LETTER

Parallel responses of species and genetic diversity to El Niño Southern Oscillation-induced environmental destruction

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Abstract

Species diversity within communities and genetic diversity within species are two fundamental levels of biodiversity. Positive relationships between species richness and within-species genetic diversity have recently been documented across natural and semi-natural habitat islands, leading Vellend to suggest a novel macro-ecological pattern termed the species-genetic diversity correlation. We tested whether this prediction holds for areas affected by recent habitat disturbance using butterfly communities in east Kalimantan, Indonesia. Here, we show that both strong spatial and temporal correlations exist between species and allelic richness across rainforest habitats affected by El Niño Southern Oscillation-induced disturbance. Coupled with evidence that changes in species richness are a direct result of local extirpation and lower recruitment, these data suggest that forces governing variation at the two levels operate over parallel and short timescales, with implications for biodiversity recovery following disturbance. Remnant communities may be doubly affected, with reductions in species richness being associated with reductions in genetic diversity within remnant species.

Keywords

Biodiversity, El Niño, extirpation, forest fire, genetic loss, recovery, species loss, species-genetic diversity correlation, time scale.

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INTRODUCTION

The well-established theory of island biogeography invokes a balance of colonization and extirpation (local extinction) for determining community diversity (MacArthur & Wilson 1967). Classic island models of population genetics invoke gene flow (from migration) and genetic drift as regulating influences on genetic diversity (Wright 1940). Small habitat patches, for example, contain small populations and communities so that both alleles and species are expected to be lost due to the effect of drift. However, immigration may counter this effect and introduce new genes and/or species. Although the factors that influence species or genetic diversity are well studied, little is known about simultaneous responses of both to variable site-specific characteristics (Vellend & Geber 2005). Recently, Vellend (2003) introduced the species-genetic diversity correlation (SGDC) as a measure of parallel responses in these two fundamental levels of biodiversity; Island Biogeography

Theory (MacArthur & Wilson 1967) was invoked as a possible governing mechanism. In a second study (Vellend 2004), farmed plots that had been recolonized by surrounding woodland vegetation over the past 70 years were censused and found to have reduced diversity of both species and genes of forest herbs relative to primary forest. The exploration of common processes is now under way (Vellend & Geber 2005; Vellend 2005).

Here, we ask whether a system undergoing extreme habitat disturbance shows evidence for such common mechanisms operating at the (same) rapid timescale; if so, this would have implications for biodiversity recovery following such disturbances as well as shining light on common mechanisms governing these two scales of diversity.

El Niño Southern Oscillation (ENSO)- and human-mediated (Siegert *et al.* 2001) forest fires greatly increase extirpation rates of butterflies and other invertebrates (Harrison 2000; Cleary 2003; Cleary & Genner 2004) and

may be expected to decimate remaining populations. Genetic drift due to, and following, such bottlenecks is expected to decrease genetic diversity, suggesting the SGDC may hold in these non-equilibrial situations. The 1997–1998 ENSO-induced forest fires resulted in destruction of vast tracts of rainforest throughout Borneo (Siegert *et al.* 2001), with over 5 million ha burning in the province of east Kalimantan alone (Cleary 2003). We chose butterfly assemblages as biodiversity indicators (Dennis 1993; Fuller *et al.* 1998; Howard *et al.* 1998; Parmesan *et al.* 1999; Cleary 2004) and measured species richness and a genetic analogue, allelic richness, both spatially and temporally.

METHODS

Spatially (Fig. 1), each sample was in a 450-ha landscape: three unburned isolate landscapes surrounded by burned forest and three landscapes within the burned forest in east Kalimantan sampled in 2000. Temporally, we sampled one 450-ha plot (B2) in 1997 prior to the wildfires, and then subsequently in 1998, 1999, 2000 and 2004. In total 26 162 individuals and 419 butterfly species were sampled.
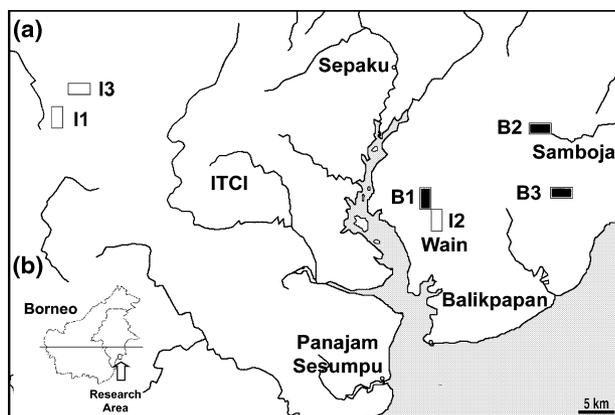
Study area

All six landscapes in the Balikpapan–Samarinda region of East Kalimantan, Indonesia were located in the 5.2 million ha of East Kalimantan, that burned during the 1997–1998 ENSO event (Siegert *et al.* 2001) and is now a habitat mosaic dominated by secondary (burned) forest with remnant unburned isolates. The sampled isolates (areas of unburned habitat surrounded by burned forest) include the two largest remaining contiguous areas of unburned lowland forest within the affected area and are therefore probably

Figure 1 (a) Research area with locations of sampled landscapes within the Balikpapan–Samarinda region of east Kalimantan, Indonesia. Shaded landscapes are burned and unshaded landscapes are unburned. (b) Research area on Borneo.

crucial for recovery in the area. The unburned isolate landscapes were not directly affected by the 1997–1998 ENSO event, but were completely surrounded by forest that burned during this event and although unburned were subjected to pronounced drought stress (Slik 2004). The I1 (unlogged primary: 0°58′ S, 116°19′ E) and I3 (logged in 1993–1994: 0°57′ S, 116°21′ E) landscapes were located in a large (108 000 ha) unburned isolate located in part of the International Timber Concessions Indonesia and adjacent Balikpapan Forest Industries concessions, including the Gunung Meratus Protected Forest Reserve (*c.* 30 000 ha). The I2 landscape (1°06′ S, 116°49′ E) was located in a small (3500 ha) unburned primary isolate that is all that remains of the Sungai Wain Protected Forest; 6500 ha of the original 10 000 ha burned during the 1997–1998 ENSO event. All these unburned landscapes were dominated by dipterocarp species, typical for intact lowland dipterocarp rainforest in Borneo (Yamakura *et al.* 1986).

The burned landscapes are not isolates, but rather representative of burned habitats within the 5 million ha area and include pristine forest that burned for the first time during the 1997–1998 ENSO event and forest that was partially burned during an earlier event. The burned landscape B1 (1°05′ S, 116°48′ E) burned for the first time during the 1997–1998 ENSO event and was located in the burned part of the Sungai Wain Nature Reserve. The burned landscape B2 (0°59′ S, 116°57′ E) was partially burned during the 1982–1983 ENSO event and severely burned during the 1997–1998 ENSO event; it was located in the Wanariset Samboja Research Forest. The burned landscape B3 (1°03′ S, 116°57′ E) was located in an area frequently affected by slash and burn agriculture along 30 km of the Balikpapan to Samarinda highway. None of the burned landscapes have been commercially logged although they may have been subjected to unrecorded illegal logging. During the 2000 surveys, grasses dominated B3 (especially *Imperata cylindrica*). Ferns (especially the cosmopolitan *Pteridium aquilinum*, Dennstaedtiaceae or bracken) and pioneer trees (e.g. *Macaranga gigantea*) dominated B1, and euphorb pioneer trees dominated B2 (especially *Macaranga* spp.). In Sungai Wain (B1) and Wanariset (B2) burned forests were characterized by networks of low-lying areas in swamps and river valleys, with high tree species diversity and climax species density, surrounded by higher-lying areas with low tree diversity and high pioneer abundance (Slik & Eichhorn 2003). In B1 and B2 the area occupied by these unburned networks was estimated to be 10.6% (B1) and 8.1% (B2) of the total area (K.A.O. Eichhorn, unpublished data).

Following Vellend (2003, 2004), we chose one species to assess variation in genetic diversity. *Drupadia theda* (Felder) is a rainforest lycaenid species typical of pristine and moderately disturbed forest, and was sufficiently abundant both to

enable enough individuals to be sampled for robust estimates of genetic diversity, and importantly, for the SGDC to be expected (Vellend 2005).

Sampling

Sampling took place within sites located within each *c.* 450-ha landscape. We chose to sample a very large area (450 ha) in order to capture the natural heterogeneity involved in the disturbance. During the spatial survey in 2000, each area sampled was assessed using a completely random sampling design.

Each site was located in the field with a compass and clinometer, and then georeferenced with a handheld GPS device (Garmin 12XL; Garmin Ltd, Olathe, KS, USA). For the temporal study, eight sites were sampled in 1997, nine sites each in 1998 and 1999, 21 sites in 2000 and 11 sites in 2004. In 2000, for the spatial study 16 sites were sampled in each landscape with the exception of B2 in which 21 sites were sampled. In each landscape sample sites were randomly allocated to grids on a map of the 450-ha study area (landscape). Within each site butterflies were sampled along a demarcated 300 m transect. It is difficult, if not impossible to accurately identify most Bornean butterflies on the wing so all encountered individuals were caught with nets and identified. Individuals were marked in order to avoid multiple observations of the same individual and subsequently released. Specimens of *D. theda* were killed immediately after which three legs were removed and stored in 96% ethanol. Each individual was assigned a unique code. Voucher specimens were preserved using silica gel and are deposited in the Zoological Museum of the University of Amsterdam. Sampling took place between 9:00 and 16:00 hours. Date of capture and location were noted for each individual. Butterflies were identified to species except in a few cases where it was not possible to identify beyond a species pair or species group (e.g. *Allotinus leogoron* and *Allotinus melos*). Such individuals were then considered to belong to the same species (*A. leogoron* in this case) as diagnostic characteristics (e.g. male genital characters) could not be determined in the field. For detailed descriptions of sampling, see Cleary & Genner (2004) and Cleary *et al.* (2004).

Molecular analysis

Genomic DNA was isolated from legs using a cetyltrimethyl ammonium bromide (CTAB) protocol (Hillis & Moritz 1990). Five microsatellite loci were used: DtC1, DtD10, DtE6, DtF6 and DtN10. All polymerase chain reaction (PCR) reactions were conducted in a total volume of 10 μL containing 1x PCR buffer (HT Biotechnology Ltd, Cambridge, UK), 1.25 mM MgCl$_2$, 0.1 mM of each dNTP, 0.3 mg mL^{-1} bovine serum albumin, 0.2 μM of each primer

(with F-primers IRD700 labelled), 0.2 U Taq Polymerase (HT Biotechnology) and *c.* 3 ng DNA. PCR reactions were carried out in PTC 100 Thermocycler (MJ Research, Waltham, MA, USA): 3 min denaturation at 94 °C, 40 cycles of 30 s at 94 °C, 30 s at 58 °C and 30 s at 72 °C, and a final extension of 5 min at 72 °C. PCR products were diluted 20 times, loaded on a 6.5% acrylamide gel, and run on a Li-Cor 4200 automatic sequencer, Li-Cor, Lincoln, NB, USA. To ensure scoring accuracy and consistency across gels, a locus-specific size standard made of PCR products of individuals with known genotypes was run at both sides of each gel, as well as a commercial size standard (50–350 bp, Li-Cor). In order to assure repeatability of observed patterns, PCRs were reconducted on *c.* 10% of randomly chosen individuals. A detailed description of the protocol is presented in Fauvelot (2005). Five specific nuclear microsatellite markers were scored for a total of 571 individuals.

Data analysis

Because of differing sample sizes from landscapes, rarefaction analysis was used with the Species Diversity option of the program PRIMER (Primer-E Ltd, Plymouth, UK) for species richness and with FSTAT, version 2.9.3 (Goudet 2002) for allelic richness (El Mousadik & Petit 1996). For comparisons of mean species richness estimates were based on 57 individuals per sample site. Estimates of allelic richness were based on 15 individuals per sample. Strength of associations between species and genetic diversity were tested using Pearson Product Moment correlation tests in Statistica 6.1 (Statsoft, Tulsa, OK, USA).

RESULTS

Rarefied species richness was highest in logged forest (I3) followed by unburned forest in I1 and once-burned forest (B1). Low levels of species richness were recorded in the unburned isolate (I2) and twice-burned landscape (B2, which lacked proximate unburned forest). The lowest species richness (67 species) was recorded in the severely degraded B3 and despite a large sampling effort ($n = 3200$ individuals) *Drupadia theda* was completely absent (Fig. 2a and Table 1). Temporally, species richness was highest in B2 during pre-ENSO 1997 sampling, lowest immediately after the fires in 1998, but had increased in 2004 (Fig. 2b and Table 1). Spatial and temporal patterns of species richness have been confirmed by ANOVA tests presented previously (Cleary & Genner 2004; Cleary *et al.* 2004). The loss of species in B2 directly after the 1997–1998 ENSO event was dramatic, with reduction from 216 species ($n = 1333$ individuals) observed in 1997 to only 43 species ($n = 1800$ individuals) observed the following year. Locally extirpated species included all Bornean endemics and
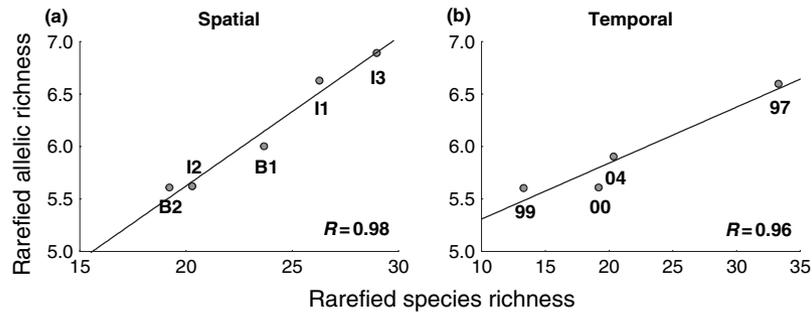
Figure 2 Relationship between mean rarefied species richness and mean rarefied allelic richness sampled: (a) spatially across five differentially disturbed landscapes; (b) temporally from 1997 to 2004 in the Wanariset Research forest B2 ($n = 57$ individuals/sample site and $n = 15$ individuals/sample). *Drupadia theda* was absent from B3 so that the data point corresponding to this landscape is not included in panel (a); it would theoretically fall at the origin.

Table 1 Summary results for each landscape

Variable	I1–00	I2–00	I3–00	B1–00	B2–97	B2–98	B2–99	B2–00	B2–04	B3–00
Number of individuals (total)	3200	3200	3200	3200	1333	1800	1800	4200	629	3200
Number of individuals (Msat)	220	41	73	25	35	2	15	87	30	
Total number of species	167	126	190	143	216	43	67	117	73	67
Mean species richness ($n = 57$ individuals)	26.3	20.3	29.0	23.7	33.3	9.1	13.3	19.2	20.4	17.4
Allelic richness ($n = 15$ individuals)	6.6	5.6	6.9	5.9	6.4		5.6	5.6	5.9	
Total alleles, DtN10	15	12	14	13	9	3	7	8	6	
Total alleles, DtF6	8	2	7	5	7	2	3	4	4	
Total alleles, DtE6	7	5	6	3	6	2	5	7	7	
Total alleles, DtC1	11	7	8	6	7	3	7	7	6	
Total alleles, DtD10	19	9	12	7	10	4	6	8	9	
Mean alleles per locus	12	7	9.4	7	8	3	5.6	6.8	6.4	
Total number of alleles	60	35	47	34	39	14	28	34	32	

Number of individuals (total), number of individuals sampled from all species; number of individuals (Msat), number of *Drupadia theda* individuals for which microsatellite data were recorded; allelic richness, mean allelic richness taken over five loci using Fstat (Goudet 2002).

virtually all Sundaic endemics. Remnant fauna was dominated by geographically widespread species.

Within the single species *D. theda*, analyses of the individual genotypes at the five microsatellite loci revealed a total of 71 alleles. Both spatially and temporally, allelic richness had virtually the same pattern found with species richness (Fig. 2). Rarefied species richness and rarefied allelic richness were strongly and linearly correlated over space in 2000 ($R = 0.98$, $P = 0.002$) and over time between 1997 and 2004 ($R = 0.96$).

DISCUSSION

Here, we have shown that strong spatial and temporal associations exist between species and allelic richness across rainforest habitats affected by ENSO-induced disturbance. At the minimum, this generalizes previous plant studies

(Vellend 2004; Sezen *et al.* 2005) that have found significant reductions in genetic diversity of disturbed forests vs. old growth forests. Very little is known about the genetic composition of animal populations in disturbed/secondary forests even though these forests cover a greater global area than old growth forests (Sezen *et al.* 2005). Here, it is likely that local environmental regimes, the nature of habitat discontinuities between habitat patches and dispersal ability of constituent taxa have determined both genetic and community structure of our species-rich butterfly assemblage. If patterns from *D. theda* are indicative, these results also support Vellend's (2003, 2004) suggestion of analogous processes affecting diversity at these scales, and support his use of plots with different farming histories to represent communities of different age. Our results also suggest that the SGDC applies to recently disturbed habitats over relatively short ($\pm$ 70 km) spatial and temporal scales.

Recovery of both species and alleles following disturbance was both relatively rapid and of similar rate (see Vellend 2004, p. 3052).

It is important to note that the type and scale of the disturbance had important implications for the sampling design as the burning occurred over very large areas, affecting millions of hectares of rainforest, and did not occur in discrete blocks. Given its scale, the phenomenon of ENSO-induced disturbance should entail multiple studies over a larger spatial scale and including diverse taxa (Oksanen 2001). Like Oksanen (2001), we believe that the appropriate scale of assessment, especially when dealing with large-scale phenomena such as landscape patterns in fire-affected habitat, must have priority over replication.

The large sampling scale we used should reduce the importance of spatial autocorrelation as an explanatory factor. Indeed, site B1 is geographically proximate to I2 (< 5 km) and distant from I1 (> 70 km) but its species richness is closer to that of I1. Likewise, there are substantial and parallel differences in species and allelic richness between the nearby (< 5 km apart) landscapes I1 (unlogged) and I3 (logged). Elsewhere (Cleary *et al.* 2004; Cleary & Genner in press), we found a very sharp decline in the similarity of butterfly assemblages at very small distances (< 2 km) and little change in mean similarity over much greater distances (see also Condit *et al.* 2002). Simulations of genetic population differentiation also showed a rapid increase of divergence over small spatial scales with little change over larger distances (Palumbi 2003).

The higher species richness we recorded in the logged I3 over pristine I1 falls in line with previous studies that have recorded higher species richness in moderately disturbed forest than in proximate pristine forest (Hamer *et al.* 1997; Spitzer *et al.* 1997; Walpole & Sheldon 1999; Willott *et al.* 2000); this is consistent with theories that moderate levels of disturbance may enhance diversity by providing additional ecological niches and preventing competitive exclusion of rarer species (Caswell 1976; Connell 1978; Rosenzweig 1995). In the study area, logging was highly selective, opening up the canopy in areas while maintaining areas of unlogged forest. Resultant increases in habitat heterogeneity may have provided new niches for rare opportunistic colonizing species and reduced abundance of previous common competitive dominants (Rosenzweig 1995). However, we know of no theory that predicts that allelic richness for species that occur in both habitats should show parallel patterns, as we find here.

Temporally, although both allelic and species richness increased quickly, neither species nor allelic richness had recovered 7 years after the 1997–1998 ENSO event and it is unclear whether a new equilibrium has been reached or will be reached in the near future (see also Vellend 2004).

Our results also have potential conservation implications. While the low levels of species and allelic richness recorded here may be predominantly due to severe habitat disturbance, the loss of allelic richness, combined with a reduction in immigration (C. Fauvelot, unpublished results) may make the remaining species more prone to extinction because of reduced population fitness (Allendorf 1986; Pease *et al.* 1989; Petit *et al.* 1998) and therefore adversely affect future levels of species richness. This may make the remnant species such as *D. theda* more vulnerable to future disturbance events. It is important to note that ENSO-induced fires are increasing in magnitude and frequency because of the prevalence of logging, habitat fragmentation, increases in ignition sources and increasing frequency and intensity of ENSO-induced droughts (Laurance 2003). Only a couple of decades ago, forest fires were not considered an important conservation issue but are now considered a major threat to tropical biodiversity (Guilderson & Schrag 1998; Salafsky 1998; Timmermann *et al.* 1999; Siegert *et al.* 2001; Laurance 2003).

If genetic and species diversity are closely correlated, this could help to inform management decisions concerning natural biodiversity resources threatened by overexploitation or disturbance. Preserving genetic diversity appears to be critical to species survival under changing environmental conditions (Spielman *et al.* 2004), but is not often measured (except for flagship species, see e.g. Nichols *et al.* 2001). At the least, one level of diversity may predict the other. In practice, as little extra is actively performed to conserve genetic diversity in natural environments over that which was carried out to conserve community diversity, by focusing management initiatives on community diversity, genetic diversity may also be conserved.

Results from this study suggest that disturbance events such as severe ENSO-induced drought and associated fires are doubly destructive for tropical rainforest biodiversity: reduced species diversity has potentially important repercussions for ecosystem functioning (Tilman 1999), and remnant genetically depauperate species may have decreased resilience to future disturbance events (Pease *et al.* 1989). However, field-based assessments in species-rich environments are lacking, and further evidence of the generality of the pattern is required across systems and levels of taxonomic diversity.

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