Ibis (2007), **149**, 298–312

Impacts of a volcanic eruption on the forest bird community of Montserrat, Lesser Antilles

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Volcanic eruptions are an important and natural source of catastrophic disturbance to ecological communities. However, opportunities to study them are relatively rare. Here we report on the effects of the eruption of the Soufrière Hills volcano on the forest bird community of the Lesser Antillean island of Montserrat. The island's species-poor avifauna includes 11 restricted-range species, including the Critically Endangered endemic Montserrat Oriole *Icterus oberi*. Analysis of monitoring data from 1997 to 2005 indicates that counts of most species were substantially lower following major ashfalls. However, this effect was short-lived, with rapid population recovery in subsequent years. Furthermore, levels of seasonal rainfall appear to have been at least as important in determining population trends as ashfall. Overall, most species were at least as abundant at the end of the study as at the start, and no forest bird species have been extirpated from Montserrat. We discuss potential ecological drivers of ashfall impacts on populations: there is some evidence that terrestrial foragers were most severely affected.

Environmental catastrophes are predicted to have a major influence on the survival of small, isolated animal populations. However, catastrophic events are rare, ephemeral and unpredictable, and are therefore difficult to study. The bird communities of the Lesser Antilles Endemic Bird Area (EBA) are heavily shaped by such events. The land area of the EBA is relatively small (6400 km^2), comprising numerous small islands (Stattersfield *et al*. 1998). The current biogeography of Lesser Antillean birds has emerged from this distribution of land masses, but has also been profoundly shaped by frequent hurricanes (Wauer & Wunderle 1992, Wunderle *et al*. 1992, Wunderle 1995) and volcanic eruptions. Most islands in the Lesser Antilles are volcanic in origin, and during historical times major eruptions have been moderately frequent, with 16 volcanoes recorded as active in the Holocene (www.volcano.si.edu/gvp/). A mass extinction related to explosive volcanism in the Caribbean region occurred in the late Palaeocene (Bralower *et al*. 1997). The region is also one of the hottest of the world's biodiversity hotspots (Myers *et al*. 2000), and the EBA holds 24 restricted-range bird species; within the island chain, there are 12 single-island endemic bird species.

Pyroclastic flows and explosive blasts of hot gases and solids are characteristic of eruptions of Caribbean andesite volcanoes and can cause complete destruction of biota in impacted areas. However, a far wider area can be affected by the ashfalls and acid rain that are also associated with such eruptions. These do not cause total destruction of biota, but may still have a major effect on ecosystems. Little is known about the effects of volcanic eruptions on bird populations, and almost all the information

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available comes from the eruption of Mount St Helens, USA, on 18 May 1980 (Hayward *et al*. 1982, Andersen & MacMahon 1986, Manuwal *et al*. 1987). Such information is relevant to the conservation of 15 globally threatened bird species that are threatened by volcanic activity, and in particular the two bird species – Black-breasted Puffleg *Eriocnemis nigrivestris* and Mount Karthala White-eye *Zosterops mouroniensis* – that have their entire ranges on the slopes of currently active volcanoes (BirdLife International 2004).

Here we examine the influence of the eruption of the Soufrière Hills volcano on the forest bird community in Montserrat (16°N, 62°W, 109 km^2), a UK Overseas Territory at the northern end of the Lesser Antilles. One would predict that, on small islands, volcanic eruptions might result in temporary population bottlenecks and, possibly, extirpation, with recolonization occurring once the volcano has fallen dormant. The current eruption of the Soufrière Hills volcano began in 1995 and continues at the time of writing. The volcano also erupted in 1640, though information about this eruption is scant. Briefly, the eruption has been characterized by the growth of an andesite lava dome with associated pyroclastic flows, vulcanian explosion and debris flows (www.mvo.ms). Pyroclastic flows caused the almost complete destruction of tropical forest in the southern hill ranges of the island by late 1997. In the remaining forested hill range, the Centre Hills, ashfalls and acid rains have been frequent and heavy during 1996–2005, interspersed with periods of recovery. This pattern of localized obliteration of ecological communities, accompanied by much more widespread impacts of ash/acid rainfall, has presumably been the pattern in previous eruptions, although direct evidence is lacking. Montserrat's avifauna is of considerable conservation importance, as it includes the critically endangered single-island endemic Montserrat Oriole (Hilton *et al*. 2003), the vulnerable four-island endemic Forest Thrush, and nine other restricted-range species (Stattersfield *et al*. 1998, Arendt *et al*. 1999, Hilton *et al*. 2001) (see Table 1 for scientific names of the study species).

Regular forest bird monitoring commenced in the Centre Hills in December 1997, and these data allow a rare glimpse of the response of a bird community to such a major disturbance event. In this paper, we report population changes between 1997 and 2005, encompassing four major ashfalls and the intervening recovery periods. We examine whether ashfalls have caused temporal changes in species' abundances – both decline and recovery – and whether birds redistribute themselves in the immediate aftermath of ashfalls. We also examine the effect of variations in seasonal rainfall on population trends.

METHODS

Study area and study species

Montserrat has a moist tropical climate, with rainfall varying between 1000 and 2500 mm per year. The natural climax vegetation is a succession from xerophytic scrub, through seasonal forest, evergreen rainforest, and elfin woodland as precipitation and altitude increase (Blankenship 1990). There are three main hill ranges – the South Soufrière Hills, Soufrière Hills and Centre Hills, rising to 700–900 m asl. Prior to 1995, forests covered most land above *c*. 250 m in these hill ranges (Fig. 1). At lower altitudes, there are narrow strips of riparian forest only.

The current eruption has destroyed all of the hill forest in the South Soufrière and Soufrière Hills, with the exception of a small (*c*. 200-ha) patch in the southeast of the South Soufrière Hills. Several narrow fringes of degraded riparian forest in the lowlands of the north of the island continue to support small populations of some forest bird species, including Forest Thrush. Other than this, Montserrat's forest bird community is now confined to the Centre Hills forest (*c*. 1400 ha). The Centre Hills were affected by major ashfalls in August–October 1997. There was a strong ashfall gradient within the Centre Hills, such that sites in the south of the range received ash to a depth of *c*. 50 mm, whereas in the north of the range, *c*. 5 mm of ash fell (Montserrat Volcano Observatory unpubl. data). Another substantial ashfall occurred on 3 July 1998. A third major ashfall occurred on 29 July 2001. Accurate data on ash levels are not available, but ash depths were similar to the 1997 events (C.G.R. Bowden pers. comm.). On 12/13 July 2003, a major dome collapse deposited 150 mm of ash over southwestern parts of the Centre Hills, decreasing to only 5 mm in the northeast (Montserrat Volcano Observatory unpubl. data). In the intervening periods, there were numerous minor ashfalls. In addition, the large quantity of ash in the soil was frequently re-circulated by wind action during dry periods.

During forest bird monitoring in the Centre Hills, 12 resident forest birds were recorded in sufficient numbers to be statistically analysed (Table 1). Arendt *et al*. (1999) report absolute population densities for these species in the Centre Hills, based

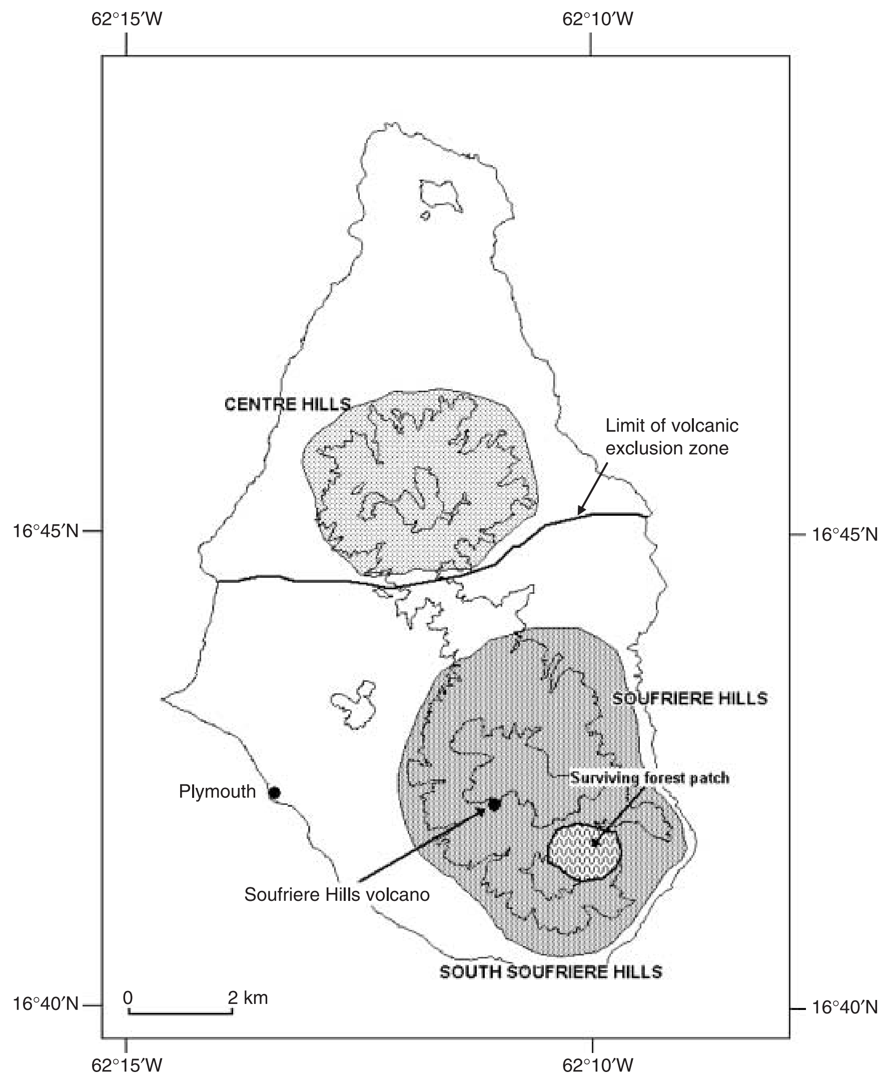

Figure 1. Map of Montserrat, showing location of Soufrière Hills volcano, Soufrière Hills, South Soufrière Hills and the Centre Hills study area. Shaded areas show approximate outlines of hill forest areas: the extant Centre Hills forest, the destroyed forest in the Soufrière and South Soufrière Hills, and the surviving forest patch in the South Soufrière Hills.

on distance-sampling (Buckland *et al.* 1993). This set includes all of the restricted-range bird species known to occur on Montserrat, except Green-throated Carib, Antillean Euphonia and Lesser Antillean Bullfinch, which reach highest densities in drier, lowland sites on the island (Montserrat Forest Department unpubl. data).

Bird census

All bird count data consist of point-counts, conducted at 47 fixed points that were visited repeatedly over the course of the monitoring scheme. The points were taken from a systematic grid of 140 points placed across the entire Centre Hills (see Arendt *et al.* 1999). All points were > 300 m apart, so they are independent with respect to detections of individual birds. For pragmatic reasons, the 47 points sampled from the main grid could not be chosen entirely at random. Rather, they were chosen to create a series of routes that could be walked in a single day and to cover a representative sample of habitats in the Centre Hills. In practice, this means that they are slightly spatially autocorrelated, and tend to be in more accessible areas of the forest. However, they give good overall coverage of the

Table 1. Study species of resident forest bird in the Centre Hills, Montserrat.

Species	Global status*	Mass (g)†	Diet‡	Feeding zone‡
1 Scaly-naped Pigeon *Columba squamosa*	Least Concern	288	Frugivore/herbivore	Arboreal (terrestrial)
2 Bridled Quail-dove *Geotrygon mystacea*	Restricted-range	230†	Granivore/insectivore	Terrestrial
3 Mangrove Cuckoo *Coccyzus minor*	Least Concern	64	Insectivore	Understorey
4 Purple-throated Carib *Eulampis jugularis*	Restricted-range	9	Nectarivore/insectivore	Understorey & canopy
5 Antillean Crested Hummingbird *Orthorynchus cristatus*	Restricted-range	3.8	Nectarivore/insectivore	Understorey & canopy
6 Caribbean Elaenia *Elaenia martinica*	Restricted-range	22.6	Insectivore/frugivore	Aerial
7 Forest Thrush *Cichlherminia lherminieri*	Restricted-range Vulnerable	100	Insectivore/frugivore	Terrestrial (understorey & canopy)
8 Scaly-breasted Thrasher *Margarops fuscus*	Restricted-range	72	Frugivore/insectivore	Canopy
9 Pearly-eyed Thrasher *Margarops fuscatus*	Restricted-range	105	Frugivore/insectivore/ carnivore	Canopy
10 Brown Trembler *Cinclocerthia ruficauda*	Restricted-range	53	Insectivore	Terrestrial (understorey)
11 Bananaquit *Coeroba flava*	Least Concern	10	Nectarivore/Insectivore	Understorey
12 Montserrat Oriole *Icterus oberi*	Restricted-range Critically Endangered	35	Insectivore	Understorey

*Based on BirdLife International (2004) and Stattersfield *et al*. (1998).
†Mist-net capture data from Montserrat (RSPB/MALHE unpubl. data) and Dunning (1992).
‡Authors' pers. obs., Raffaele *et al*. (1998) and del Hoyo *et al*. (1997, 1999).

Centre Hills and the habitats contained therein, including the full altitudinal range.

Each point-count was conducted for 10 min, following a 3-min settling down period. Counts were conducted by two or more observers, at least one of whom was experienced with the Montserratian avifauna. Counts were conducted between 05:45 and 15:00 h, and were suspended during heavy rain. All bird detections were recorded. Full details of census techniques are reported in Arendt *et al*. (1999) and Hilton *et al*. (2003).

The 47 points were visited repeatedly, beginning in December 1997, until June 2005. Censuses were conducted in four seasons: Dec/Jan, Mar/Apr, Jun/Jul and Sep/Oct. Most species in Montserrat breed during March–June, so that the Jun/Jul census includes fledglings from the breeding season just completed, whereas the subsequent Mar/Apr census represents the pre-breeding situation. Because of this, we defined discrete 'years' in analysis as running from the Jun/Jul census to the Mar/Apr census. During December 1997 to November 2001, censuses were conducted quarterly. Following this, censuses were conducted less frequently. In most censuses, a few points were missed. Overall, data are available for 25 censuses.

Spatial distribution of ashfall

Spatial variation in ashfall was determined from isopach maps provided by the Montserrat Volcano Observatory for two of the four major ashfalls (August–October 1997 and July 2003). For each of these events, the isopach maps were used to estimate depth of ash coverage for each census point, and an overall average ash depth ('Ash-level') was derived, and used as a score of the local level of ashing. The spatial pattern of ashfall differed somewhat between the two events. During 1997, heaviest ashing was in the south of the Centre Hills, declining toward the north. In 2003, ashing was heaviest in the southwest, declining towards the northeast. The 1998 and 2001 ashfalls were broadly speaking heaviest in the south and lowest in the north, but detailed information is lacking.

Other environmental variables

Four habitat characteristics of each point were measured during August 2003 (Table 2). These variables capture major axes of variation in the Centre Hills environment, particularly vegetation structure and water availability, but are relatively simple to measure. Precipitation data from the Hope Ghaut (southwest Centre Hills, 16°45′N, 62°13′W) rain gauge were used to assess the effect of rainfall on population trends. Data were missing for 1997 and 1998. For those years, we therefore interpolated values by linear regression, using data available from the nearby island of Nevis (ftp://ftp.ncdc.noaa.gov/pub/data/inventories/COUNTRY-LIST.TXT; ftp://ftp.ncdc.noaa.gov/pub/data/inventories/GLOBAL-SFC-1900-98D.TXT). Long-term data indicate an extremely high correlation between Nevis and Montserrat rainfall (1982–96 annual totals, $r = 0.93$, $P < 0.001$).

Data analysis

Counts for each species were initially modelled as Poisson distributed data, with a log link function. Where data were underdispersed in a Poisson model (deviance/*df* < 0.9), we modelled the data as a binary distribution (present or absent), with a binomial error structure and logit link function (Crawley 1993). Binomial models were used for Bridled Quail-dove, Purple-throated Carib, Caribbean Elaenia, Brown Trembler and Mangrove Cuckoo. For these species, > 75% of counts were zero, and < 10% of counts were of two or more birds. All Poisson models had deviance/*df* < 1.6, and therefore overdispersion effects were minor.

We used PROC GENMOD in the statistic package SAS v.9.1 for the analysis. In all models, 'Point' × 'Season' was declared as a repeated-measures variable with a first-order autoregressive covariance structure, to account for autocorrelation among successive counts at the same points, while also controlling for seasonal variation in abundance and detectability. All Poisson models were rescaled using the DSCALE option. Type III Generalised Estimating Equations (GEE) were used to estimate the Wald χ^2 statistic, and hence *P*-value for each explanatory variable.

Species' population trends

We first examined annual variation in bird counts, using 'Year' ($n = 8$ years) as a categorical explanatory variable. 'Year' was numbered from the Jun/Jul census in calendar year_t to the Mar/Apr census in calendar year_{t+1}. The parameter estimates given for each year by this model were used as the Population index values (see following section).

Effects of ashfall and rainfall on population trends

We next modelled bird counts as a function of ashfall and rainfall, while accounting for possible density dependence in counts. For ashfall, we modelled for each species:

$$\text{'Count'}_{\text{year } t+1} = \text{'Recent ashfall'} + \text{'Population index'}_{\text{year } t}$$

where 'Recent ashfall' is a binary variable, which is given a value of 1 in censuses that were completed between a major ashfall (i.e. August–October 1997, July 1998, July 2001, July 2003, see above) and the subsequent breeding season (commencing in April), and 'Population index' is the modelled annual population index (previous section). For rainfall analyses, we replaced 'Recent ashfall' with 'Wet season rainfall'$_{\text{year } t}$ and 'Dry season rainfall'$_{\text{year } t}$.

Table 2. Habitat variables measured at each point on the census grid.

Variable	Variable type	Method of measurement
Distance to watercourse	Continuous (m). Assigned to one of four distance bands: 0–25 m, 25–50 m, 50–100 m, and > 100 m, with the midpoint of each distance band being used to develop a continuous variable	Visually estimated in the field by forest rangers who know the area well
Rainfall	Continuous (mm yr^{-1})	Derived from isohyet map of Montserrat for the period 1935–64
Altitude	Continuous (m asl)	Hand-held altimeter
Canopy cover	Continuous (arcsine transformed percentage)	Estimates were made vertically through a hand-held tube 10 times along a 20-m transect through the census point

We separately analysed wet and dry season rainfall, because we *a priori* expected them to have differing and perhaps opposing effects on bird counts. The wet season in Montserrat is the hurricane season (July–December), and is prone to periods of cool weather, strong winds and heavy rain, whereas the dry season (January–June) is prone to occasional periods of drought. The bulk of the birds' breeding season occurs during the dry season. The effects of rainfall are expected to arise primarily through medium-term impacts on forest ecology (e.g. plant growth and flowering, insect abundance). Hence, we modelled the effect of rainfall in the study year prior to the counts. Conversely, ashfalls are relatively instantaneous events, the effects of which (covering surfaces with ash) are likely to be initially large, and then to diminish rapidly. Therefore, we modelled ashfall effects on subsequent counts in the same study year.

Spatial and temporal effects of ash on species' abundances

To assess the effect of ashfall on counts in more detail, models were developed for each species using both spatial and temporal variation in ashfall as explanatory variables (and again accounting for density dependence):

$$\text{'Count'}_{\text{year } t+1} = \text{'Recent ashfall'} + \text{'Ash-level'} + \text{'Recent ashfall'} \times \text{'Ash-level'} + \text{'Population index'}_{\text{year } t}$$

where 'Ash-level' reflects spatial variation in the quantity of ash falling across the Centre Hills over the entire course of the eruption (see above). Hence, this model evaluates (1) whether counts vary in response to recent ash deposition in the Centre Hills (significant effect of 'Recent ashfall'); (2) whether counts over the whole study period vary in response to spatial variations within the Centre Hills in the amount of ash falling (significant effect of 'Ash-level'); and (3) whether the temporal response to ashfall varies between high-ash and low-ash areas (significant effect of 'Recent ashfall' × 'Ash-level').

As spatial variation in the amount of ash may be confounded by variation in other habitat features, we also analysed counts in relation to 'Ash-level', after controlling for habitat associations. We developed habitat association models for each species, using the explanatory habitat variables described in Table 2. Quadratic altitude, canopy cover and rainfall effects were included in the initial models, but no interaction terms were permitted. *t*-tests indicated that altitude and rainfall differ significantly between low and high ash points (low ash points being lower altitude and higher rainfall), but that values of other habitat variables did not differ significantly between the two ash-level categories.

Full habitat association models were developed, with subsequent step-wise deletion of non-significant interaction terms and then main effects, until a minimal adequate model (MAM) with all variables significant ($P < 0.05$) was obtained. A categorical 'Year' term was included in all models, to account for temporal variation in counts. 'Point' × 'Season' was, as in all models, declared as a repeated-measures subject. The normally distributed standardized residuals from the MAM were then used as a response variable, with 'Ash-level' as an explanatory variable in a GEE model (with 'Point' × 'Season' as a repeated measure) to test for significant effects of 'Ash-level' on bird counts.

RESULTS

Species' population trends

Species trends across eight years showed a rather high degree of concordance. Most species increased during 1997/8–2000/1, and almost all species decreased in abundance between 2001/2 and 2002/3 (Fig. 2). Trends subsequent to 2003 were varied. In contrast to the general pattern, Caribbean Elaenia and Montserrat Oriole decreased between 1997 and 2001, Bananaquit showed a remarkably smooth trend followed by a sharp drop between 2002/3 and 2003/4, and Purple-throated Carib and Caribbean Elaenia doubled in abundance between 2001/2 and 2002/3. Figure 3 shows that the mean population multiplication rate (λ) tended to vary systematically by year among the study species, being high initially, and then declining gradually to a low point in the interval 2001/2–2002/3, with a subsequent increase in the final years of the study period. Mean λ across all species exceeded 1 in all time-intervals except for 2000/1–2001/2 and 2001/2–2002/3.

Effects of ashfall and rainfall on population trends

Given that there is a common temporal pattern in λ among most species (Fig. 3), does this relate to temporal environmental variation? Four species

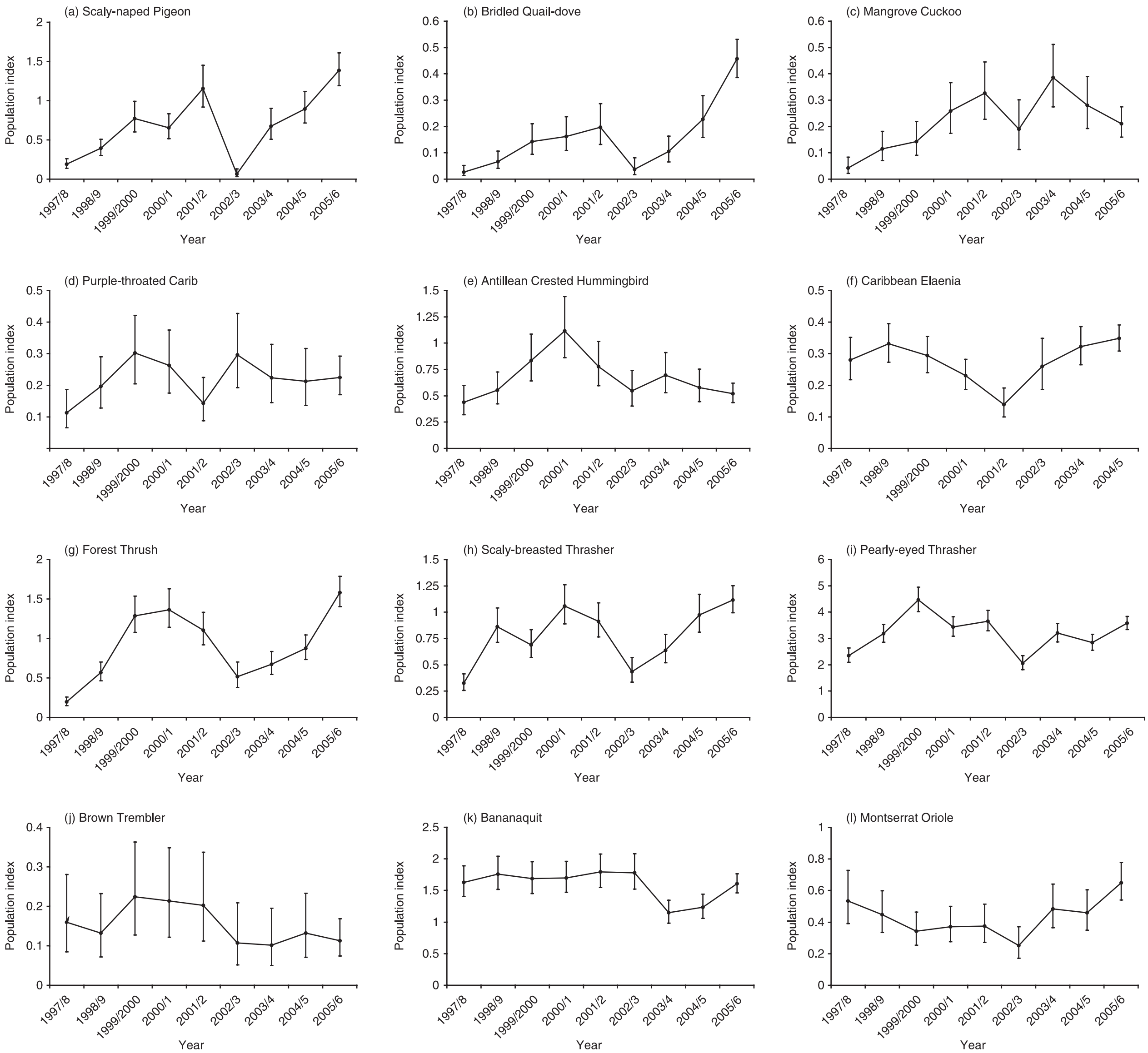

Figure 2. Population trends of resident forest birds in the Centre Hills, Montserrat, 1997–2005. Points and solid lines: fitted annual estimates from Generalised Estimating Equations (GEEs), using *'Year'* as a categorical factor, ± 95% confidence limits. Values are back-transformed parameter estimates from GEEs. Hence, for Poisson models (Scaly-naped Pigeon, Antillean Crested Hummingbird, Forest Thrush, Scaly-breasted Thrasher, Pearly-eyed Thrasher, Bananaquit and Montserrat Oriole), values represent estimated count per point. For binomial models (Bridled Quail-dove, Purple-throated Carib, Caribbean Elaenia, Brown Trembler and Mangrove Cuckoo), values represent estimated probability of detecting the species per point.

– Scaly-naped Pigeon, Bridled Quail-dove, Forest Thrush and Brown Trembler – showed strong and significant declines in response to 'Recent ashfall' (Table 3). Perversely, Mangrove Cuckoo appeared to increase substantially following ashfalls. No effect of recent ashfall was detected in counts of the remaining seven species. Hence, for a significant part but not a majority of the forest bird community there was evidence that ashfalls induce relatively sharp short-term declines in counts.

However, the models suggested that rainfall in the previous year had an even stronger impact on bird counts. Most species abundances responded significantly to rainfall in the previous year (Table 4). A group of species (Scaly-naped Pigeon, Bridled Quail-dove, Purple-throated Carib, Forest Thrush

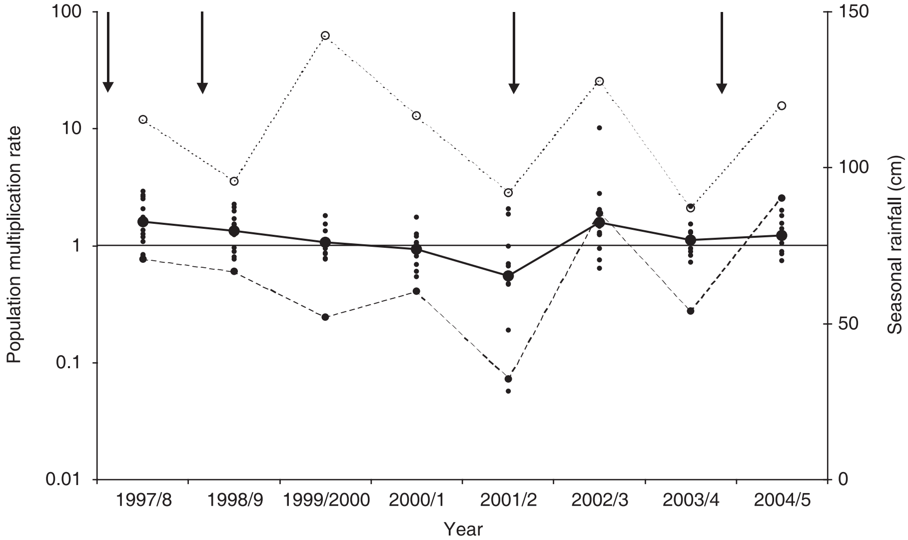

Figure 3. Population multiplication rate of 12 forest bird species, in relation to rainfall and ashfall, in Montserrat's Centre Hills, 1997–2005. Small dots: values of population multiplication rate (λ, = population index$_{\text{year } t+1}$/population index$_{\text{year } t}$) for individual species in each year interval. Thick continuous line: geometric mean value of λ; large open circles: wet-season rainfall in year$_t$; large closed circles: dry-season rainfall in year$_t$; vertical arrows: time intervals in which a major ashfall occurred in year$_t$.

Table 3. Effect of recent volcanic ashfall on population trends of forest birds.

	Recent ashfall		
Species	Effect (% change)*	Wald χ^2 (*df* = 1)	*P*
Scaly-naped Pigeon	**–51%**	**22.9**	**< 0.0001**
Bridled Quail-dove	**–32%**	**4.09**	**0.043**
Mangrove Cuckoo	**+30%**	**4.55**	**0.033**
Purple-throated Carib	–13%	1.37	0.24
Antillean Crested Hummingbird	–11%	1.84	0.17
Caribbean Elaenia	+12%	0.89	0.35
Forest Thrush	**–27%**	**12.8**	**0.0003**
Scaly-breasted Thrasher	–3.9%	0.25	0.61
Pearly-eyed Thrasher	–8.6%	2.88	0.090
Brown Trembler	**–28%**	**3.86**	**0.049**
Bananaquit	+0.71%	0.01	0.90
Montserrat Oriole	+13%	0.85	0.36

Based on Generalised Estimating Equations, with 'Recent ashfall' as a binary variable, 'Year' as a fixed effect, and 'Point' × 'Season' as a repeated-measures effect.
Rows in bold are significant effects ($P < 0.05$).
*Modelled percentage difference in counts between a census conducted following a recent ashfall, and censuses conducted in the absence of recent ashfall. Positive values indicate that counts increased following ashfalls, and vice versa.

and Pearly-eyed Thrasher) responded positively to wet-season rainfall, by increasing in abundance in the subsequent year. None of these species showed the same positive response to dry-season rainfall: Scaly-naped Pigeon and Pearly-eyed Thrasher decreased following wet dry seasons, Forest Thrush showed a near-significant trend in the same direction, while Purple-throated Carib and Bridled Quail-dove showed no response to dry-season rainfall. Antillean Crested Hummingbird and Brown Trembler both

Table 4. Effect of seasonal rainfall on population trends of forest birds.

Species	Wet-season rainfall: Effect (% change)*	Wald χ^2 (df = 1)	P	Dry-season rainfall: Effect (% change)*	Wald χ^2 (df = 1)	P
Scaly-naped Pigeon	**+15%**	**5.47**	**0.019**	**–19%**	**26.1**	**< 0.0001**
Bridled Quail-dove	**+25%**	**6.10**	**0.014**	+2.3%	0.12	0.73
Mangrove Cuckoo	**–22%**	**9.25**	**0.0024**	**–15%**	**8.87**	**0.0029**
Purple-throated Carib	**+20%**	**19.5**	**0.0021**	+6.6%	1.55	0.21
Antillean Crested Hummingbird	+6.2	1.78	0.18	**–8.1%**	**5.33**	**0.021**
Caribbean Elaenia	–12%	2.38	0.12	**+18%**	**9.00**	**0.0027**
Forest Thrush	**+29%**	**39.4**	**< 0.0001**	–5.6%	2.82	0.093
Scaly-breasted Thrasher	+0.90%	0.03	0.87	+2.6%	0.64	0.42
Pearly-eyed Thrasher	**+11%**	**20.7**	**< 0.0001**	**–12%**	**49.2**	**< 0.0001**
Brown Trembler	+14%	2.19	0.14	–14%	3.18	0.074
Bananaquit	+3.0%	0.79	0.37	–3.0%	0.78	0.38
Montserrat Oriole	–1.2%	0.02	0.88	+3.9	0.31	0.58

Based on Generalised Estimating Equations, with 'Wet-season rainfall' or 'Dry-season rainfall' in the previous years as a covariate, 'Year' as a fixed effect, and 'Point' × 'Season' as a repeated-measures effect.
Rows in bold are significant effects ($P < 0.05$).
*Modelled percentage change in counts if rainfall is 1 sd above the mean, relative to abundance if rainfall takes the mean value (n = 8 years of rainfall data). Positive values indicate that counts increased following high rainfall, and vice versa.

showed the same positive responses to wet-season rain and negative responses to dry-season rain, but without such strong statistical support.

In contrast to this pattern across seven of the study species, Caribbean Elaenia increased following dry seasons, but showed no response to wet-season rainfall. Mangrove Cuckoo showed a different response altogether: it increased following years of low rainfall in wet and dry seasons. The remaining species – Scaly-breasted Thrasher, Bananaquit and Montserrat Oriole – showed no suggestion of a population response to rainfall.

In full models including both rainfall and ashfall variables simultaneously, the idea that rainfall was the more important determinant of population trends was borne out (Table 5). However, these full models suggested that dry-season rather than wet-season rainfall may be the more important factor. Five species showed a negative trend in response to dry-season rainfall, i.e. they tended to increase when the previous dry season was relatively dry. For Brown Trembler, there was a similar, marginally non-significant effect. Caribbean Elaenia showed a reverse pattern, increasing after wet dry seasons. Three species (Purple-throated Carib, Forest Thrush and Pearly-eyed Thrasher) responded positively to wet-season rainfall in the full models.

Conversely, the effects of recent ashfall tended to weaken when rainfall effects were controlled for in the full models. There was evidence of strong negative effects of ash on counts of Scaly-naped Pigeon and Brown Trembler only. For Antillean Crested Hummingbird there was a marginally non-significant negative effect of ash. For Bridled Quail-dove and Forest Thrush, the negative effects of ash that were apparent from the ash-only models disappeared in the full models. The perverse positive effect of ash on Mangrove Cuckoos disappeared when rainfall was accounted for.

Spatial and temporal effects of ash on species' abundances

The outcomes of models analysing the effect of recent major ashfall, spatial variation in ash levels and the interaction between them are shown in Table 6. These models suggest that the effects of ash were relatively slight, and not widespread across the avifauna. Temporal effects were apparent only in the two Columbid species, which were significantly less abundant in counts conducted after recent ashfalls. Spatial effects were found in Montserrat Oriole, which tended to be less abundant in areas with high ashfall. Conversely, Mangrove Cuckoo was significantly more abundant in high ash areas. For Forest Thrush alone there was evidence of a redistribution away from high ash areas in immediate response to ashfalls.

Table 5. Effect of seasonal rainfall and ashfall on population trends of forest birds.

	Wet-season rainfall			Dry-season rainfall			Ashfall		
Species	Effect (% change)*	Wald χ^2 (*df* = 1)	*P*	Effect (% change)*	Wald χ^2 (*df* = 1)	*P*	Effect (% change)	Wald χ^2 (*df* = 1)	*P*
Scaly-naped Pigeon	–24%	38.4	< 0.0001	–	–	–	–56%	29.8	< 0.0001
Bridled Quail-dove	–	–	–	–	–	–	–	–	–
Mangrove Cuckoo	–11%	4.05	0.044	–18%	2.98	0.084	–	–	–
Purple-throated Carib	–	–	–	+26%	11.1	0.009	–	–	–
Antillean Crested Hummingbird	–13%	13.0	0.0003	–	–	–	–19%	3.47	0.063
Caribbean Elaenia	+22%	15.8	< 0.0001	–	–	–	–	–	–
Forest Thrush	–14%	15.8	< 0.0001	+30%	18.8	< 0.0001			
Scaly-breasted Thrasher	–	–	–	–	–	–	–	–	–
Pearly-eyed Thrasher	–14%	52.2	< 0.0001	+14	22.2	< 0.0001			
Brown Trembler	–23%	7.76	0.054	–	–	–	–39%	4.87	0.027
Bananaquit	–	–	–	–	–	–	–	–	–
Montserrat Oriole	–	–	–	–	–	–	–	–	–

Based on Generalised Estimating Equations, with 'Wet-season rainfall', 'Dry-season rainfall' and 'Recent ashfall' as explanatory variables, 'Year' as a fixed effect, and 'Point' × 'Season' as a repeated-measures effect. Non-significant explanatory variables were sequentially deleted. All effects with $P < 0.10$ are shown in the table.

*Modelled percentage change in counts if rainfall is 1 sd above the mean, relative to abundance if rainfall takes the mean value ($n = 8$ years of rainfall data). Positive values indicate that counts increased following high rainfall, and vice versa.

Table 6. Effects of spatial and temporal variation in volcanic ash forest bird counts.

	Recent ashfall		Ash-level		'Recent ashfall' × 'Ash-level'	
Species	Direction of effect	*P*	Direction of effect	*P*	Direction of effect*	*P*
Scaly-naped Pigeon	–	**0.0003**	+	0.065	+	0.82
Bridled Quail-dove	–	**0.035**	**–**	0.066	+	0.58
Mangrove Cuckoo	+	0.27	**+**	**< 0.0001**	+	0.49
Purple-throated Carib	–	0.71	–	0.50	–	0.42
Antillean Crested Hummingbird	–	0.59	–	0.37	–	0.51
Caribbean Elaenia	+	0.65	+	0.68	+	0.69
Forest Thrush	–	0.19	+	0.055	–	**0.043**
Scaly-breasted Thrasher	+	0.95	+	0.32	–	0.41
Pearly-eyed Thrasher	–	0.61	–	0.89	–	0.087
Brown Trembler	–	0.12	+	0.20	+	0.87
Bananaquit	–	0.42	+	0.24	+	0.062
Montserrat Oriole	+	0.74	–	**0.025**	**–**	0.50

Based on Generalised Estimating Equations, with 'Recent ashfall', 'Ash-level' and 'Recent ashfall' × 'Ash-level' as explanatory variables, 'Year' as a fixed effect, and 'Point' × 'Season' as a repeated-measures effect.

P-values marked in bold are significant ($P < 0.05$).

*A negative effect implies that counts in areas experiencing high ashfalls were relatively lower during censuses when there had been 'Recent ashfall', and vice versa.

The models in which habitat associations were controlled for also gave little evidence for avoidance of high ash areas by forest birds. Only one species, Bridled Quail-dove, showed a significantly lower abundance in high ash areas, after habitat associations were controlled for (Table 7).

DISCUSSION

These analyses provide some of the first information concerning the effect of the Soufrière Hills volcanic eruption on Montserrat's bird community. It also gives a unique insight into the response of avifaunas

Table 7. Effect of spatial variation in volcanic ash on forest bird counts, after controlling for habitat associations.

Species	Habitat variables in model*				'Ash-level' parameter estimate†	Wald χ^2 (*df* = 1)	*P*
	Altitude	Rainfall	Canopy cover	Distance to watercourse			
Scaly-naped Pigeon	–				0.0016	0.63	0.43
Bridled Quail-dove					**–0.0027**	**6.06**	**0.014**
Mangrove Cuckoo	n	+	+	+	0.0014	0.83	0.36
Purple-throated Carib	n			–	–0.0001	0.01	0.91
Antillean Crested Hummingbird	+	–	n	–	0.0017	2.32	0.13
Caribbean Elaenia	–			+	–0.0003	0.03	0.87
Forest Thrush	–			–	0.0016	0.65	0.42
Scaly-breasted Thrasher	–				0.0005	0.09	0.76
Pearly-eyed Thrasher	–				–0.0005	0.06	0.80
Brown Trembler					0.0010	0.50	0.48
Bananaquit	+	n	–	–	0.0000	0.00	0.99
Montserrat Oriole	n				–0.0024	2.32	0.13

Habitat association models were developed using Generalised Estimating Equations, with habitat variables (linear and quadratic) and 'Year' as explanatory variables, and 'Point' × 'Season' as a repeated-measures effect. Standardized residuals from these models were then used as response variables in General Linear Models, with 'Ash-level' as a continuous explanatory variable. Values in bold indicate significant effects ($P < 0.05$) of spatial variation in volcanic ash on forest bird counts, after controlling for habitat associations.
*Symbols used to describe the relationship between bird abundance and habitat variables: +, positive association; –, negative association; n, quadratic association, with peak bird abundance at intermediate values of the explanatory variable.
†Positive values indicate that counts were higher at points with relatively high ash levels, and vice versa.

to volcanic ashfalls. The generality of the responses observed in Montserrat is unclear. Volcanic eruptions in different parts of the world vary in the quantity and nature of ash falling, and its persistence in the environment. The bird community sampled here contains a mix of forest insectivores, omnivores, nectarivores and frugivores, although, being from a small island that has a history of catastrophic ecological disturbance, it is characterized by generalist species, which may be more adaptable to disturbance than some other avifaunas.

The loss of *c.* 60% of the forested land was coupled with massive disruption of the remaining forest in the Centre Hills. Major ashfalls resulted in large-scale defoliation, and anecdotal reports from 1997/8 describe insect die-offs within the forest. Major ashfalls substantially depress canopy arthropod numbers (Marske 2004). Despite this, the Montserratian bird community has remained qualitatively unaltered: no resident forest bird species have been extirpated. Furthermore, the relative abundance of species has not changed greatly (Fig. 2). By contrast, major hurricanes are thought to have caused extreme population crashes on other Caribbean islands, in particular of nectarivores/frugivores (e.g. Wauer & Wunderle 1992, Rathcke 2000).

The volcano shifted from a period of intense activity and very frequent ashfalls in 1997 to a period of relative quiet, interspersed with occasional (less than annual) major ashfalls during 1998–2001. During this time, the majority of forest bird species showed very large-scale population increases (Fig. 2). Superficially, this suggests dramatic quantitative effects of ashfall on the abundance of most bird species in the Centre Hills, and the 1997–2001 increases can be interpreted as a recovery phase following the peak of volcanic activity. Furthermore, the pattern for several species was for very substantially lower counts in censuses following ashfalls (Table 3), suggesting an immediate acute effect of major ashfalls on bird populations. However, for eight of the 12 study species, there was no evidence of a reduction in counts immediately following an ashfall. In addition, when the influence of seasonal rainfall was examined, it appeared to explain a substantial part of the variation in bird numbers, and to reduce the apparent importance of ashfalls (Tables 4 & 5). Finally, the large variation in the quantity of ash falling in different parts of the Centre Hills should generate strong spatial variation in the observed bird population responses, and yet there was little evidence for reduced counts in areas that were most affected by ash, nor of redistribution of birds in response to ashfall (Tables 6 & 7). Redistribution of Bullock's Orioles *Icterus bullockii* away from high ash areas following ashfalls was observed at Mount St. Helens

(Butcher 1981). We therefore suggest that, although there were reductions in populations of some species immediately following ashfalls, these were relatively short-lived, and several species seemed remarkably unaffected.

The proximate causes of the low counts following ashfalls are not clear. Possibly, changes in the birds' behaviour might make them less conspicuous to observers (e.g. if stress and food shortage made them less vocal). However, this seems rather unlikely: in the immediate aftermath of ashfalls, birds are particularly visible because of the pale-coloured ash background and the extensive defoliation.

Nest failure resulting from abandonment and covering of eggs with ash was recorded in Bullock's Orioles and California Gulls *Larus californicus* following the Mount St. Helens eruption (Butcher 1981, Hayward *et al.* 1982). Andersen and MacMahon (1986) showed that predation rates were extremely high in ashfall areas. During major ashfalls on Montserrat, active nests of Montserrat Orioles were directly destroyed by falling ash (RSPB/MALHE unpubl. data) and this probably applies to all other open-nesting species. However, the major ashfalls in Montserrat occurred late in or shortly after the breeding season, so breeding failure seems relatively unlikely as a cause of population declines.

As the major ashfalls occurred near the start of the post-breeding period, low counts in the censuses that occurred between the ashfalls and the subsequent breeding season imply that temporarily increased mortality of adult and fledged juveniles was the proximate cause of the declines.

Reductions in arthropod numbers following ashfalls appear to be ephemeral but pronounced (Marske 2004), which may cause temporary food shortages. At Mount St. Helens there was also evidence of markedly lower insect abundance shortly after the eruption (Foster & Myers 1982), as ash from the eruption was lethal to insects (Edwards & Schwartz 1981). Following ashfalls, birds may also be more conspicuous to predators – in this instance primarily American Kestrels *Falco sparverius*, Merlins *Falco columbarius* and Pearly-eyed Thrashers (Arendt 2006). Hayward *et al.* (1982) showed that conjunctivitis can occur in birds following ashfall. It has also been shown that exposure to ash affects the human respiratory system (Searl *et al.* 2002). However, during mist-netting of *c.* 400 birds in the Centre Hills during 1997–2005, no externally obvious signs of ill-health were observed among Montserrat's avifauna. Immigration of large numbers of birds into the Centre Hills from the southern hill ranges might have occurred as these latter forests were destroyed; however, the pattern of population changes in the Centre Hills strongly suggests that this was not the case. The southern forests were effectively destroyed by late 1997, while forest bird populations in the Centre Hills at that time were apparently at their lowest (Fig. 2).

The apparently rapid population recovery following ashfall may indicate density-dependent improvements in demographic rates following ash-induced population decreases. Alternatively, the forest may be highly productive following an ashfall, due to the input of nutrients from ash, and a flush of new plant growth following defoliation. In either scenario, the recovery is likely to be driven by relatively high reproductive success in the breeding season following an ashfall. The net result is that, following an 8-year period in which there were four major ashfalls, most species were at least as abundant as at the outset. Similarly, at Mount St. Helens, songbird populations, having been depressed in the year of the eruption, were largely back to pre-eruption levels in the subsequent year (Foster & Myers 1982). Manuwal *et al.* (1987), who studied community-level effects of the Mount St. Helens eruption 2–5 years after the event, found that at a site that was lightly ashed, bird communities were little different from those in similar habitats in unaffected areas. At a second site, which suffered heavy vegetation loss through scorching, the numbers of tree-foliage insectivores and tree seed-eaters were dramatically reduced relative to ground-foraging birds. We were unable to study forest bird communities in scorched areas of Montserrat, because such areas occur only in the 'exclusion zone' in the south of the island where the volcano's continued activity makes access impossible.

Our data suggest that seasonal variation in rainfall plays a strong role in the population dynamics of Montserrat's forest birds, with the majority of species showing a significant response to either dry-season rainfall or wet-season rainfall. The most frequent response to rainfall was for species to decrease if the preceding dry season was relatively wet, and to increase if the preceding wet season was relatively wet. This implies that dry breeding seasons (dry season) resulted in high fecundity, and/or that survival of fledglings and adults was high in wet non-breeding seasons. Anecdotal observations suggest that the former is unlikely as a general response: a dry-season drought in 2001 caused widespread breeding deferral and failure in the Centre Hills (RSPB/MALHE unpubl. data).

A complication arises because during the study years, there was a tendency for wet-season rainfall (July–December) to be positively correlated with dry-season rainfall in the following year (January–June) (Fig. 3). Hence, it is rather difficult to discern which season is the key driver of population trend. Furthermore, there was a tendency for ash-years to follow dry years (Fig. 3), so again the effects of ashfall and rainfall are difficult to separate. Thus, although we have some evidence that rainfall may be an important driver of forest bird population dynamics in Montserrat, more data are needed before the effect can be separated from that of ashfall, and its exact form can be determined.

It is difficult to discern whether any ecological traits predispose species to be sensitive to ashfall. The species that show evidence of declines and/or redistributions away from ashfalls are Scaly-naped Pigeon, Bridled Quail-dove, Antillean Crested Hummingbird, Forest Thrush, Brown Trembler and Montserrat Oriole (although the evidence is equivocal for some of these). Assigning Lesser Antillean bird species to feeding guilds is problematic, because they are almost all generalists, feeding on more than one major food type (Table 1). This in itself may be a response to the high level of environmental stochasticity in Lesser Antillean habitats, which militates against specialization. Although one food type may be dominant under normal conditions, diet may change in response to stressful conditions such as ashfalls; for example, Montserrat Orioles have been observed feeding on fruit during ashfall episodes, but very rarely at other times (RSPB/MALHE unpubl. obs.). Butcher (1981) suggested that, in general, small insectivorous birds were most affected by the ash from the Mount St. Helens eruption, but there is no evidence for this in the Montserrat forest bird community, and indeed no particular diet type appears to be more sensitive than others, nor does body size seem to predict sensitivity. There are, however, signs of a link between primary feeding zone and sensitivity: all of the terrestrially foraging species show evidence of declines or redistribution in response to ashfall. This is in agreement with Marske's (2004) suggestion that canopy arthropods are less severely affected by ashfall than terrestrial arthropods, because ash is removed from the canopy relatively quickly by rainfall and leaf-fall, whereas it remains in the soil far longer.

Overall, the effects of the eruption are perhaps less severe than might be anticipated for resident birds on such a small island. These results are in contrast to data concerning the fruit-bat community in Montserrat, which has been profoundly altered. Two of the nine fruit-bat species present on the island in the mid-1990s are apparently extirpated, and capture rates of all species declined greatly in 1997/8 (Adams & Pedersen 1999, Pedersen 2000). Data concerning the impact of the eruption on the terrestrial reptiles and amphibians of Montserrat have not been published.

One might expect the massive ash deposition to cause longer-term changes to the ecology of the Centre Hills. Volcanic ash is known to change soil characteristics (Nammah *et al.* 1986), to reduce growth of plant seedlings (Caruso *et al.* 1990) and to stress especially sensitive plants (Sadler & Grattan 1999). The effects of acid rain on forest plants and decomposers are still debated (e.g. Bormann 1985, Larkin & Kelly 1987, Chen *et al.* 1991, Sherman & Fahey 1994, Chang & Lee 1995, Heneghan & Bolger 1996). One might also predict indirect effects on bird communities. The introduced rat population in the Centre Hills increased dramatically from 1998 to 2001 (both Black Rat *Rattus rattus* and Brown Rat *R. norvegicus* are abundant, although whether one or both species increased is not known), before subsequently declining. It is unclear whether this was in response to volcanic disturbance, but it is known that nest predation by rats on Montserrat Orioles, and hence presumably other sensitive bird species, was extremely high in 2001. However, such long-term and indirect effects will be superimposed on an ecosystem that is already substantially influenced by human activity. The forest is largely secondary, following clearance in the plantation era (Beard 1949), and still contains numerous non-native fruit trees. Introduced Pigs *Sus scrofa* and rats are widespread. Agricultural and built areas fringe the hills, with consequent benefits for species that thrive in anthropogenic landscapes, such as Pearly-eyed Thrasher, a major nest-predator (Arendt 2006). The effect of the eruption might be surprisingly small relative to other external influences on the forest.

If the current eruption continues, one can expect further temporary reductions in Montserratian forest bird populations. However, as long as the ashfalls are intermittent, and are not compounded by other catastrophes, forest bird populations appear able to persist. After 9 years of the current eruption, Montserrat remains a major site for many of the restricted-range species of the Lesser Antilles EBA.

This study was funded by the UK Foreign & Commonwealth Office, American Bird Conservancy, WWF/Novo

Nordisk and University of Aarhus. We are grateful to Tony Hill (DFID), Richard Allcorn, Chris Bowden, Ken Smith, Mark Hulme, Joah Madden, Liz Mackley and Debbie Pain (RSPB) and Phil Atkinson (British Trust for Ornithology) for valuable discussion and fieldwork assistance, and to David Buckingham, Richard Bradbury and Paul Donald (RSPB), and Preben Blæsild (University of Aarhus) for statistical suggestions. David Robinson and John Guilbert kindly provided Nevis rainfall data. The Montserrat Volcano Observatory (MVO) provided ashfall data for the Centre Hills. Professor Mike Ivie and Katie Marske (Montana State University) provided valuable additional data and discussion. The manuscript was greatly improved by the suggestions of Gavin Siriwardena and an anonymous referee.

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Received 11 April 2006; revision accepted 11 August 2006.