

## RANGE-RESTRICTED, SPECIALIST BORNEAN BUTTERFLIES ARE LESS LIKELY TO RECOVER FROM ENSO-INDUCED DISTURBANCE

N. A. CHARRETTE,<sup>1</sup> D. F. R. CLEARY,<sup>2</sup> AND A. Ø. MOOERS<sup>3,4</sup>

<sup>1</sup>Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V6A 1S6 Canada

<sup>2</sup>Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands

<sup>3</sup>Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V6A 1S6 Canada

**Abstract.** The forest fires induced by the El Niño Southern Oscillation (ENSO) in 1997–1998 resulted in the temporary extirpation of more than 100 lowland butterfly species at a forest site in Borneo. Species with more restricted ranges were less likely to recover over the following four years. Matched-pair analyses revealed that species with lower initial abundances, restricted geographic ranges, and more specialized larvae were less likely to return. Specialization differed predictably between the (more generalist) wide-range and (more specialized) restricted-range species in our data set, and both geographic range and level of specialization were important in multivariate models. These are the first observations directly linking extent of occurrence, ecological specialization, and observed recovery following local extirpation. If recovery time exceeds the frequency of disturbance, local extirpation can lead to local extinction. Given that ENSO-induced disturbances are increasing in frequency, in severity, and in geographic scale, these results suggest that specialist species with restricted geographic ranges could be at particularly high risk of global extinction.

**Key words:** *El Niño; endemic; extirpation; forest fire; generalist; geographic range; specialist.*

### INTRODUCTION

Endemic species with restricted geographic ranges are of special conservation concern because local extirpation is more likely to result in global extinction. The comparative study presented here is motivated by our observation that tropical forest fires induced by the El Niño Southern Oscillation (ENSO) on the island of Borneo had a disproportionate negative demographic effect on butterflies endemic to the island (Cleary and Genner 2004). The ENSO, with a periodicity of 2.5–7 years, is the largest interannual climatic fluctuation in the world, causing pronounced effects on ecosystem functioning (Tudhope et al. 2001). The 1997–1998 ENSO caused a record-breaking drought in East Kalimantan that affected more than 5 million hectares of forest. Importantly, the drought and fire greatly increased the risk of future fire because of the large amount of flammable dead wood (Siegert et al. 2001). The context for our observation is the evidence that ENSO events are increasing in frequency, severity, and geographic scale (Timmerman et al. 1999, Holmgren et al. 2001, Tudhope et al. 2001).

Our observation of increased vulnerability of island endemics is consistent with previous surveys suggesting that restricted-range butterflies are more sensitive to disturbance (Hill et al. 1995, 2001, Spitzer et al. 1997,

Willott et al. 2000; but see Lewis 2001) and more likely to go locally extinct over historical time (Koh et al. 2004). Several factors may explain this increased vulnerability. First, perturbations on the same scale as a species' geographic range will affect all populations of the species, and geographically smaller perturbations are more common than larger ones (for forest fires see, e.g., Malamud et al. [1998]). This means that recovery of range-restricted species will be less aided by immigration. Second, local abundance and geographic range are often positively correlated (Brown 1984, Gaston and Lawton 1990, Kouki and Häyrinen 1991, Gaston et al. 1997, Quinn et al. 1997; but see also Päävinen et al. 2005). Such a correlation makes endemics locally rare and more vulnerable to stochastic events. It also makes endemics susceptible to deterministic (e.g., Allee effects; Courchamp et al. 1999) and stochastic (MacArthur and Wilson 1967) demographic events following decimation (for a theoretical treatment of the relative strengths of these forces, see Lande [1993]). Indeed, many empirical studies demonstrate that populations at lower abundances are more susceptible to disturbances (Bolger et al. 1991, Newmark 1991, Spiller et al. 1998, Barlow et al. 2002, Davies et al. 2004, Henle et al. 2004: Table 2). Third, other attributes of range-restricted endemics may make them susceptible to disturbance (Gaston et al. 1997). For example, if endemic species are small in size, they may recover more slowly because of slower recolonization. Evidence has connected size with dispersal in a beetle (Davis 1984, 1986), midges (McLachlan 1983), insects and fish (Roff 1991), and butterflies

Manuscript received 30 September 2005; revised 3 January 2006; accepted 23 January 2006; final version received 14 February 2006. Corresponding Editor: M. F. Antolin.

<sup>4</sup> Corresponding author. E-mail: amooers@sfu.ca

(Kuussaari et al. 1996). Endemics can also have specific ecologies. For butterflies, Thomas (1991) provides evidence that endemic species in Costa Rica are less likely to use human-modified habitat (see also Lewis et al. 1998), and Spitzer et al. (1997) present evidence that endemic species in North Vietnam tend to be confined to closed forest canopies, while nonendemics tend to be gap specialists. Endemic butterflies also are more commonly found in forests of later successional status in Vietnam (Leps and Spitzer 1990, Spitzer et al. 1993; but see also Wood and Gillman 1998). Finally and importantly, endemics might be specialists, and specialists might be at greater risk of disturbance (the flexibility hypothesis; Lawton 1993). Henle et al. (2004) presented a review of data, and evidence exists from birds (Barlow et al. 2002, Gage et al. 2004) and butterflies (Koh et al. 2004, Päävinen et al. 2005).

The above examples suggest that life history traits of restricted-range endemics increase their susceptibility to disturbance. Independent of the direct effects of restricted geographic range, such traits will place endemic species at higher risk if the habitats required by those species are altered or eliminated. Importantly, if the recovery rate of range-restricted species is less than that of disturbance events like those produced by the ENSO, then temporary extirpations could lead to global extinction.

We can test whether geographic range, abundance, and host specialization in butterflies are correlated to postdisturbance recovery by examining the impact of disturbance from recent and widespread ENSO-induced fires in the rainforests of Borneo. These occurred in 1982–1983 and much more dramatically in 1997–1998 (Siegert et al. 2001). Directly following the 1997–1998 fire, no visible herbs or animals were present in most burned (but intact) forest, but the burned areas began to rejuvenate within a few weeks (Cleary 2003). At Wanariset (116°57' E, 0°59' S), a large (3000-ha) research forest (now a fragment) found in East Kalimantan, Indonesian Borneo, we have extensive collections both before and after the 1997–1998 ENSO event, allowing us to distinguish between returning and nonreturning species.

Nine Bornean endemic species were collected at Wanariset preceding the 1997–1998 event. None of these species returned, but this sample size is too small to perform a meaningful analysis. In contrast, a large number of nonendemic species have either returned to Wanariset (“returners”) or have not (“nonreturners”). Therefore, we begin our analysis of recovery ability by excluding the nine Bornean endemic species, and consider only the remaining nonendemic species. We first test hypotheses on a set of related pairs of nonendemic species that differ in their pattern of recovery, chosen to control for phylogenetic nonindependence among species. Because these phylogenetically contrasted species comprise only a small portion of our species set (78 of 207 species), we then analyze data from

the entire nonendemic community. We test the following hypotheses contrasting returning and nonreturning species: (1) nonreturners had smaller geographic ranges, (2) nonreturners were at lower initial abundance at Wanariset, (3) nonreturning species were smaller in size, and (4) nonreturners had distinct ecologies, specifically that they were more specialized.

## MATERIALS AND METHODS

### *Study site*

Cleary (2002, 2003) described the Wanariset study site, a 3000-ha protected lowland dipterocarp-dominated forest contiguous with large tracts of intact forest prior to the 1997–1998 El Niño Southern Oscillation (ENSO) event. The site was partly burned in the ENSO event of 1982–1983, but recovered such that surveys before the 1997–1998 fires identified butterfly communities very similar to unburned sites (Cleary and Mooers 2004). Roughly 8.0% of the forest remained intact following the 1997–1998 fire, and a secondary forest consisting of pioneer trees (*Trema*, *Mallotus*, and *Macaranga*) returned by 2000 (Cleary et al. 2004).

### *Sampling*

Cleary (2003) presented a full description of sampling. Sampling was in eight 0.9-ha plots (300 × 30 m strips) in 1997 ( $n = 1333$  individuals), nine plots in 1998 and 1999 ( $n = 1800$  individuals), and 21 plots in 2000 ( $n = 4200$  individuals), assigned fully at random in a 450-ha area in the Wanariset Samboja Research Forest. Butterflies were caught in nets if encountered within the boundaries of a plot and identified in the field, with vouchers kept for all species. In 1997 (predisturbance), each plot was traversed on foot from one end to the other until at least 130 butterflies were collected. In postdisturbance sampling in 1998, 1999, and 2000, sample size was 200 butterflies per plot. In all, we collected 216 species in 1997, and these comprise our primary dataset.

### *Larval feeding guilds*

Butterflies use almost all major seed plant families and even a few nonseed plants (Janz and Nylin 1998). Host use is, however, strongly clustered. Of the butterfly species, 69% use rosids and 73% use trees and/or shrubs. Growth form is in fact a more evolutionarily conservative aspect of butterfly–host plant associations than is plant phylogeny (Janz and Nylin 1998). Because plant growth form is such an important aspect of host association in butterflies, factors other than plant chemistry, such as habitat or community structure, might play an important role in shaping the large-scale patterns of butterfly–host plant association. Each species was categorized into a feeding guild as follows (Cleary 2003): *herb specialists* feed on monocotyledonous and/or dicotyledonous herbs, and/or other herb-like plants; *liana specialists* feed on monocotyledonous and/or dicotyledonous vines; *tree specialists* feed on woody monocotyledonous and/or dicotyledonous shrubs and/

or trees; *carnivores* feed on insects; and *generalists* fit into at least two of the previously mentioned guilds. In our data, species with carnivorous larvae are always paired with each other, and thus do not affect the results of the analysis. We used data from Otsuka (1988), Maruyama and Otsuka (1991), Seki et al. (1991), Elliot (1992:595), Igarashi and Fukuda (1997, 2000), Fiedler (1998), and Robinson et al. (2001). For some of our species we were able to reliably score host family diversity. The correlation between host form generalism and host family generalism (species scored as feeding on one plant family or more than one family) is significant and positive (Spearman  $\rho = 0.3$ ,  $P = 0.008$ ,  $N = 79$ ).

For the geographic distribution, each species was ranked on a scale of one to four, as follows: 1, endemic to the island of Borneo ("endemics"; nine spp.); 2, endemic to the Sundaland Region (Malaysia, Southern Thailand, Sumatra, Java, Borneo, and satellite islands; 78 spp.); 3, found in Sundaland and surrounding biogeographic regions (Indo-Burma, Wallacea, and/or the Philippines; "moderate"; 81 spp.); 4, Sundaland and extending into more distant biogeographic regions (e.g., Australia, Africa, Europe; "wide ranging"; 48 spp.). Range data were compiled from Otsuka (1988), Maruyama and Otsuka (1991), Seki et al. (1991), and Igarashi and Fukuda (1997, 2000).

#### *Species pairs*

Our primary data set consists of species that are not endemic to Borneo and that were present in the 1997 (prefire) collection at Wanariset. Attributes of non-returner species (i.e., not present in any of the four postfire collections) were compared to closely related species that returned (i.e., present in at least one postfire collection). Using each nonendemic nonreturning species as our starting point, we used taxonomic treatments to identify returning relatives, using the method of phylogenetically independent contrasts presented by Burt (1989). We chose species pairs such that no part of the path along the phylogenetic tree (represented by the taxonomy) linking a pair of species is shared by paths linking other pairs of species. In this way, evolved differences between one pair of species are independent of evolved differences between other such pairs (Burt 1989). The Appendix lists the 39 pairs (nonreturner vs. returner) that we identified. Most of these pairs are close relatives, but the independent contrast method can identify more distantly related pairs (e.g., *Chersonesia intermedia* and *Cethosia hypsea*) as long as the phylogenetic path linking them is independent of other pairs. For none of the three tested variables did the taxonomic depth of the contrast predict its direction (results not shown). For recent examples of this methodology see, e.g., Stockley (2003) and Hone et al. (2005).

Relatedness was determined based on the taxonomy in Otsuka (1988), Maruyama and Otsuka (1991), and Seki et al. (1991). Species relatedness for the Nymphalidae were further resolved utilizing Ackery and Vane-

Wright (1984), Harvey (1991), and Wahlberg et al. (2003, 2005); the subfamily Satyrinae was further resolved using Miller (1968). When these sources were in contradiction with each other over the grouping of species, we deferred to Otsuka (1988), Maruyama and Otsuka (1991), and Seki et al. (1991) for consistency.

In cases where there were several candidate species for a matched pair because phylogenies are unresolved, the species with the mean forewing length closest to that of the average forewing length of all the candidate species was chosen as the most representative of the clade. When two or more species have mean forewing lengths equally close to this average, the species with name highest in alphabetical order was chosen (considered as a random choice).

*Abundance* was measured as the number of individuals caught of each species (prefire) across all plots; *size* was the mean of minimum and maximum wing size as recorded in Otsuka (1988), Maruyama and Otsuka (1991), and Seki et al. (1991).

Data were analyzed using SPSS 13.0. We first undertook a conservative set of univariate nonparametric (one-tailed) analyses using the phylogenetically matched pairs, following Burt (1989). We then treated species as independent observations, considered all our variables together, and performed multiple binary logistic regression using backward elimination of variables based on the decrease in  $-2$  log-likelihood of the logistic regression models when each variable was removed. Goodness of fit of the final model was tested with the Hosmer-Lemeshow statistic that indicates a poor fit if the significance value is less than 0.05. This statistic is a reliable test of model fit because it aggregates observations into groups of similar cases and bases the statistic upon these groups. Finally, we used pseudo- $R^2$  statistics, which measure the variability in the dependent variable that is explained by a regression model. These statistics are designed to have similar properties to true  $R^2$  statistics for linear regression. In the present case, we present the Nagelkerke  $R^2$  statistic (Burnham and Anderson 2002). We retained all predictor variables that significantly contribute to the model (at  $\alpha = 0.05$ ). We report results from the 207 nonendemic species. Because we know that the Bornean endemics did not return, including them would bias results in favor of a significant effect of range size.

## RESULTS

### *Univariate tests*

*Geographic range.*—Fully consistent with our motivating observation from the nine Bornean endemics, nonreturners in the nonendemic data set had smaller geographic ranges than their paired returning species for 20 of 39 cases and had larger geographic ranges for only 7 of 39 cases (12 ties; Wilcoxon signed ranks test,  $P = 0.002$ ).

*Abundance.*—Nonreturners were at lower initial abundance than their paired returning species in 22 of

TABLE 1. Multiple logistic regression for probability of return (0 or 1) for all butterflies at Wanariset (minus Bornean endemics).

Variable	B	SE	Wald	df	P	e <sup>B</sup>	95.0% CI for e <sup>B</sup>	
							Lower	Upper
Geographic range†			29.324	2	0.000			
Sundaic endemics (G2)	-2.831	0.523	29.321	1	0.000	0.059	0.021	0.164
Moderate (G3)	-1.691	0.472	12.833	1	0.000	0.184	0.073	0.465
Generalism‡			26.565	4	0.000			
Generalist (SG)	2.091	0.431	23.499	1	0.000	8.093	3.475	18.850
Herb specialist (SH)	1.077	0.526	4.189	1	0.041	2.937	1.047	8.242
Carnivore (SC)	2.016	0.735	7.531	1	0.006	7.509	1.779	31.695
Liana specialist (SL)	0.461	0.707	0.426	1	0.514	1.586	0.397	6.342
Constant	0.365	0.446	0.668	1	0.414	1.440		

Notes: Regression is based on the following model:  $\ln[p/(1-p)] = 0.365 + 2.091x_{SG} + 1.077x_{SH} + 2.016x_{SC} + 0.461x_{SL} - 2.831x_{G2} - 1.691x_{G3}$ ; for this model,  $\chi^2 = 83.586$ ,  $df = 6$ ,  $P < 0.001$ . B is the regression coefficient in the logistic model; Wald is Wald's  $\chi^2$  statistic, which tests for the effect of a variable; e<sup>B</sup> is the odds ratio, computed relative to widespread species and tree specialists, respectively.

† Listed variables are compared to "widespread species."

‡ Listed variables are compared to "tree specialists."

39 cases and were at higher initial abundance for 8 of 39 cases (9 ties; Wilcoxon signed ranks test,  $P = 0.013$ ).

Size.—Nonreturners were smaller than returners in 23 of 39 cases and were larger than returners in 15 of 39 cases (1 tie; Wilcoxon signed ranks test,  $P = 0.102$ ).

Ecology.—For host growth form, returners were more generalist than their nonreturner counterparts in 9 of 39 cases, and nonreturners were more generalist in 2 of 39 cases (28 ties; Wilcoxon signed ranks test,  $P = 0.018$ ).

Multivariate tests

The final model (Table 1) following backward elimination retains only geographical range and specialization, with abundance and body size offering no additional predictive value. The Hosmer-Lemeshow statistic ( $\chi^2 = 8.870$ ,  $df = 6$ ,  $P = 0.181$ ) indicates that the model adequately fits the data. The Nagelkerke  $R^2$  statistic is 0.449. Even though the Bornean endemics were not included in this analysis, both geographical range and specialization are highly significant. Although they are also significantly related (likelihood ratio  $\chi^2 = 32.76$ ,  $P < 0.001$ ,  $N = 207$ ), the model is stable with both factors included. For example, generalist butterfly species were more than eight times more likely to return than were tree specialists. Butterfly species with the widest geographic ranges were more than five times more likely to return than were those with moderate ranges and almost 17 times more likely to return than were species restricted to the Sundaland region (Fig. 1). Among feeding guilds, 72% of generalists, 50% of carnivorous species, 40% of herb specialists, 27% of liana specialists, and 19% of tree specialists returned (Table 2). Analyses on other subsets of the data set (pairs only, the difference between all nonendemics and the pairs, and the entire community including the endemics) gave completely congruent patterns (results not shown).

DISCUSSION

El Niño Southern Oscillation (ENSO)-induced disturbance is increasing in its possible detrimental effects and thus could be an important force shaping future biodiversity. The ENSO-induced forest fires at Wanariset had a disproportionate effect on butterfly species of smaller geographic range, in that nonreturning species had smaller ranges than returning species. This holds not only for the Bornean endemics but much more generally. If we classify each of the species into one of the four range size classes (see Fig. 1), all pairwise comparisons indicate that the smaller range class also had lower proportion of returning species (Wilcoxon signed rank test, all with nominal  $P < 0.05$ , except in the

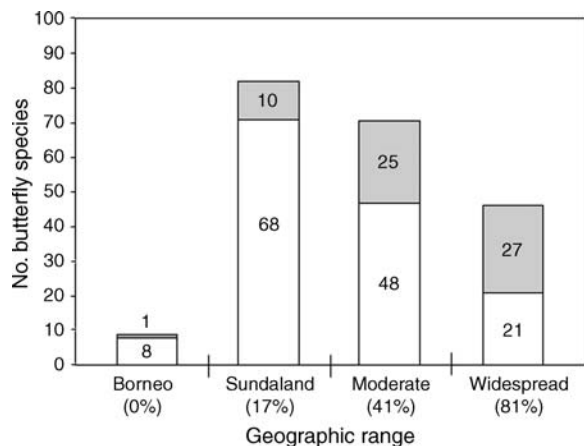


FIG. 1. Number of specialist and generalist butterfly species in each geographic range category at Wanariset, Borneo: plant form generalists (gray) and plant form specialists (open). The percentage values associated with each geographic range indicate the proportion of species within that range category that returned within four years.

TABLE 2. Number of species (and percentages) in each larval feeding guild that returned and that did not return to Wanariset following the 1997–1998 forest fire event.

Variable	Returners	Nonreturners
Generalists	46 (72)	18 (28)
Liana specialists	4 (27)	11 (73)
Herb specialists	12 (40)	18 (60)
Carnivorous	5 (50)	5 (50)
Tree specialists	18 (19)	79 (81)
Total	85 (39)	131 (61)

case of the Bornean endemics compared to Sundaland endemics, where  $P = 0.068$ ). This suggests a general link between the range size of tropical butterfly species and their rate of recovery from disturbance.

From the univariate matched-pair tests, low abundance, small size, and specialist ecology were all correlated with failure to return, but it was not true that species with smaller ranges tend to be smaller in size or at lower abundance at Wanariset. Using our crude measures of abundance, species from two of the middle geographic range classes (Sundaland and moderate) had nominally higher initial abundances than the species from the most widespread class, in contrast to our prediction (Wilcoxon signed rank test,  $P = 0.02$  and  $0.03$ , respectively), while all other comparisons were not significant (Wilcoxon signed rank test, all  $P > 0.6$ ). This pattern may not be surprising (see, e.g., Thomas and Mallorie 1985, Arita 1993, Cowley et al. 2001, Päävinen et al. 2005). Likewise, there were no significant differences between the average sizes of species of different geographic range (Wilcoxon signed rank test, all  $P > 0.15$ ). So while being a small and low abundance butterfly might predict slow recovery after ENSO-induced disturbance, it does not seem to be why butterflies of restricted range are disproportionately affected.

The most consistent trait linking increased recovery and larger ranges seems to be generalism. The univariate contrasts strongly suggest that host plant growth form generalists were more likely to recover from disturbance-mediated extirpation. In the best-fit logistic regression predicting recovery, only level of specialization and geographic range remain as attributes that predict recovery. Critically, and in contrast to size and abundance, our measure of generalism is also strongly associated with butterfly species range sizes at Wanariset, (Fig. 1). For host growth form, Bornean endemics, Sundaic endemics, and species with moderate distributions each have a higher proportion of specialist species than does the class of most widespread species (Bornean endemics, 8 specialists and 1 generalist,  $P = 0.02$ ; Sundaic endemics, 68 specialists and 10 generalists,  $P < 0.0001$ ; moderate range species, 55 specialists and 26 generalists,  $P = 0.006$ ; Fisher exact tests; wide-range species, 21 specialists and 27 generalists); the Sundaic endemic species' class even has a higher proportion of

specialists than does the class of species with a moderate distribution ( $P = 0.007$ ).

Our results strongly suggest that, at Wanariset, butterfly species with smaller ranges are both more likely to be specialized and are less likely to recover from ENSO-induced forest fires. Of the nine Bornean endemics, eight are larval plant growth form specialists. We suggest that a common explanation links host plant specialization to range size and to the ability to recover from disturbance. One simple possibility is that generalists are more likely to be able to exploit early-recovering growth forms and so recover more quickly. Although denuded of vegetation immediately after the drought and fire, living trees (e.g., *Fordia splendidissima*) resprouted quickly, and pioneer saplings (e.g., *Trema*, *Mallotus*, and *Macaranga*), forbs (e.g., *Eupatorium odoratum*), and ferns were abundant a year later in 1999 (Slik et al. 2002, Slik and Eichhorn 2003, Cleary and Grill 2004, Slik 2004; D. Cleary, personal observation). By 2000, less severely burned areas (~8% of Wanariset) established a closed canopy with a dense undergrowth of forest herbs (predominantly Zingiberaceae and Maranthaceae), while the burned areas were dominated by relatively large pioneer saplings. These observations do not suggest host growth forms return in any clear successional order, although more quantitative data are needed. So while it is true that none of the 42 *Arhopala* tree specialists returned, being a tree specialist per se might not be indicative of recovery ability: of the 17 phylogenetically matched pairs that included tree specialists, in nine pairs (53%) the tree specialist did not recover, in five pairs both the recovering and the nonrecovering species were tree specialists, and in the last three pairs it was the tree specialist that recovered.

Brown (1984) developed the niche breadth hypothesis, which predicts that species that can exploit a wide range of resources become geographically widespread and locally abundant. Although Gaston et al. (1997) criticized the theory for its lack of convincing evidence, this study and several others have found that generalists do maintain greater geographic ranges even if they are not more locally abundant; evidence spans butterflies (Thomas and Mallorie 1985), birds (Kouki and Häyriinen 1991), moths (Quinn et al. 1997), and small mammals (Glazier and Eckert 2002). Directly related to our observations, Quinn et al. (1997) found a positive relationship between host range and geographic range of macrolepidoptera in Britain, while Hughes (2000) found that the continental range of lycaenid butterfly species was positively correlated with the number of host plant species used. In Britain, specialist species were much more likely to have their ranges reduced over the past 40 years (Warren et al. 2001). The connection between range size and generalist lifestyle seems quite strong.

Both Lawton (1993) and Gaston et al. (1997) pointed to several studies that show that species that are more abundant and widespread in their native environment are more likely to establish themselves when introduced

to foreign areas. If introductions are analogous in any way to recovery, this is consistent with our main result. The recent review by Henle et al. (2004) found that most studies support the notion that ecological specialists are generally more prone to extinction, and this is supported by a comparison of extant and historical extinctions of butterflies in Singapore (Koh et al. 2004; note this study also found that cosmopolitan species were less likely to have disappeared from Singapore than were "Oriental" species). While less extensive, a correlation between niche breadth and vulnerability might also be general. Our data link these two aspects of restricted range: restricted-range species are more likely to be vulnerable to temporary extirpation and perhaps to global extinction because they tend to be more specialized.

We note that some species may use a few food sources in a given area, while using a wide variety of food sources over their entire range; indeed, a correlation between total range and the total number of host plants used might be expected from first principles. Importantly, our measure of species generalism was evaluated over their entire range (Cleary 2003), and it is not known if these species are generalists at Wanariset. Hughes (2000) presents evidence that local and continental specialization on host plants are correlated for North American lycaenid butterflies, although statistical power is weak (Spearman rank correlation = 0.61,  $P < 0.10$ ,  $N = 11$ ). Recent genetic analyses raise the possibility that at least one wide-ranging generalist neotropical butterfly actually might be a series of partially sympatric specialist lineages (Hebert et al. 2004). The wide distribution of a "generalist" species consisting of the summed distributions of its component specialist lineages seems reasonable. The appropriate life history for recovery might be more likely to be found among its component lineages than in any one uniform specialist species. Such phenomena would be consistent with our results.

Another intriguing possibility is that widely distributed species might be inherently "more adaptable" and better able to exploit a wider range of ecological niches, as has been suggested for birds (Jones et al. 2001) and primates (Harcourt et al. 2002). Perhaps growth form generalists are less constrained (e.g., more plastic) on axes such as developmental time or temperature tolerance. Such plasticity might both allow for larger ranges and make burned forest more hospitable, enhancing recovery. This is a testable prediction, but will require experimental data. It is also important to note that the guilds most affected by the forest fires are liana and tree specialists. The great majority of species in these guilds are forest dependent, a confirmation of Koh et al.'s (2004) finding that butterfly extinctions in Singapore are particularly prevalent in forest-dependent species.

The connection we have documented leads to the prediction that an increase in the scale and frequency of local disturbance could increase the probability that temporary extirpation will lead to global extinction for

restricted-range specialist butterfly species in the tropics, and perhaps for other taxa. This should be considered when designing conservation interventions, particularly for species not yet so rare as to be deemed "at risk" using conventional measures.

#### ACKNOWLEDGMENTS

We thank the many field assistants in Kalimantan for help with data collection and R. De Jong for help with identification of species. The FAB\*-Lab and BERG at Simon Fraser University, Anna Drake, Diane Srivastava, several reviewers, and especially Jessica Hellmann offered helpful input and/or comments on earlier versions of the manuscript. We are particularly grateful to the expert referees and to Niklas Wahlberg for his review of our taxonomic treatment. The Netherlands Foundation for the Advancement of Tropical Research (through S. B. J. Menken) funded D. Cleary's dissertation research; NSERC Canada funded N. A. Charrette and this submission. All three authors contributed equally to this article.

#### LITERATURE CITED

- Ackery, P. R., and R. I. Vane-Wright. 1984. Milkweed butterflies, their cladistics and biology: being an account of the natural history of the Danainae, a subfamily of the Lepidoptera, Nymphalidae. British Museum of Natural History, London, UK.
- Arita, H. T. 1993. Rarity in neotropical bats: correlations with phylogeny, diet, and body mass. *Ecological Applications* **3**: 506–517.
- Barlow, J., T. Haugaasen, and C. A. Peres. 2002. Effects of ground fires on understorey bird assemblages in Amazonian forests. *Biological Conservation* **105**:157–169.
- Bolger, D. T., A. C. Alberts, and M. E. Soulé. 1991. Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. *American Naturalist* **137**:155–166.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* **124**:255–279.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Burt, A. 1989. Comparative methods using phylogenetically independent contrasts. Pages 33–53 in P. H. Harvey and L. Partridge, editors. Oxford surveys in evolutionary biology. Volume 6. Oxford University Press, Oxford, UK.
- Cleary, D. F. R. 2002. Biodiversity and environmental change in the rainforests of Borneo. Ph.D. Dissertation. University of Amsterdam, The Netherlands.
- Cleary, D. F. R. 2003. An examination of scale of assessment, logging and ENSO-induced fires on butterfly diversity in Borneo. *Oecologia* **135**:313–321.
- Cleary, D. F. R., and M. J. Genner. 2004. Changes in rain forest butterfly diversity following major ENSO-induced fires in Borneo. *Global Ecology and Biogeography* **13**:129–140.
- Cleary, D. F. R., and A. Grill. 2004. Butterfly response to severe ENSO-induced forest fires in Borneo. *Ecological Entomology* **29**:666–676.
- Cleary, D. F. R., and A. Ø. Mooers. 2004. Butterfly species richness and community composition in forests affected by ENSO-induced burning and habitat isolation in Borneo. *Journal of Tropical Ecology* **20**:359–367.
- Cleary, D. F. R., A. Ø. Mooers, K. A. O. Eichhorn, J. van Tol, d R. de Jong, and S. B. J. Menken. 2004. Diversity and community composition of butterflies and odonates in an ENSO-induced fire affected habitat mosaic: a case study from East Kalimantan, Indonesia. *Oikos* **105**:426–446.

- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the allee effect. *Trends in Ecology and Evolution* **14**:405–410.
- Cowley, M. J. R., C. D. Thomas, D. B. Roy, R. J. Wilson, J. L. León-Cortés, D. Gutiérrez, C. R. Bulman, R. M. Quinn, D. Moss, and K. J. Gaston. 2001. Density–distribution relationships in British butterflies. I. The effect of mobility and spatial scale. *Journal of Animal Ecology* **70**:410–425.
- Davies, K. F., C. R. Margules, and J. F. Lawrence. 2004. A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* **85**:265–271.
- Davis, M. A. 1984. The flight and migration ecology of the red milkweed beetle (*Tetraopes tetraophthalmus*). *Ecology* **65**:230–234.
- Davis, M. A. 1986. Geographic patterns in the flight ability of a monophagous beetle. *Oecologia* **69**:407–412.
- Elliot, J. N. 1992. The butterflies of the Malay Peninsula. Fourth revised edition. Malayan Nature Society, Kuala Lumpur, Malaysia.
- Fiedler, K. 1998. Diet breadth and host plant diversity of tropical vs temperate-zone herbivores: South-East Asian and West Palearctic butterflies as a case study. *Ecological Entomology* **23**:285–297.
- Gage, G. S., M. D. Brooke, M. R. E. Symonds, and D. Wege. 2004. Ecological correlates of the threat of extinction in neotropical bird species. *Animal Conservation* **7**:161–168.
- Gaston, K. J., T. M. Blackburn, and J. H. Lawton. 1997. Interspecific abundance–range size relationships: an appraisal of mechanisms. *Journal of Animal Ecology* **66**:579–601.
- Gaston, K. J., and J. H. Lawton. 1990. Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos* **58**:329–335.
- Glazier, D. S., and S. E. Eckert. 2002. Competitive ability, body size and geographical range size in small mammals. *Journal of Biogeography* **29**:81–92.
- Harcourt, A. H., S. A. Coppeto, and S. A. Parks. 2002. Rarity, specialization, and extinction in primates. *Journal of Biogeography* **29**:445–456.
- Harvey, D. J. 1991. Higher classification of the Nymphalidae. Pages 255–273 in H. F. Nijhout, editor. The development and evolution of butterfly wing patterns. Smithsonian Institution Press, Washington, D.C., USA.
- Hebert, P. D. N., E. H. Penton, J. M. Burns, D. H. Janzen, and W. Hallwachs. 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences (USA)* **96**:992–995.
- Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**:207–251.
- Hill, J. K., K. C. Hamer, L. A. Lace, and W. M. T. Banham. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* **32**:754–760.
- Hill, J. K., K. C. Hamer, J. Tangah, and M. Dawood. 2001. Ecology of tropical butterflies in rainforest gaps. *Oecologia* **128**:294–302.
- Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution* **16**:89–94.
- Hone, D. W. E., T. M. Keeseey, D. Pisani, and A. Purvis. 2005. Macroevolutionary trends in the Dinosauria: Cope's rule. *Journal of Evolutionary Biology* **18**:587–595.
- Hughes, J. B. 2000. The scale of resource specialization and the distribution and abundance of lycaenid butterflies. *Oecologia* **123**:375–383.
- Igarashi, S., and H. Fukuda. 1997. The life histories of Asian butterflies. Volume 1. Tokai University Press, Tokyo, Japan.
- Igarashi, S., and H. Fukuda. 2000. The life histories of Asian butterflies. Volume 2. Tokai University Press, Tokyo, Japan.
- Janz, N., and S. Nylin. 1998. Butterflies and plants: a phylogenetic study. *Evolution* **52**:486–502.
- Jones, M. J., M. S. Sullivan, S. J. Marsden, and M. D. Linsley. 2001. Correlates of extinction risk in birds from two Indonesian islands. *Biological Journal of the Linnean Society* **73**:65–79.
- Koh, L. P., N. S. Sodhi, and B. W. Brook. 2004. Ecological correlates of extinction proneness in tropical butterflies. *Conservation Biology* **18**:1571–1578.
- Kouki, J., and U. Häyrinen. 1991. On the relationship between distribution and abundance in birds breeding on Finnish mires: the effect of habitat specialization. *Ornis Fennica* **68**:170–177.
- Kuussaari, M., M. Nieminen, and I. Hanski. 1996. An experimental study of migration in the Glanville fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65**:791–801.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**:911–927.
- Lawton, J. H. 1993. Range, population abundance and conservation. *Trends in Ecology and Evolution* **8**:409–413.
- Leps, J., and K. Spitzer. 1990. Ecological determinants of butterfly communities (Lepidoptera, Papilionoidea) in the Tam Dao mountains, Vietnam. *Acta Entomologica Bohemoslovica* **87**:182–194.
- Lewis, O. T. 2001. Effect of experimental selective logging on tropical butterflies. *Conservation Biology* **15**:389–400.
- Lewis, O. T., R. J. Wilson, and M. C. Harper. 1998. Endemic butterflies on Grande Comore: habitat preferences and conservation priorities. *Biological Conservation* **85**:113–121.
- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Malamud, B. D., G. Morein, and D. L. Turcotte. 1998. Forest fires: an example of self-organized critical behavior. *Science* **281**:1840–1842.
- Maruyama, K., and K. Otsuka. 1991. Butterflies of Borneo. Volume 2., no. 2. Hesperidae. Tobishima Corporation, Tokyo, Japan.
- McLachlan, A. 1983. Life-history tactics of rain-pool dwellers. *Journal of Animal Ecology* **52**:545–561.
- Miller, L. D. 1968. The higher classification, phylogeny, and zoogeography of the Satyridae. *Memoirs of the American Entomological Society*. Volume 24. The American Entomological Society at the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
- Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. *Conservation Biology* **5**:67–78.
- Otsuka, K. 1988. Butterflies of Borneo. Volume 1. Tobishima Corporation, Tokyo, Japan.
- Päivinen, J., A. Grappuo, V. Kaitala, A. Komonen, J. S. Kotiaho, K. Saarinen, and N. Wahlberg. 2005. Negative density–distribution relationship in butterflies. *BMC Biology* **3**:5.
- Quinn, R. M., K. J. Gaston, T. M. Blackburn, and B. C. Eversham. 1997. Abundance–range size relationships of macrolepidoptera in Britain: the effects of taxonomy and life history variables. *Ecological Entomology* **22**:453–461.
- Robinson, G. S., P. R. Ackery, I. J. Kitching, G. W. Beccaloni, and L. M. Hernández. 2001. Hostplants of the moth and butterfly caterpillars of the Oriental Region. The Natural History Museum and Southdene Sdn Bhd, United Selangor Press Sdn Bhd, Kuala Lumpur, Malaysia.
- Roff, D. A. 1991. Life History consequences of bioenergetic and biomechanical constraints on migration. *American Zoologist* **31**:205–215.
- Seki, Y., Y. Takanami, and K. Maruyama. 1991. Butterflies of Borneo. Volume 2, no. 1. Lycaenidae. Tobishima Corporation, Tokyo, Japan.

- Siegert, F., G. Ruecker, A. Hinrichs, and A. A. Hoffmann. 2001. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* **414**:437–44.
- Slik, J. W. F. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* **141**:114–120.
- Slik, J. W. F., and K. A. O. Eichhorn. 2003. Fire survival of lowland tropical rain forest trees in relation to stem diameter and topographic position. *Oecologia* **137**:446–455.
- Slik, J. W. F., R. W. Verburg, and P. J. A. Kessler. 2002. Effects of fire and selective logging on the tree species composition of lowland dipterocarp forest in East Kalimantan, Indonesia. *Biodiversity and Conservation* **11**:85–98.
- Spiller, D. A., J. B. Losos, and T. W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. *Science* **281**:695–697.
- Spitzer, K., J. Jaros, J. Havelka, and J. Leps. 1997. Effect of small-scale disturbance on butterfly communities of an Indochinese montane rainforest. *Biological Conservation* **80**:9–15.
- Spitzer, K., N. Vojtech, M. Tonner, and J. Leps. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera, Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography* **20**:109–121.
- Stockley, P. 2003. Female multiple mating behaviour, early reproductive failure and litter size variation in mammals. *Proceedings of the Royal Society of London B* **270**:271–278.
- Thomas, C. D. 1991. Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation* **55**:269–281.
- Thomas, C. D., and M. C. Mallorie. 1985. Rarity, species richness and conservation: butterflies of the Atlas Mountains in Morocco. *Biological Conservation* **33**:95–117.
- Timmermann, A., J. Obernuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**:694–697.
- Tudhope, A. W., C. P. Chilcott, M. T. McCulloch, E. R. Cook, J. Chappell, R. M. Ellam, D. W. Lea, J. M. Lough, and G. B. Shimmield. 2001. Variability in the El Niño Southern Oscillation through a glacial–interglacial cycle. *Science* **291**:1511–1517.
- Wahlberg, N., A. V. Z. Brower, and S. Nylin. 2005. Phylogenetic relationships and historical biogeography of tribes and genera in the subfamily Nymphalinae (Lepidoptera: Nymphalidae). *Biological Journal of the Linnean Society* **86**:227–251.
- Wahlberg, N., E. Weingartner, and S. Nylin. 2003. Towards a better understanding of the higher systematics of Nymphalidae (Lepidoptera: Papilionoidea). *Molecular Phylogenetics and Evolution* **28**:473–484.
- Warren, M. S., et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**:65–69.
- Willott, S. J., D. C. Lim, S. G. Compton, and S. L. Sutton. 2000. Effects of selective logging on the butterflies of a Bornean rainforest. *Conservation Biology* **8**:388–397.
- Wood, B., and M. P. Gillman. 1998. The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. *Biodiversity Conservation* **7**:597–616.

#### APPENDIX

Phylogenetic pairs of returning and non-returning butterflies at Wanariset (*Ecological Archives* E087-140-A1).