). Both are based on the expected species shared between two distinct and random draws of a particular size (number of individuals, represented as parameter m) from a sample (Grassle & Smith 1976). In the calculation of NNESS, m individuals are replaced before the second random draw (Trueblood *et al.* 1994). The NNESS value ranges from 0 (no common species) to 1 (samples are random from the same assemblage). The index value varies depending on parameter m , becoming more sensitive to rare species as m increases. Because comparisons of the index values between the two periods are important, rather than exact determination of the absolute values, our analyses were based on the two extremes of NNESS, $\text{NNESS}_{m=1}$ and $\text{NNESS}_{m \text{ max}}$ ($m \text{ max}$: the highest value of a pair, as

per Brehm & Fiedler 2004); the former analysis is biased against abundant species, and the latter is biased against rare species. For the calculations, we used the COMPAN program (<http://www.es.umb.edu/edgwebp.htm>). The similarity indices were calculated based on pairs of monthly catches in pre-drought period, considered as 'pre-drought similarity', and in the period during which the 1998 drought occurred, as 'across-drought similarity' (Figure 1). The interval between two catches for the index calculations was 23 mo, which was adopted to maximize the replications of index under a fixed interval (Figure 1). Thus, similarity indices were calculated using 21 and 16 pairs of monthly catches for pre-drought and across-drought periods, respectively (Figure 1). To confirm whether different intervals cause different results from the result for 23-mo interval, we calculated similarity indices using all other possible time-intervals that contain at least 10 pairs of monthly catches for pre- or across-drought period. In total, 17 time-intervals (17–22 mo and 24–34 mo) were used for the calculations. To compare the index values between pre- and across-drought periods, we performed Wilcoxon two-sample test using Proc NPAR1WAY in SAS.

We caught 17 336 individuals in total representing 304 species. The number of species in a monthly catch varied from 19 to 89 throughout the study period (Figure 2). The mean number of species during the first collection period immediately following the drought was 27.7 (April–June 1998), while that of all other periods was 59.0.

The proportion of species loss ranged between 0.20 and 0.57 during pre- and post-drought periods, with the mean being 0.40, while the only species-loss proportion across the drought was 0.78 (Figure 3). The frequency distribution of the 44 arcsine-transformed values other than that across the drought was not significantly different from the expected frequencies of the normal distribution (mean = 0.41, SD = 0.095; $W = 0.99$, $P = 0.912$, Shapiro–Wilk test), suggesting that we could approximate the frequency distribution of the 44 species-loss proportions to the normal distribution with the mean

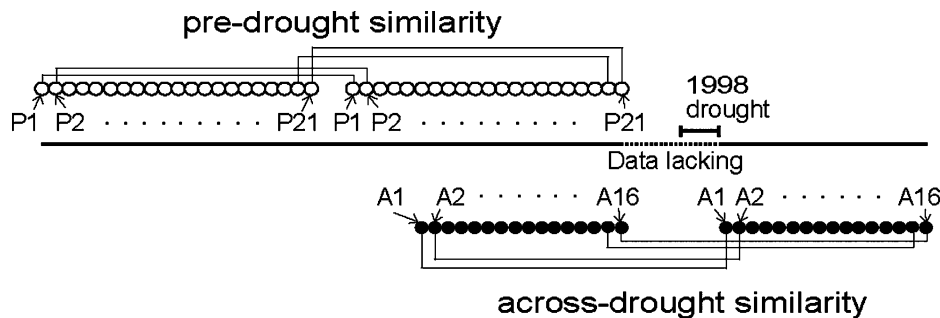


Figure 1. The design for analysing similarity indices for pre- and across-drought periods. A circle represents a monthly catch. The interval between two catches of a pair for calculation of an index value was 23 mo. Each type of the similarity index was calculated for 21 pairs for the pre-drought period and 16 pairs for across-drought period. The index values were compared between pre- and across-drought periods for each type of index.

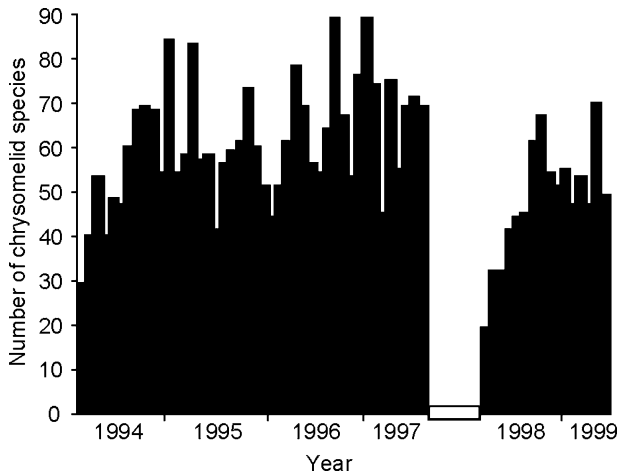


Figure 2. Temporal variation in the monthly catches of chrysomelid species during the study. The open box on the horizontal axis indicates the period of no data.

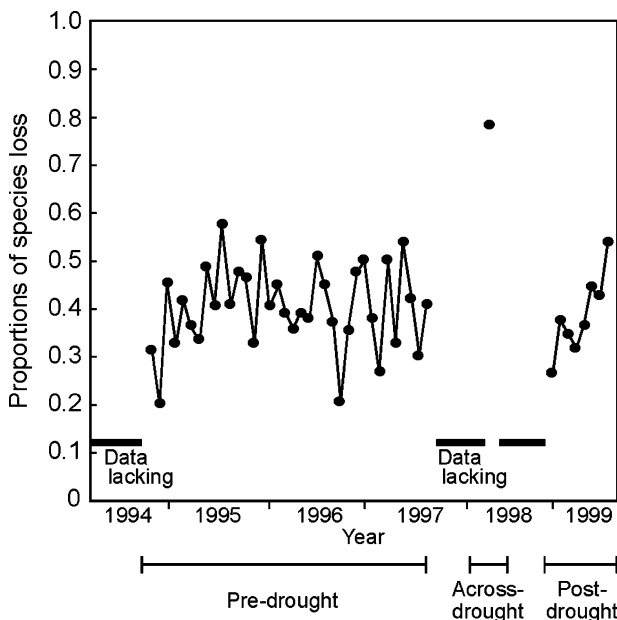


Figure 3. Temporal variation in the proportions of species loss during the pre-, across-, and post-drought periods.

and SD mentioned above. The only proportion across the drought period deviated from the mean of the 44 proportions at approximately 5.12 times the SD of the 44 proportions, on the arcsine-transformed base. Assuming that arcsine-transformed species-loss proportions obey to the normal distributions estimated from the frequency distribution of the 44 proportions, the probability that a proportion might deviate at 5.12 times SD from the mean was expected to be smaller than 0.00003%. This suggests that the observed species-loss proportion across the drought period was extremely high. There was no substantial difference if different time intervals were used

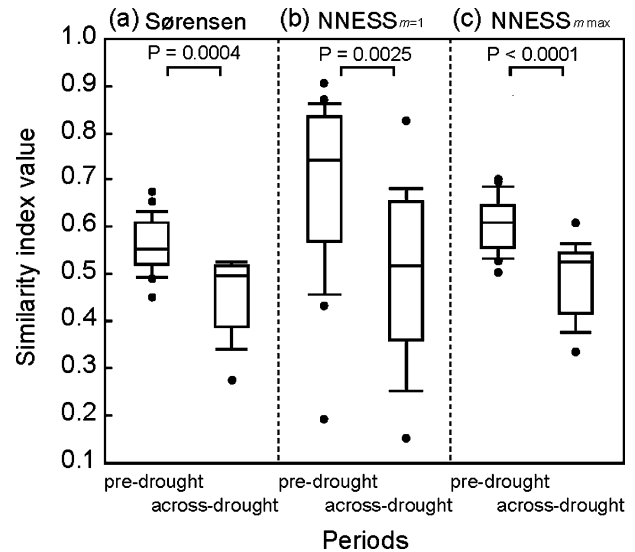


Figure 4. Box-plots of the values of the (a) Sørensen, (b) $NNESS_{m=1}$, and (c) $NNESS_{mmax}$ indices for the pre-drought similarity (left side of each column) and for the across-drought similarity (right side of each column). The five horizontal lines of each box plot represent 10th, 25th, 50th, 75th and 90th percentiles, respectively. All individual values above the 90th and below the 10th percentile are plotted (closed circles).

(mean: 0.39 for non-drought periods; mean: 0.68 for across drought period, $t = 12$).

Of the 274 species caught before the drought, approximately 47% (129 species) were not caught after the drought. In addition, approximately 19% (30 species) of the 166 species caught after the drought appeared for the first time in the post-drought period.

The Sørensen ($S\phi$), $NNESS_{m=1}$ (M1), and $NNESS_{mmax}$ (MM) for the across-drought period were significantly lower than those for the pre-drought period ($S\phi$; $z = -3.88$, $P = 0.0004$, M1; $z = -3.02$, $P = 0.0025$, MM; $z = -4.14$, $P < 0.0001$ for 23-mo intervals, Wilcoxon two-sample tests, Figure 4), suggesting that species composition changed at a higher rate during the across-drought period than during the pre-drought period. Similar significant difference was detected for almost all the comparisons of different intervals. For only two (M1 for 28- and 30-mo intervals) of the 81 comparisons, the difference was not significant, but the mean score was high for the pre-drought period.

Our results indicate that the number of species of light-attracted chrysomelid at the study site remarkably decreased after the drought associated with the 1997–1998 ENSO (Figure 2), and that the degree of species loss across the drought period was extremely high, compared with usual levels of species loss during the non-drought periods (Figure 3). These suggest that ENSO-related severe droughts, which occur irregularly and supra-annually, substantially influence the chrysomelid populations, and that they could cause drastic local loss of species. The

disappearance of some species after the drought probably reflects a drastic decrease in their populations or even local extinction caused directly or indirectly by the drought.

Although the precise causal factors of lower post-drought chrysomelid species numbers are difficult to specify at present, a shortage of food resources brought about by increased leaf-shedding during the drought period (Harrison 2005, Itioka & Yamauti 2004) is likely to be one critical causal factor at our study site. Predation pressure by parasitoids (Van Bael *et al.* 2004), egg hatchability, and adult residence time (Inoue *et al.* 1993, Nakamura *et al.* 1990) may also change and subsequently affect chrysomelid population growth during severe drought.

The recovery of the total number of chrysomelid species approximately 4 mo after the end of the drought does not reflect a recovery of all populations observed in the pre-drought period. Approximately half of all species collected at least once throughout the pre-drought period were not caught after the drought, probably due to local extinction. The comparisons of the similarity index values suggested that species composition changed more greatly during the period across the severe drought than during the non-drought periods. These results indicate that severe ENSO-related droughts could have a major impact on the species composition of chrysomelid assemblages by heavily suppressing populations of some species, while providing opportunities for other species to colonize areas from which they previously were excluded.

The present study suggests that ENSO-related drought has a great influence on the structure of chrysomelid assemblages in aseasonal areas. Considering that the frequency and strength of ENSO-related events have increased in recent decades (Guilderson & Schrag 1998, Harrison 2001, Salafsky 1998) and are predicted to increase more in coming decades (Timmermann *et al.* 1999), future intensive investigations should focus on the effects of ENSO-related drought on the biodiversity and ecosystems of tropical forests.

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