

## Effect of El Niño and La Niña on abundance of frugivorous and nectarivorous terrestrial birds in three tropical forests

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**Abstract:** El Niño and La Niña climatic oscillations have dramatic effects on population dynamics and community structure of different animals. For marine birds, El Niño phenomenon drastically increases their mortality and reduces their reproductive success. In terrestrial ecosystems, the lack of long-term longitudinal data limits our understanding of the impact of El Niño and La Niña on bird populations and communities. We analyzed changes in abundance of frugivorous (large, medium, and small) and nectarivorous birds on three tropical forest types (lowland, premontane and montane) during El Niño, La Niña and neutral years using data from 16 Christmas' Bird Counts in Costa Rica. Abundance of large and medium size frugivores increased during La Niña events, and the abundance of nectarivores during El Niño in the lowland forest, but neither of these events affected the abundance of small frugivores. In the montane forest, abundance of all four bird groups increased during El Niño, but decreased during La Niña events. Abundance of large, and small frugivores increased in the premontane forest during La Niña events, but other bird groups were not affected by La Niña. The abundance of small frugivores also increased during El Niño. We hypothesize that changes in abundance of frugivores and nectarivores during La Niña and El Niño events is probably correlated with fluctuations in food resources as it has been reported for other terrestrial tropical ecosystems.

**Key words:** El Niño; La Niña; nectarivorous birds; frugivorous birds; climatic change.

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The evaluation of the changes in patterns of bird abundance is important for our understanding of factors that could affect population dynamics (survival and mortality) and animal communities (changes in species composition) (Holt, 1993; Yodzis, 1993; Brown, 1995). In bird communities, species often adjust the timing of molting, migration and reproduction to fluctuations in food resources, which in turn respond to predictable, seasonal climatic changes (Stiles, 1985; Loiselle & Blake, 1991; Worthington, 1996). Unpredictable climatic

anomalies such as El Niño Southern Oscillation (hereafter El Niño) and presumably La Niña phenomenon, have a strong impact on survivorship and reproduction in many bird populations, and consequently affect the community structure (Grant & Grant, 1983; Stiles, 1992; Jaksic & Laso, 1999). El Niño occurs approximately every 4.1 years (Glynn, 1988), but oscillates between two and ten years (Philander, 1985). El Niño and La Niña represent extremes in sea-surface temperatures, with El

Niño being above mean temperature and La Niña below it (Andreoli & Kayano, 2005).

The impact of El Niño and La Niña on bird populations often varies between taxonomic groups. Seabirds are presumably more strongly affected than land-bird species. For example, rates of survivorship and reproduction of many marine bird species (e.g., *Phalacrocorax bougainvilli*, *Sula variegata*, *Pelecanus thagus*, *Nonnapternum harrisi*, *Diomedea irrorata*, and *Spenicus mendiculus*) that nest in the area of maximum impact of El Niño are drastically reduced, particularly during strong El Niño events (Idyll, 1973; Boersma, 1978; Tovar, Guillen, & Cabrera, 1987; Rechten, 1985; Hays, 1986; Valle, Cruz, Cruz, Merlen, & Coulter, 1987; Glynn, 1988). During the strong El Niño events food supply for marine birds (e.g., the sardine *Sardinops sagax* and the anchovy *Engraulis ringens*) decrease strikingly, precluding birds to reproduce or greatly increasing mortality, particularly of juveniles (Ashmole, 1971; Hays, 1986; Anderson, 1989).

The effect of El Niño events on terrestrial bird populations in the Neotropics is difficult to evaluate for several reasons. First, occurrence, duration and intensity of El Niño are unpredictable (Cai et al., 2014). Second, the occurrence and intensity of La Niña is even less predictable (Grimm, Ferraz, & Gomes, 1998). Third, there is a lack of long-term monitoring data needed to evaluate the impact of these unpredictable climatic phenomena on the dynamics of bird populations in tropical forests (Wolfe & Ralph, 2009). During El Niño events, precipitation in general decreases in the Neotropical region, producing extensive droughts in areas where rains dominate year-round under normal conditions (Nobre & Shukla, 1996; Andreoli & Kayano, 2005; Paxton, Cohen, Paxton, Németh, & Moore, 2014), although precipitation at more localized scales could be higher in some areas during El Niño years (Villalobos & Retana, 2000). On the contrary, La Niña which sometimes occurs right after El Niño or not at all is often considered the anti-Niño because it has roughly the opposite effect on climatic conditions (Philander,

1985; Brenes & Bonilla, 2012). Our main objective here is then to test the effect of El Niño and La Niña events on the abundance of terrestrial bird populations in three different forest types in Costa Rica. We used data from Christmas Bird Counts from 1984 to 2011, the longest data set of bird abundance in Costa Rica. The effect of the El Niño is extremely variable over Central America (Ropelewski & Halpert, 1987; Enfield & Mayer, 1997; Sheffield & Wood, 2008). For instance, Waylen, & Caviades (1996) and Giannini, Kushnir, & Cane (2000) show that El Niño events in Costa Rica produce contrasting climatic conditions between Pacific (decreases rainfall) and Caribbean slopes (increases rainfall). Thereby, we expect contrasting results on bird abundance among forest types since the effect of El Niño could affect differently each forest.

## MATERIALS AND METHODS

**Study sites:** We selected three localities for which long term monitoring data ( $\geq 16$  years) on bird abundance and species composition is available. This data set allows comparisons among multiple events of El Niño, La Niña, and neutral years. The three localities include three forest types: lowland rain forest (La Selva Biological Station, Caribbean slope), premontane forest (Grecia, Pacific slope), and montane forest (Monteverde, continental divide that includes portions of both Caribbean and Pacific slopes). Forest vegetation for La Selva and Monteverde were described by Hartshorn, (1983) and Haber, (2000) respectively. Vegetation in Grecia consists of a matrix of large sugar cane and coffee plantations, urban habitats and large fragments of riparian premontane forest.

**Bird abundance data:** We obtained bird species abundance from Christmas' Bird Counts (CBC) conducted in each locality under Audubon protocol (National Audubon Society, 2010). CBCs use a standard protocol that consists of counting bird species and abundance inside a circle of 24 km in diameter

(452.4 km<sup>2</sup> area). In each locality, the circle includes the largest area of most forest types in that locality; the location of the circular sampling area is set prior to the first CBC and this location is maintained through time. Additionally, CBCs are conducted during a single 24 h period started at 00:00 h and finished at 24:00 h on the same routes year after year, which increases the comparative power of the data over time. The period of time analyzed varied across localities: lowland rain forest from 1985 to 2011, premontane forest from 1984 to 2003, and montane forest from 1994 to 2010. Data on CBC were obtained from The Organization for Tropical Studies (OTS, 2010) ([http://www.ots.ac.cr/cbc\\_laselvea](http://www.ots.ac.cr/cbc_laselvea)) and National Audubon Society (<http://www.christmasbirdcount.org>).

For each locality, we selected resident large frugivorous (> 30 g), medium size frugivorous (20 - 30 g), small frugivorous (< 20 g), and nectarivorous bird species (Table S1). We selected this subset of species because they fulfilled the following criteria: (1) species are conspicuous reducing their false-positive identification, and (2) species main food resource (fruits and nectar) are seasonal and influenced by rainfall levels that change according to El Niño and La Niña occurrence. We only used species recorded in 50 % or more of the CBC in each locality.

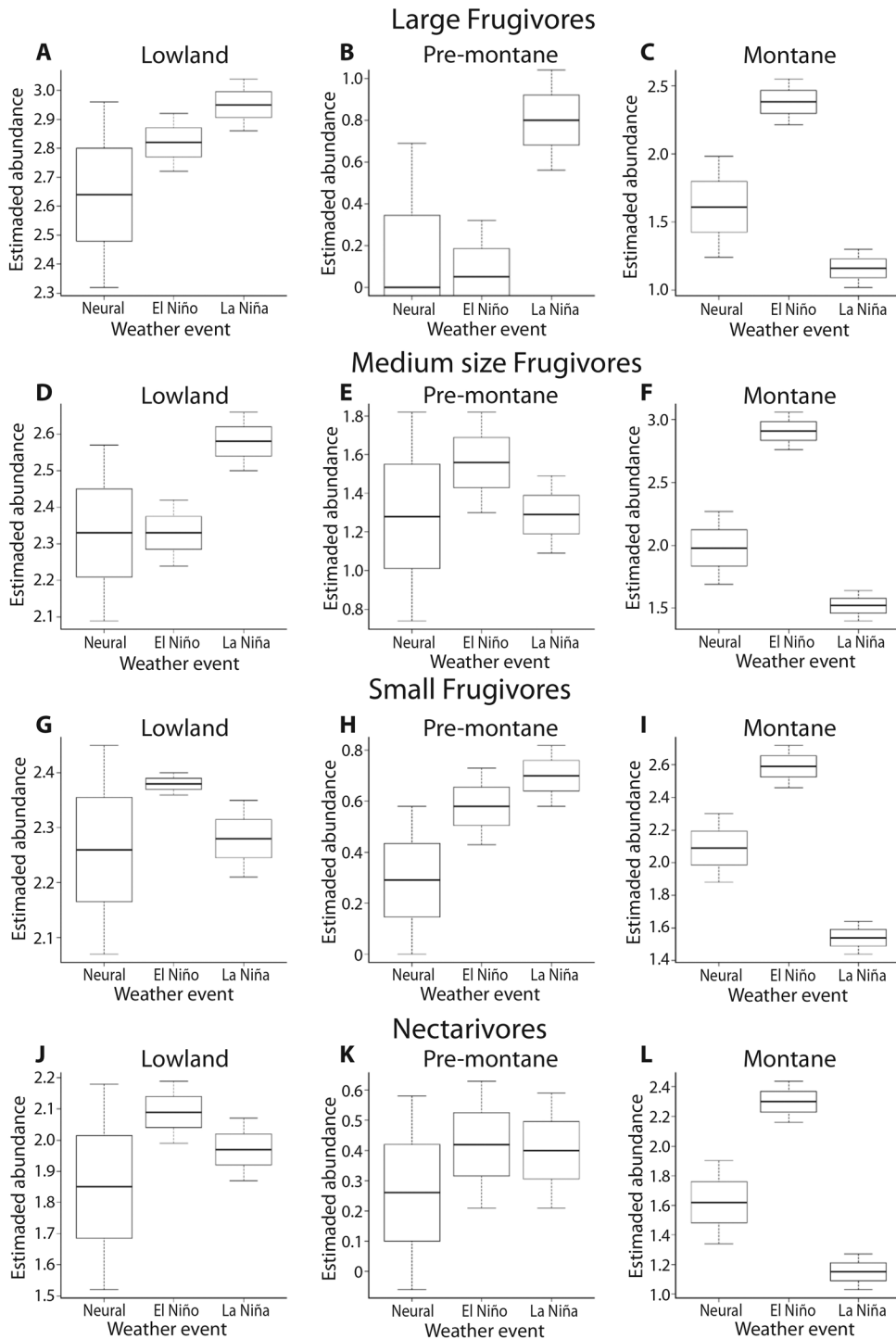
**Statistical analyses:** We compared bird abundance (e.g. count frequency) of species included in each of the four-bird diet-categories for each of the forest types and three weather events (i.e., El Niño, La Niña, neutral years) using Generalized Linear Models with a Poisson distribution or quasipoisson distribution when residuals were over-dispersed (GLM, library MASS). We used Zero Inflated Models (library glmmADMB) with a negative binomial probability distribution when the number of ceros exceed those expected by a Poisson (or quasipoisson) distribution. With the negative binomial probability distribution, we could accomplish the assumptions of normality of residuals and homoscedasticity. El Niño, La Niña, or neutral years were defined

with the Oceanic Niño Index (ONI), obtained from <https://ggweather.com/enso/oni.htm>. Events are defined by the National Oceanic and Atmospheric Administration (<https://www.noaa.gov/>) as five consecutive overlapping 3-month periods with values of the ONI index above the +0.5° anomaly for warm (El Niño) events, or below the -0.5° anomaly for cold (La Niña) events. For the analyses we included the median value (negative or positive) of the 3-month periods for each year defined as El Niño, La Niña, or neutral. Thus, the statistical models included bird-diet categories, weather events, the co-variable “ONI”, which account for the variation in climatic conditions during of El Niño, La Niña, and neutral years, and the total number of person-hours per bird count as another covariate in the analyses (i.e., time) to account for yearly-variation in effort and total distance covered, and species as random factors within the model. All analyses were done using the R statistical language, version 3.0.1 (R Core Team, 2013).

## RESULTS

The number of El Niño, La Niña, and Neutral years were similar for all three study sites. Lowland rain forest included seven years in each of the three weather categories; the premontane forest included six El Niño and La Niña years, and seven neutral years; and the montane forest included six El Niño years, seven La Niña years, and five neutral years.

**Lowland rain forest:** We tested the effect of weather events on the abundance of 17 large frugivorous (LF), 27 medium size frugivorous (MF), 36 small frugivorous (SF), and 12 nectarivorous (Nc) bird species in the lowland forest (Table S1). The abundance of large and medium size frugivores increased significantly during La Niña events in comparison to neutral years (Table 1, Fig. 1), and the abundance of Nc during the El Niño events relative to neutral years. Abundance of SF was not affected by La Niña or El Niño events; nor El Niño affected significantly the abundance in any of the three



**Fig. 1.** Mean, standard error, and confidence intervals for three groups frugivorous birds (large, medium size, and small), and nectarivorous birds in three forest types (lowland, pre-montane, and montane). The mean was estimated from the intercept of the statistical models, which directly correlate with the mean values of the variables included in the models.

TABLE 1  
 Comparison between climatic events (El Niño, La Niña, and Neutral years) for Large frugivores,  
 Medium size frugivores, Small frugivores, and Nectarivores in three forest types based on  
 Generalized Linear Models with a Poisson probability distribution.

<b>Lowland rain forest</b>					
<b>Large frugivores</b>					
Effect	Coefficient	SE	T	P	
Neutral	2.64	0.32	8.13 (446)	0.0000	
Niño - Neutral	0.18	0.10	1.81 (446)	0.0708	
Niña - Neutral	0.31	0.09	3.27(446)	0.0011	
Niña - Niño	01.2	0.16	0.79 (446)	0.4274	
ONI	0.05	0.05	0.92 (446)	0.3532	
Counting hours	0.00	0.00	8.79 (446)	0.0000	
<b>Medium frugivores</b>					
Effect	Coefficient	SE	T	P	
Neutral	2.33	0.24	9.55 (696)	< 0.0001	
Niño - Neutral	0.00	0.09	0.40 (696)	0.9681	
Niña - Neutral	0.25	0.08	2.99 (696)	0.0029	
Niña - Niño	0.25	0.14	1.75 (696)	0.0806	
ONI	0.09	0.05	1.90 (696)	0.0581	
Counting hours	0.00	0.00	8.25(696)	< 0.0001	
<b>Small frugivores</b>					
Effect	Coefficient	SE	T	P	
Neutral	2.26	0.19	11.57 (896)	< 0.0001	
Niño - Neutral	0.12	0.02	1.60 (896)	0.1089	
Niña - Neutral	0.02	0.07	0.23 (896)	0.7881	
Niña - Niño	-0.10	0.11	-0.85 (896)	0.3928	
ONI	-0.01	0.04	-0.19 (896)	0.8428	
Counting hours	0.00	0.00	11.33 (896)	< 0.0001	
<b>Nectarivores</b>					
Effect	Coefficient	SE	T	P	
Neutral	1.85	0.33	5.11 (321)	< 0.0001	
Niño - Neutral	0.24	0.10	2.33 (321)	0.0203	
Niña - Neutral	0.12	0.10	1.19 (321)	0.2352	
Niña - Niño	-0.12	0.16	-0.76 (321)	0.4491	
ONI	0.00	0.06	0.08 (321)	0.9382	
Counting hours	0.00	0.00	5.66 (321)	< 0.0001	
<b>Pre-montane forest</b>					
<b>Large frugivores</b>					
Effect	Coefficient	SE	T	P	
Neutral	0.00	0.69	0.00 (104)	0.9968	
Niño - Neutral	0.05	0.27	0.19 (104)	0.8485	
Niña - Neutral	0.80	0.24	3.27 (104)	0.0015	
Niña - Niño	0.74	0.44	1.70 (104)	0.0913	
ONI	0.22	0.14	1.62 (104)	0.1069	
Counting hours	0.03	0.00	6.00 (104)	< 0.0001	

TABLE 1 (Continued)

<b>Medium frugivores</b>				
Effect	Coefficient	SE	Z	P
Neutral	1.28	0.54	2.40 (228)	0.017
Niño - Neutral	0.28	0.26	1.10 (228)	0.272
Niña - Neutral	0.01	0.20	0.07 (228)	0.942
Niña - Niño	-0.27	0.40	-0.67 (228)	0.504
ONI	-0.07	0.13	-0.49 (228)	0.623
Counting hours	0.02	0.00	4.92 (228)	< 0.001

<b>Small frugivores</b>				
Effect	Coefficient	SE	T (339)	P
Neutral	0.29	0.29	0.98 (338)	0.3254
Niño - Neutral	0.29	0.15	1.99 (338)	0.0469
Niña - Neutral	0.41	0.12	3.29 (338)	0.0011
Niña - Niño	-0.29	0.15	-1.99 (338)	0.5462
ONI	0.10	0.07	1.49 (338)	0.1370
Counting hours	0.02	0.00	5.96 (338)	< 0.0001

<b>Nectarivores</b>				
Effect	Coefficient	SE	T	P
Neutral	0.26	0.32	0.82 (266)	0.4147
Niño - Neutral	0.16	0.21	0.75 (266)	0.4522
Niña - Neutral	0.14	0.19	0.72 (266)	0.4680
Niña - Niño	-0.02	0.35	-0.05 (266)	0.9611
ONI	0.13	0.11	1.21 (266)	0.2244
Counting hours	0.02	0.00	4.99 (266)	< 0.0001

<b>Montane forest</b>				
<b>Large frugivores</b>				
Effect	Coefficient	SE	T	P
Neutral	1.61	0.37	4.35 (268)	< 0.0001
Niño - Neutral	0.77	0.17	4.42 (268)	< 0.0001
Niña - Neutral	-0.45	0.14	-3.20 (268)	0.0016
Niña - Niño	-1.23	0.27	-4.65 (268)	< 0.0001
ONI	-0.42	0.09	-4.39 (268)	< 0.0001
Counting hours	0.00	0.00	4.22 (268)	< 0.0001

<b>Medium frugivores</b>				
Effect	Coefficient	SE	T	P
Neutral	1.98	0.29	6.73 (506)	< 0.0001
Niño - Neutral	0.93	0.15	5.98 (506)	< 0.0001
Niña - Neutral	-0.46	0.12	-3.81 (506)	0.0002
Niña - Niño	-1.39	0.23	-6.14 (506)	< 0.0001
ONI	-0.52	0.08	-6.15 (506)	< 0.0001
Counting hours	0.00	0.00	2.78 (506)	0.0055

TABLE 1 (Continued)

Small frugivores				
Effect	Coefficient	SE	T	P
Neutral	2.09	0.21	10.06 (829)	< 0.0001
Niño - Neutral	0.50	0.13	3.77 (829)	< 0.0001
Niña - Neutral	-0.55	0.10	-5.24(829)	< 0.0001
Niña - Niño	-1.05	0.13	-3.77 (829)	< 0.0001
ONI	-0.30	0.07	-4.18 (829)	< 0.0001
Counting hours	0.00	0.00	4.69 (8.29)	< 0.0001
Nectarivores				
Effect	Coefficient	SE	Z	P
Neutral	1.62	0.28	5.87 (468)	< 0.0001
Niño - Neutral	0.68	0.14	4.66 (468)	< 0.0001
Niña - Neutral	-0.47	0.12	-4.14 (468)	< 0.0001
Niña - Niño	-1.15	0.21	-5.57 (468)	< 0.0001
ONI	-0.41	0.08	-5.35 (468)	< 0.0001
Counting hours	0.00	0.00	3.06 (468)	< 0.0001

The intensity of the climatic event (ONI Index) was included in the model.

The corresponding degrees of freedom are included in parentheses besides the T-values.

The Z-values correspond to the Zero Inflated Models.

groups of frugivores (Table 1). Neither we found significant differences in the abundance of frugivores and nectarivores between La Niña and El Niño events (Table 1). The ONI did not have a significant effect on frugivorous and nectarivorous birds in the lowland rain forest (Table 1).

**Pre-montane forest:** For the premontane forest, we analyzed the abundance of 6 LF, 12 MF, 19 SF, and 15 Nc bird species. In this forest, the abundance of LF and SF increased significantly during La Niña events when compared with neutral years (Table 1, Fig. 1), but it did not affect the abundance of MF nor Nc. The abundance of SF also increased during El Niño, but it did not affect the abundance of other groups. The ONI had no effect on abundance of any of the bird groups (Table 1).

**Montane forest:** For the montane forest, we analyzed the abundance of 17 LF, 30 MF, 49 SF, and 26 Nc bird species. In this forest the abundance of all three groups of frugivores and the nectarivores increased during El Niño events in comparison to neutral years,

but decreased for all bird groups during La Niña events (Table 1, Fig. 1). The abundance of all four groups correlated negatively with ONI index values (Table 1). Thus, the abundance of birds in the montane forests has a strong increment during El Niño events, despite that bird abundance decreased as the index ONI increased.

The total number of person-hours per bird count correlated positively with bird abundance in all cases. However, the ONI index had only a significant effect on bird abundance in the Montane forest.

## DISCUSSION

The variation in the abundance of frugivorous and nectarivorous birds detected in this study could be the result of temporal and spatial changes in the phenology of flowering and fruiting species (food resources) caused by El Niño and La Niña events. The shifting in the pattern of precipitation, intensity of rainfall, and radiation caused by El Niño and La Niña directly affect the periodicity of phenological



phases, the distribution, and mortality of plants (Wright, Carrasco, Calderón, & Paton, 1999; Villalobos & Retana, 2000; Holmgren, Scheffer, Ezcurra, Gutiérrez, & Mohren, 2001; Jaksic, 2001; McPhaden, Zebiak, & Glantz, 2006; Chen & Cane, 2008). For instance, flowering and fruiting of understory plant species correlate with increasing temperature and radiation (Kimura, Yumoto, Kikuzawa, & Kitayama, 2009). Increasing variation of food resources (Wright et al., 1999) could force birds to change their movement patterns or to move to areas where the effect of these climatic anomalies is milder. Such variation could also increase mortality of birds if food resources decrease drastically (Wolfe & Ralph, 2009; Boyle, Norris, & Guglielmo, 2010), and all these factors could affect the abundance of species locally (Jaksic & Laso, 1999).

The fluctuation in bird abundance across bird groups in this study is similar to that reported for other terrestrial ecosystems in the Neotropics. For instance, in Barro Colorado island (Panama) fruit production greatly increases during El Niño events but decreases drastically when a mild dry season (e.g., the Niña event) follows El Niño, thus increasing mortality of frugivorous mammals (Foster, 1982; Wright et al., 1999). In the Galapagos Islands, reproduction and recruitment of *Geospiza fortis* significantly increased as a result of high production of seeds during the strong rainy season of El Niño 1982-1983 (Grant, 1986). In Chile, the diversity and density of several groups of landbirds increased during El Niño 1997-1998 (Jaksic & Laso, 1999). These changes in diversity and density are presumably a direct consequence of increasing rainfall in the region during El Niño years (Jaksic & Laso, 1999).

The effect of El Niño on climate varies among events and geographical scales. In Chile, total rainfall increases during El Niño but in Barro Colorado Island, rainfall actually decreases during these events, although increases in food resources have in both cases been attributed to El Niño events (Wright et al., 1999; Jaksic, 2001). In Costa Rica,

precipitation during the El Niño and La Niña events also varies between slopes and across events (Waylen, Quesada, & Caviedes, 1994; Waylen, & Caviedes, 1996; Waylen, Caviedes, Poveda, Mesa, & Quesada, 1998; Brenes & Bonilla, 2012). This variation affects differently the abundance of the bird groups in different forests. In the lowland forest abundance of frugivores (large and medium size) increased during La Niña years, but El Niño years did not have a significant effect on frugivores abundance, though abundance of nectarivores increased during these events (Table 1, Fig. 1). The montane forest showed an entirely opposite pattern for frugivores. In this forest, the abundance increased consistently for all frugivorous and nectarivorous birds during El Niño events, but their abundance decreased during La Niña. It is notable in the montane forest that El Niño has a strong positive effect on bird abundance, but this abundance tends to decrease if intensity of El Niño increases (Table 1). This suggests that there are at least two different processes affecting bird abundance in montane forests. One that likely makes birds to move uphill during El Niño, and another, perhaps less intense, affecting negatively their abundance at high elevation. In the premontane forest these climatic events had little effect on bird abundance. Only abundance of SF increased during La Niña events, but had no effect on LF, MF, and Nc (Table 1, Fig. 1). It is likely that differences in climatic conditions at small geographical scales affects differently plant phenology, and so avian food resources in each forest type, but until we have detailed information on the climatic conditions along the mountain slopes and their effect on bird food resources, the response to fluctuation in frugivores and nectarivores will remain elusive (Williams-Linera & Meave, 2002).

The changes in abundance during El Niño and La Niña events could be attributed to temporal and spatial fluctuation in food resources, but these climatic events may also affect bird reproduction and survivorship (Wolfe, Ralph, & Elizondo, 2015). Both climatic events may have drastic negative effects at the level



of population and community structure. For instance, some populations of Darwin's finches (*Geospiza* spp.) fail to reproduce during extremely dry years, which usually coincide with La Niña events, and mortality increases up to 85 % during these years and sex ratio skewed toward males (Boag & Grant, 1981; 1984; Grant & Grant, 1983; Grant, 1986). These factors delayed the recovery of populations (Boag & Grant, 1984). Similarly, survivorship of the Long-billed Hermit (*Phaetornis longirostris*) drastically decreased in a Costa Rican rain forest as a consequence of a flower shortage caused by a severe drought during El Niño event 1972-1973 (Stiles, 1992). Recovery of this population lasted about four years. Bird survival may also depend on the specific habitat features. For instance, in Costa Rica Survivorship of the White-collared Manakin (*Manacus candei*) was drastically affected by el Niño in disturbed forests but not in near mature forests (Wolfe et al., 2015).

Climate scenario models predict that El Niño events will increase in frequency as global, greenhouse warming increases (Cai et al., 2014). Considering that some populations of terrestrial birds require nearly four years to recover after the impact caused the by El Niño and that the mean period of El Niño occurrence is 4.1 yrs (Glynn, 1988), an increase in frequency of these events would increase the probability of some avian populations to become extinct if they are not capable to recover in a shorter time. We finally highlight the importance of long-term data on bird abundance and phenology of plants to evaluate more precisely the effects of the El Niño and La Niña climatic anomalies on population's dynamics and community structure of tropical birds.

**Ethical statement:** authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgements

section. A signed document has been filed in the journal archives.

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## RESUMEN

**El efecto de El Niño y La Niña sobre la abundancia de aves frugívoras y nectarívoras terrestres en tres bosques tropicales.** Las oscilaciones climáticas causadas por el fenómeno de El Niño y La Niña tienen efectos drásticos sobre la dinámica de las poblaciones y la estructura de las comunidades. Para aves marinas, el fenómeno de El Niño incrementa drásticamente su mortalidad y reduce su éxito reproductivo. En ecosistemas terrestres, la falta de datos a largo plazo limita nuestro entendimiento sobre el impacto de El Niño y La Niña sobre la dinámica de las poblaciones y comunidades de aves. Nosotros analizamos los cambios en la abundancia de aves frugívoras (grandes, medianos y pequeños) y nectarívoras en tres tipos de bosque tropical (lluvioso de tierras bajas, premontano y montano) durante los años de El Niño, La Niña, y años neutrales usando datos de al menos 16 conteos de navidad (Christmas' Bird Counts) en Costa Rica. La abundancia de frugívoros grandes y medianos incrementó durante los años de La Niña, y la abundancia de nectarívoros durante el Niño en el bosque lluvioso de tierras bajas, pero ninguno de estos eventos afectó la abundancia de frugívoros pequeños en este bosque. En el bosque montano, la abundancia de los cuatro grupos de aves incrementó durante los años de El Niño, pero disminuyó durante los años de La Niña. La abundancia de frugívoros grandes y pequeños aumentó en el bosque pre-montano durante los años de La Niña; sin embargo, la abundancia de los frugívoros medianos y los nectarívoros no fue afectada por los eventos por La Niña o El Niño. La abundancia de frugívoros pequeños también aumentó durante El Niño en este bosque. Proponemos la hipótesis de que los cambios en la abundancia de las aves frugívoras y nectarívoras reflejan fluctuaciones en

el recurso alimentario, como ha sido reportado en otros ecosistemas terrestres tropicales.

**Palabras clave:** El Niño; La Niña; aves nectarívoras; aves frugívoras; cambio climático.

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## Supporting Information

TABLE S1  
Bird species used in the analysis of effect of El Niño and La Niña in three forests of Costa Rica according to the effects of El Niño and La Niña

	English name	Category	Size (cm)	Forest type		
				Lowland rainforest	Premontane forest	Monatane forest
<b>TINAMIFORMES</b>						
<b>Tinamidae</b>						
	<i>Nothocercus bonapartei</i>	Highland Tinamou	Large frugivorous			X
	<i>Tinamus major</i>	Great Tinamou	Large frugivorous	X		X
	<i>Crypturellus soui</i>	Little Tinamou	Medium frugivorous	X		
	<i>Crypturellus boucardi</i>	Slaty-breasted Tinamou	Large frugivorous	X		
<b>GALLIFORMES</b>						
<b>Cracidae</b>						
	<i>Ortalis cinereiceps</i>	Gray-headed Chachalaca	Large frugivorous	X		X
	<i>Penelope purpurascens</i>	Crested Guan	Large frugivorous	X		X
	<i>Chamaepetes unicolor</i>	Black Guan	Large frugivorous		X	X
	<i>Crax rubra</i>	Great Curassow	Large frugivorous	X		
<b>Odontophoridae</b>						
	<i>Odontophorus leucolaemus</i>	Black-breasted Wood-Quail	Medium frugivorous			X
<b>COLUMBIFORMES</b>						
<b>Columbidae</b>						
	<i>Patagioenas cayennensis</i>	Pale-vented Pigeon	Large frugivorous	X		
	<i>Patagioenas speciosa</i>	Scaled Pigeon	Large frugivorous	X		
	<i>Patagioenas flavirostris</i>	Red-billed Pigeon	Large frugivorous		X	X
	<i>Patagioenas fasciata</i>	Band-tailed Pigeon	Large frugivorous		X	X
	<i>Patagioenas subvinacea</i>	Ruddy Pigeon	Medium frugivorous		X	X
	<i>Patagioenas nigrirostris</i>	Short-billed Pigeon	Medium frugivorous	26.5	X	X
	<i>Columbina inca</i>	Inca Dove	Medium frugivorous	20		X
	<i>Columbina passerina</i>	Common Ground-Dove	Small frugivorous	16		X
	<i>Columbina talpacoti</i>	Ruddy Ground-Dove	Small frugivorous	16.5	X	
	<i>Claravis pretiosa</i>	Blue Ground-Dove	Medium frugivorous	20	X	
	<i>Leptotila verreauxi</i>	White-tipped Dove	Medium frugivorous	26	X	X
	<i>Leptotila cassinii</i>	Gray-chested Dove	Medium frugivorous	24	X	
	<i>Geotrygon veraguensis</i>	Olive-backed Quail-Dove	Medium frugivorous	21.5	X	X
	<i>Geotrygon chiriquirensis</i>	Chiriqui Quail-Dove	Medium frugivorous	30		X
	<i>Geotrygon lawrencii</i>	Purplish-backed Quail-Dove	Medium frugivorous	25		X
	<i>Geotrygon costaricensis</i>	Buff-fronted Quail-Dove	Medium frugivorous	28		X
	<i>Geotrygon montana</i>	Ruddy Quail-Dove	Medium frugivorous	23	X	
<b>APODIFORMES</b>						
<b>Trochilidae</b>						
	<i>Glaucois aeneus</i>	Bronzy Hermit	Nectarivorous		X	
	<i>Threnetes ruckeri</i>	Band-tailed Barbthroat	Nectarivorous		X	

TABLE S1 (Continued)

	English name	Category	Size (mm)	Forest type		
				Lowland rainforest	Premontane forest	Montane forest
<i>Phaethornis guy</i>	Green Hermit	Nectarivorous				X
<i>Phaethornis longirostris</i>	Long-billed Hermit	Nectarivorous		X		X
<i>Phaethornis striigularis</i>	Stripe-throated Hermit	Nectarivorous		X		X
<i>Doryfera ludovicae</i>	Green-fronted Lancebill	Nectarivorous				X
<i>Colibri delphinae</i>	Brown Violetear	Nectarivorous				X
<i>Colibri cyanotus</i>	Lesser Violetear	Nectarivorous			X	X
<i>Heliophryx barroti</i>	Purple-crowned Fairy	Nectarivorous		X		X
<i>Anthracothorax prevostii</i>	Green-breasted Mango	Nectarivorous		X	X	X
<i>Heliodoxa jacula</i>	Green-crowned Brilliant	Nectarivorous				X
<i>Panterpe insignis</i>	Fiery-throated Hummingbird	Nectarivorous			X	X
<i>Heliomaster constantii</i>	Plain-capped Starthroat	Nectarivorous			X	X
<i>Lampornis hemileucus</i>	White-bellied Mountain-gem	Nectarivorous				X
<i>Lampornis calolaemus</i>	Purple-throated Mountain-gem	Nectarivorous			X	X
<i>Calliphlox bryantae</i>	Magenta-throated Woodstar	Nectarivorous				X
<i>Selasphorus flammula</i>	Volcano Hummingbird	Nectarivorous			X	
<i>Selasphorus scintilla</i>	Scintillant Hummingbird	Nectarivorous			X	X
<i>Chlorostilbon canivetii</i>	Canivet's Emerald	Nectarivorous			X	X
<i>Klais guimeti</i>	Violet-headed Hummingbird	Nectarivorous		X		X
<i>Phaechroa cuvierii</i>	Scaly-breasted Hummingbird	Nectarivorous		X		
<i>Campylopterus hemileucurus</i>	Violet Sabrewing	Nectarivorous			X	X
<i>Eupherusa eximia</i>	Stripe-tailed Hummingbird	Nectarivorous			X	X
<i>Elvira cupreiceps</i>	Coppery-headed Emerald	Nectarivorous				X
<i>Chalyburauochrysia</i>	Bronze-tailed Plumeleteer	Nectarivorous		X		
<i>Thalurania colombica</i>	Crowned Woodnymph	Nectarivorous		X		X
<i>Amazilia amabilis</i>	Blue-chested Hummingbird	Nectarivorous		X		
<i>Amazilia saucerrottei</i>	Steely-vented Hummingbird	Nectarivorous			X	X
<i>Amazilia tzacatl</i>	Rufous-tailed Hummingbird	Nectarivorous		X	X	X
<i>Amazilia rutila</i>	Cinnamon Hummingbird	Nectarivorous			X	X
<i>Hylcocharis eliciae</i>	Blue-throated Goldentail	Nectarivorous			X	
<b>TROGONIFORMES</b>						
<b>Trogonidae</b>						
<i>Trogon clathratus</i>	Lattice-tailed Trogon	Medium frugivorous	30	X		X
<i>Trogon massena</i>	Slaty-tailed Trogon	Medium frugivorous	30	X		X
<i>Trogon caligatus</i>	Gartered Trogon	Medium frugivorous	23	X		X
<i>Trogon rufus</i>	Black-throated Trogon	Medium frugivorous	23	X		
<i>Trogon collaris</i>	Collared Trogon	Medium frugivorous	25		X	
<i>Trogon aurantiiventris</i>	Orange-bellied Trogon	Medium frugivorous	25			X
<i>Pharomachrus mocinno</i>	Resplendent Quetzal	Large frugivorous	36		X	X
<b>PICIFORMES</b>						
<b>Capitonidae</b>						
<i>Eubucco bourcierii</i>	Red-headed Barbet	Small frugivorous	15			X
<b>Semnornithidae</b>						
<i>Semnornis frantzii</i>	Prong-billed Barbet	Small frugivorous	17			X
<b>Ramphastidae</b>						
<i>Aulacorhynchus prasinus</i>	Emerald Toucanet	Medium frugivorous	29		X	X
<i>Pteroglossus torquatus</i>	Collared Aracari	Large frugivorous	41	X		X
<i>Selenidera spectabilis</i>	Yellow-eared Toucanet	Large frugivorous	36			X
<i>Ramphastos sulfuratus</i>	Keel-billed Toucan	Large frugivorous	47	X	X	X
<i>Ramphastos ambiguus</i>	Yellow-throated Toucan	Large frugivorous	56	X		

TABLE S1 (Continued)

	English name	Category	Size (mm)	Forest type		
				Lowland rainforest	Premontane forest	Montane forest
<b>PSITTACIFORMES</b>						
<b>Psittacidae</b>						
<i>Eupsittula nana</i>	Olive-throated Parakeet	Medium frugivorous	23	X		
<i>Eupsittula canicularis</i>	Orange-fronted Parakeet	Medium frugivorous	22.5			X
<i>Ara ambiguus</i>	Great Green Macaw	Large frugivorous	79	X		
<i>Psittacara finschi</i>	Crimson-fronted Parakeet	Medium frugivorous	28	X	X	X
<i>Bolborhynchus lineola</i>	Barred Parakeet	Small frugivorous	16			X
<i>Brotogeris jugularis</i>	Orange-chinned Parakeet	Small frugivorous	18	X	X	X
<i>Touit costaricensis</i>	Red-fronted Parrotlet	Small frugivorous	17			X
<i>Pyrilia haematotis</i>	Brown-hooded Parrot	Medium frugivorous	21	X		X
<i>Pionus senilis</i>	White-crowned Parrot	Medium frugivorous	24	X	X	X
<i>Amazona albifrons</i>	White-fronted Parrot	Medium frugivorous	25			X
<i>Amazona autumnalis</i>	Red-lore Parrot	Large frugivorous	34	X		
<i>Amazona farinosa</i>	Mealy Parrot	Large frugivorous	38	X		
<b>PASSERIFORMES</b>						
<b>Tyrannidae</b>						
<i>Elaenia flavogaster</i>	Yellow-bellied Elaenia	Small frugivorous	15	X	X	X
<i>Elaenia frantzii</i>	Mountain Elaenia	Small frugivorous	15		X	X
<i>Mionectes olivaceus</i>	Olive-striped Flycatcher	Small frugivorous	13			X
<i>Mionectes oleagineus</i>	Ochre-bellied Flycatcher	Small frugivorous	12.5	X	X	X
<i>Zimmerius vilissimus</i>	Paltry Tyrannulet	Small frugivorous	9.5	X		X
<i>Rhynchocyclus brevirostris</i>	Eye-ringed Flatbill	Small frugivorous	15	X		
<b>Tityridae</b>						
<i>Tityra semifasciata</i>	Masked Tityra	Medium frugivorous	21	X	X	X
<i>Tityra inquisitor</i>	Black-crowned Tityra	Small frugivorous	18.5	X		
<i>Pachyramphus versicolor</i>	Barred Becard	Small frugivorous	12			X
<i>Pachyramphus cinnamomeus</i>	Cinnamon Becard	Small frugivorous	14	X		X
<i>Pachyramphus polychopterus</i>	White-winged Becard	Small frugivorous	14.5	X		
<i>Pachyramphus aglaiae</i>	Rose-throated Becard	Small frugivorous	16.5			X
<b>Cotingidae</b>						
<i>Querula purpurata</i>	Purple-throated Fruitcrow	Medium frugivorous	28	X		
<i>Cephalopterus glabricollis</i>	Bare-necked Umbrellabird	Large frugivorous	41	X		X
<i>Lipaugus unirufus</i>	Rufous Piha	Medium frugivorous	23	X		
<i>Procnias tricarunculatus</i>	Three-wattled Bellbird	Medium frugivorous	30	X		
<i>Carpodectes nitidus</i>	Snowy Cotinga	Medium frugivorous	22.5	X		
<b>Pipridae</b>						
<i>Corapipo altera</i>	White-ruffed Manakin	Small frugivorous	10			X
<i>Chiroxiphia linearis</i>	Long-tailed Manakin	Small frugivorous	11.5		X	X
<i>Dixiphia pipra</i>	White-crowned Manakin	Small frugivorous	10	X		
<i>Ceratopipra mentalis</i>	Red-capped Manakin	Small frugivorous	10	X		
<i>Manacus candei</i>	White-collared Manakin	Small frugivorous	11	X		
<b>Oxyruncidae</b>						
<i>Oxyruncus cristatus</i>	Sharpbill	Small frugivorous	16.5			X
<b>Vireonidae</b>						
<i>Vireo leucophrys</i>	Brown-capped Vireo	Small frugivorous	12			X
<i>Vireo lanispulchellus</i>	Green Shrike-Vireo	Small frugivorous	14	X		
<i>Cyclarhis gujanensis</i>	Rufous-browed Peppershrike	Small frugivorous	14			X



TABLE S1 (Continued)

	English name	Category	Size (mm)	Forest type		
				Lowland rainforest	Premontane forest	Montane forest
<b>Corvidae</b>						
<i>Cyanolyca cucullata</i>	Azure-hooded Jay	Medium frugivorous	29			X
<i>Calocitta formosa</i>	White-throated Magpie-Jay	Large frugivorous	46			X
<i>Psilorhinus morio</i>	Brown Jay	Large frugivorous	39	X	X	X
<b>Turdidae</b>						
<i>Myadestes melanops</i>	Black-faced Solitaire	Small frugivorous	17		X	X
<i>Catharus aurantirostris</i>	Orange-billed Nightingale-Thrush	Small frugivorous	16		X	X
<i>Catharus fuscater</i>	Slaty-backed Nightingale-Thrush	Small frugivorous	17			X
<i>Catharus frantzii</i>	Ruddy-capped Nightingale-Thrush	Small frugivorous	16			X
<i>Catharus mexicanus</i>	Black-headed Nightingale-Thrush	Small frugivorous	16	X		X
<i>Turdus plebejus</i>	Mountain Thrush	Medium frugivorous	24		X	X
<i>Turdus obsoletus</i>	Pale-vented Thrush	Medium frugivorous	23.5	X		X
<i>Turdus grayi</i>	Clay-colored Thrush	Medium frugivorous	23.5	X	X	X
<i>Turdus assimilis</i>	White-throated Thrush	Medium frugivorous	22			X
<b>Ptiliognatidae</b>						
<i>Phainoptila melanoxantha</i>	Black-and-yellow Silky-Flycatcher	Medium frugivorous	21			X
<i>Ptiliogomys caudatus</i>	Long-tailed Silky-Flycatcher	Medium frugivorous	24		X	
<b>Fringillidae</b>						
<i>Euphonia luteicapilla</i>	Yellow-crowned Euphonia	Small frugivorous	9.5			X
<i>Euphonia hirundinacea</i>	Yellow-throated Euphonia	Small frugivorous	11		X	X
<i>Euphonia elegantissima</i>	Elegant Euphonia	Small frugivorous	11			X
<i>Euphonia gouldi</i>	Olive-backed Euphonia	Small frugivorous	9.5	X		
<i>Euphonia minuta</i>	White-vented Euphonia	Small frugivorous	9	X		
<i>Euphonia annae</i>	Tawny-capped Euphonia	Small frugivorous	11	X		X
<i>Chlorophonia callophrys</i>	Golden-browed Chlorophonia	small frugivorous	13		X	X
<b>Passerellidae</b>						
<i>Chlorospingus flavopectus</i>	Common Bush-Tanager	Small frugivorous	13.5		X	X
<i>Chlorospingus pileatus</i>	Sooty-capped Bush-Tanager	Small frugivorous	13.5		X	X
<i>Chlorospingus canigularis</i>	Ashy-throated Bush-Tanager	Small frugivorous	13			X
<b>Icteridae</b>						
<i>Amblycercus holosericeus</i>	Yellow-billed Caciue	Medium frugivorous	23	X	X	X
<i>Psarocolius wagleri</i>	Chestnut-headed Oropendola	Large frugivorous	35	X		X
<i>Psarocolius montezuma</i>	Montezuma Oropendola	Large frugivorous	50	X	X	X
<i>Cacicus uropygialis</i>	Scarlet-rumped Caciue	Medium frugivorous	23	X		X
<i>Icterus prothemelas</i>	Black-cowled Oriole	Small frugivorous	19	X		
<i>Molothrus oryzivorus</i>	Giant Cowbird	Large frugivorous	33	X		
<b>Cardinalidae</b>						
<i>Piranga flava</i>	Hepatic Tanager	Small frugivorous	18			X
<i>Piranga bidentata</i>	Flame-colored Tanager	Small frugivorous	18		X	
<i>Habia rubica</i>	Red-crowned Ant-Tanager	Small frugivorous	18		X	X
<i>Habia fuscicauda</i>	Red-throated Ant-Tanager	Small frugivorous	19	X		
<i>Chlorothraupiscarmioli</i>	Carmioli's Tanager	Small frugivorous	17	X		X
<i>Caryothraustes poliogaster</i>	Black-faced Grosbeak	Small frugivorous	16.5	X		
<i>Passerina caerulea</i>	Blue Grosbeak	Small frugivorous	16.5		X	
<b>Thraupidae</b>						
<i>Thraupis episcopus</i>	Blue-gray Tanager	Small frugivorous	15	X	X	X
<i>Thraupis palmarum</i>	Palm Tanager	Small frugivorous	16	X	X	X
<i>Tangara larvata</i>	Golden-hooded Tanager	Small frugivorous	13	X		X
<i>Tangara guttata</i>	Speckled Tanager	Small frugivorous	13			X



TABLE S1 (Continued)

	English name	Category	Size (mm)	Forest type		
				Lowland rainforest	Premontane forest	Montane forest
<i>Tangara dowii</i>	Spangle-cheeked Tanager	Small frugivorous	13			X
<i>Tangara inornata</i>	Plain-colored Tanager	Small frugivorous	12	X		
<i>Tangara gyrola</i>	Bay-headed Tanager	Small frugivorous	13.5			X
<i>Tangara florida</i>	Emerald Tanager	Small frugivorous	12			X
<i>Tangara icterocephala</i>	Silver-throated Tanager	Small frugivorous	13			X
<i>Diglossa plumbea</i>	Slaty Flowerpiercer	Nectarivorous			X	X
<i>Chrysothlypis chrysomelas</i>	Black-and-yellow Tanager	Small frugivorous	12	X		X
<i>Chlorophanes spiza</i>	Green Honeycreeper	Small frugivorous	13	X		X
<i>Tachyphonus luctuosus</i>	White-shouldered Tanager	Small frugivorous	14	X		
<i>Tachyphonus delatarii</i>	Tawny-crested Tanager	Small frugivorous	14.5	X		
<i>Tachyphonus rufus</i>	White-lined Tanager	Small frugivorous	17	X		
<i>Lanio leucothorax</i>	White-throated Shrike-Tanager	Medium frugivorous	20	X		X
<i>Ramphocelus sanguinolentus</i>	Crimson-collared Tanager	Small frugivorous	18.5	X		X
<i>Ramphocelus passerinii</i>	Passerini's Tanager	Small frugivorous	16	X		X
<i>Cyanerpes lucidus</i>	Shining Honeycreeper	Small frugivorous	10	X		
<i>Cyanerpes cyaneus</i>	Red-legged Honeycreeper	Small frugivorous	11.5	X	X	X
<i>Dacnis venusta</i>	Scarlet-thighed Dacnis	Small frugivorous	11.5			X
<i>Dacnis cayana</i>	Blue Dacnis	Small frugivorous	11.5	X		
<i>Coereba flaveola</i>	Bananaquit	Small frugivorous	9	X		X
<i>Saltator atriceps</i>	Black-headed Saltator	Medium frugivorous	24	X		
<i>Saltator maximus</i>	Buff-throated Saltator	Medium frugivorous	20	X	X	X
<i>Saltator grossus</i>	Slate-colored Grosbeak	Small frugivorous	19	X		
<i>Saltator coerulescens</i>	Grayish Saltator	Medium frugivorous	20	X	X	X

Category refers to the classification of each species according to guild and body size. Size where obtained from Stiles and Skutch (1989).