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RESEARCH LETTER

Influences of the El Niño/Southern Oscillation and the North Atlantic Oscillation on avian productivity in forests of the Pacific Northwest of North America

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ABSTRACT

To model the effects of global climate phenomena on avian population dynamics, we must identify and quantify the spatial and temporal relationships between climate, weather and bird populations. Previous studies show that in Europe, the North Atlantic Oscillation (NAO) influences winter and spring weather that in turn affects resident and migratory landbird species. Similarly, in North America, the El Niño/Southern Oscillation (ENSO) of the Pacific Ocean reportedly drives weather patterns that affect prey availability and population dynamics of landbird species which winter in the Caribbean. Here we show that ENSO- and NAO-induced seasonal weather conditions differentially affect neotropical- and temperate-wintering landbird species that breed in Pacific North-west forests of North America. For neotropical species wintering in western Mexico, El Niño conditions correlate with cooler, wetter conditions prior to spring migration, and with high reproductive success the following summer. For temperate wintering species, springtime NAO indices correlate strongly with levels of forest defoliation by the larvae of two moth species and also with annual reproductive success, especially among species known to prey upon those larvae. Generalized linear models incorporating NAO indices and ENSO precipitation indices explain 50–90% of the annual variation in productivity reported for 10 landbird species. These results represent an important step towards spatially explicit modelling of avian population dynamics at regional scales.

Key words avian reproductive success, bird banding, bird migration, climate, defoliation, El Niño Southern Oscillation, MAPS, North Atlantic Oscillation, Pacific Northwest forests, population dynamics, weather.

INTRODUCTION

Global short-term climate variability is associated with phases of coupled oceanic and atmospheric phenomena including the El Niño/Southern Oscillation (ENSO) of the subtropical and tropical Pacific Ocean, and the North Atlantic Oscillation (NAO) between subtropical and northerly latitudes. During an ENSO warm phase (ENSO event) the equatorial Pacific Ocean surface between South America and the dateline becomes abnormally warm, which causes changes in global atmospheric circulation and associated rainfall distribution. Similarly, warm phase NAO conditions affect temperature and rainfall patterns at more northerly latitudes. Both ENSO- and NAO-induced seasonal weather conditions can affect primary productivity (Barnston & Livezey, 1987; Swetnam & Betancourt, 1998; Wiles *et al*., 2001) and insect abundance (Kemp *et al*., 1985; Swetnam & Lynch, 1993) which, in turn, may affect avian reproductive success.

In Europe, NAO influences winter and spring weather that, in turn, affects food resources for the resident European dipper (*Cinclus cinclus*) (Saether *et al*., 2000) and the timing of egg laying for the migratory pied flycatcher (*Ficedula hypoleuca*) (Both & Visser, 2001; Sokolov, 2001). Species that breed in eastern North America and winter in the Caribbean are also affected by weather patterns associated with global climate cycles. Drier conditions on Caribbean wintering grounds of neotropical migratory songbirds, such as those experienced during ENSO events, appear to limit the invertebrate prey biomass available. In Jamaica, drought conditions, such as those experienced prior to spring migration during ENSO events, reduce the invertebrate prey biomass available to ovenbirds (*Seiurus aurocapillus*) and lead to a loss of body mass that may increase the risk of mortality (Strong & Sherry, 2000). Similarly, weather patterns associated with ENSO events cause black-throated blue

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warblers (*Dendroica caerulescens*) to suffer higher mortality rates on their Jamaican wintering grounds and lower reproductive success on their New Hampshire breeding grounds presumably due to reduced prey availability (Sillett *et al*., 2000).

Conversely, in forests of western North America, the likelihood of severe insect outbreaks and enhanced prey availability for avian predators (Torgersen *et al*., 1990) increases during ENSO events (Swetnam & Lynch, 1993); thus we might expect these events to increase avian reproductive success in western North America. Other evidence, however, suggests that NAO affects forest dynamics through its influence on seasonal weather patterns (Mote *et al*., 1999) which, in turn, affect tree growth patterns across subarctic and north-temperate latitudes (D'Arrigo & Jacoby, 1993; Mote *et al*., 1999; Thompson & Wallace, 2001). Therefore, NAO might also be expected to affect the magnitude and intensity of annual insect outbreaks, which vary across the Pacific Northwest forests as a function of several environmental factors, including seasonal temperature extremes and precipitation (Kemp *et al*., 1985).

Here, we examine the relationships between these ENSO and NAO events and the reproductive success of landbird species that breed in the forests of the Pacific Northwest of North America. We report a strong relationship between a seasonal ENSO Precipitation Index (ESPI) (Curtis & Adler, 2000), springtime weather in western Mexico and subsequent reproductive success among neotropical migrants. Furthermore, on the breeding grounds in the forests of the Pacific Northwest, a strong relationship exists between an index of NAO (NAOI) (Barnston & Livezey, 1987) and springtime weather conditions that appear to determine the magnitude and extent of defoliating insect outbreaks. These factors, in turn, correlate positively with landbird reproductive success, especially among temperate wintering species.

METHODS

We collected data describing climate, weather, forest defoliation, and avian productivity to test four alternate hypotheses:

1 Both ENSO- and NAO-induced seasonal conditions influence reproductive success among landbirds that breed in forests of the Pacific Northwest.

2 Because neotropical migrants overwinter closer to the tropics, they are more influenced by ENSO activity than are species that overwinter at higher latitudes in North America (henceforth known as temperate wintering species).

3 Because temperate wintering species overwinter at higher latitude, they are more influenced by NAO activity than are neotropical migrants.

4 Annual reproductive indices increase as functions of invertebrate biomass, which in turn correlate with ENSO and/or NAO events.

ENSO precipitation and North Atlantic Oscillation Indices

Monthly ESPI values, dating back to January 1979, were collected from the National Aeronautics and Space Administration (NASA, 2001). We chose this metric because the commonly cited Southern Oscillation Index (SOI) is based on sea-level pressure differences between only two points, Tahiti and Darwin, and is therefore subject to localized noise (S. Curtis, personal communication). In contrast, ESPI is a satellite-based measure of larger-scale atmospheric circulation (Curtis & Adler, 2000) that determines the wind and storm patterns that probably affect birds' breeding or wintering habitat as well as their migratory routes. An inverse relationship exists between ESPI and SOI, such that ESPI is more positive during ENSO events when precipitation increases in the subtropical and tropical Pacific Ocean, whereas SOI is more negative during these events.

Similarly, we chose an index of NAO that reflects broad scale spatial atmospheric pressure patterns (Barnston & Livezey, 1987) in preference to other NAO indices that may also be subject to localized noise. Monthly North Atlantic Oscillation indices (henceforth referred to as NAOI) dating back to 1950 are archived at the National Oceanic and Atmospheric Administration's Climate Prediction Center website (www.cpc.ncep.noaa.gov/data/teledoc/nao.html; April 2002). A positive NAO index signifies that the atmospheric pressure over the subtropical portion of the North Atlantic is higher than normal and the atmospheric pressure over Iceland is lower than normal. This results in an increased pressure difference that causes stronger winter storms to cross the Atlantic Ocean on a more northerly track. This, in turn, leads to warm, wet winters in Europe; cold, dry winters in northern Canada and Greenland; and mild, wet winters in the eastern United States. A negative NAO index reflects a reduced pressure gradient between the subtropical North Atlantic and Iceland. This results in fewer and weaker winter storms crossing the Atlantic on a more west–east track, which brings cold air to northern Europe, moist air to the Mediterranean region, and increases the chance of snowfall in the eastern United States.

Landbird productivity indices and migratory classification

We indexed annual reproductive success (Peach *et al*., 1996) using nine years (1992–2000) of landbird banding data gathered from 33 Monitoring Avian Productivity and Survivorship (MAPS) constant-effort bird banding stations (DeSante *et al*., 1995) distributed among six national forests of the USDA Forest Service Pacific Northwest Region (USDA, 2001). We calculated the ratio of young to adults as a relative index of mean annual reproductive success (Peach *et al.*, 1996) in those species ($n = 34$) for which an average of at least four young were captured each year. This ratio-based index is unbiased by annual fluctuations in the adult population. For each species, plots of annual reproductive indices (1992–2000) can be found at http://www.birdpop.org/Results/PNW/suppdoc.htm.

MAPS stations consist of 10 12-m, four-tier, 36-mm mesh nets distributed among the central 8 hectares of a 20-hectare area. Effort was standardized in that each station was operated each year for six morning hours once during each of eight 10-day periods. In the Pacific Northwest, the first 10-day period begins 21 May after the majority of spring migrants have passed through and breeding territories have been established. The last period ends 8 August during post-fledgling dispersal but before birds have amassed enough fat to begin their autumn migration (IBP, unpublished data). We assume therefore that the majority of captures consist of breeding (or unmated) adults and young from within the boundaries of the station and from the local landscape surrounding the station. This assumption is supported by an analysis of data from six stations located at Big Oaks National Wildlife Refuge, Indiana, that showed reproductive indices for four forest-interior species increased as a function of mean size of woodland patches within a 4-km radius of the station (Nott, 2000). Clearly, if migrating individuals biased the numbers of adults and young captured, these relationships would not exist.

Capture rates may vary among species that are breeding at a station due to several behavioural factors. For instance, most captures are of species that utilize the understorey while canopy foragers are captured in smaller numbers. Also, MAPS productivity indices are considered relative indices that may vary because of behavioural differences between adults and young. The temporal patterns of these indices, however, should not be biased by behavioural differences and in fact are consistent with observed adult population changes in both MAPS data (DeSante *et al.*, 1999) and in annual point count data from the North American Breeding Bird Survey (Sauer *et al.*, 1999; DeSante *et al.*, 2001). Also, patterns of productivity indices and survival rate estimates are consistent with predictions based on life history traits such as migration strategy and nest location (DeSante, 2000).

We classified species as neotropical wintering (16 species) if the centres of their overwintering ranges lay between northern Mexico and northern South America or as temperate wintering (18 species) if the centres lay between the Pacific Northwest and northern Mexico (Howell & Webb, 1995; AOU, 1998). The temperate group included year-round residents, elevational migrants and short-distance latitudinal migrants.

Identifying seasonal determinants of reproductive success

To determine the part of the year during which ENSO or NAO most strongly affects the reproductive success of most species, we examined the relationships between annual reproductive indices for each species and seven overlapping 3-month averages (December–February to June–August) of ESPI and NAOI. Within species we ranked each 3-month period by the magnitude of Pearson correlation coefficients and then averaged the ranks for each period across species. We reversed the average rankings by subtracting them from seven, resulting in a range from 0 to 6.

Defoliation indices

Because seasonal conditions affect insect abundance (Kemp *et al.*, 1985), we indexed annual (1980–2000) defoliation levels from estimates of the spatial extent and intensity of defoliation (Sheehan, 1996) affecting the same six national forests of the Pacific Northwest in which the MAPS stations were located. Many invertebrates can cause defoliation of these Pacific Northwest forests, but between 1992 and 2000 the majority of defoliation was caused by two irruptive species: the western spruce budworm (*Choristoneura occidentalis*) and the Douglas fir tussock moth (*Orygia pseudotsugata*). Both of these species are common prey for many bird species (Torgersen *et al.*, 1990). From aerial sketch maps the USDA Pacific Northwest Region annually digitizes the boundaries of all defoliated patches of forest (Sheehan, 1996; http://www.fs.fed.us/r6/nr/fid/data.shtml). For each defoliated patch we calculated a defoliation index by multiplying the area affected by the intensity of the outbreak categorized as 1 (light), 2 (moderate) or 3 (heavy), and log-transforming the annual totals.

Weather data analysis

Many of the neotropical-wintering species that breed in the Pacific Northwest either overwinter in, or migrate through, the Pacific slope region of Mexico where they experience annual variation in environmental conditions relating to ENSO activity.

To evaluate the annual variation in weather across this region we averaged precipitation and temperature data (NOAA, 2001) across five high-elevation NOAA Weather Bureau Army Navy (WBAN) weather monitoring stations located in Mexico between latitudes 16°N and 30°N (station numbers 76220; 76323; 76471; 76665; and 76485) on a latitudinal transect close to the continental divide. Similar data were averaged across seven Pacific coastal stations in Mexico (station numbers 76160; 76255; 76458; 76556; 76658; 76762; 76903). We chose the February–April period over the March–May period (see below) because many neotropical wintering birds may have already migrated north by May and may not be impacted by May rainfall. In addition, substantial rainfall is expected during May and could mask the lower levels of rainfall experienced during the normally drier period of February to April.

RESULTS

For both ESPI and NAOI, the March–May mean monthly indices (henceforth referred to as springtime ESPI and springtime NAOI) correlated most strongly with annual reproductive success (1992–2000) across 34 species (Fig. 1). A correlation matrix (Table 1) shows the relationships between these indices, averaged annual reproductive indices for neotropical- and temperate-wintering species, seasonal weather in Mexico and defoliation levels in Pacific Northwest forests. Line plots of temporal variation in these variables are shown in Fig. 2. Annual reproductive indices for neotropical-wintering species increased significantly ($r = 0.73$, $P < 0.05$) with springtime ESPI, and annual reproductive indices for temperate-wintering species increased significantly ($r = 0.69$, $P < 0.05$) with springtime NAOI (Table 1). However, we detected no statistically significant correlation between ESPI and NAOI ($r = 0.16$, $P > 0.10$).

Individually, for 25 of the 34 species, annual reproductive indices increased with both springtime ESPI and springtime NAOI (Table 2). As suggested by the averaged results, the relationships with ESPI were generally stronger for neotropical-wintering species than for temperate-wintering species and conversely, the relationships between reproductive success and NAOI were generally stronger for temperate-wintering species than for neotropical-wintering species. A comparison of the probabilities associated with partial regressions from generalized linear models (GLM) of ESPI and NAOI on reproductive success revealed that these differences were significant ($\chi^2 = 4.13$, $P < 0.05$). Models for 10 species were significant ($P < 0.05$) either overall or in one parameter (Fig. 3) and described between 50% and 90% (mean 71%, SD 11%) of the annual variation in reproductive index. Using annual reproductive indices averaged across species in each migratory group, GLMs again revealed a significant ($P = 0.044$) ESPI effect for the neotropical-wintering group and a near significant NAOI effect ($P = 0.065$) for the temperate-wintering group. Figure 2c,d shows this temporal variation in reproductive indices for each migratory group.

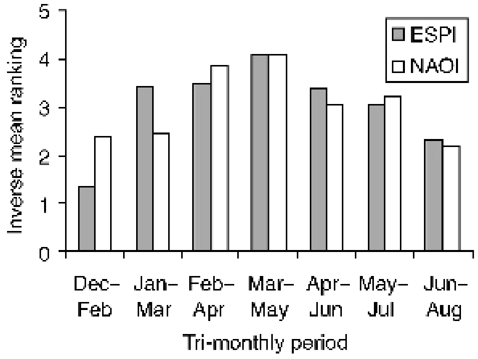

Fig. 1 Levels of the mean reverse rankings (high values indicate high ranking) of the magnitude of correlations between seasonal ESPI and NAOI values and reproductive success among 34 landbird species that breed in forests of the Pacific North-west.

Table 3 shows the group means from a multiple analysis of variance (MANOVA) of the strengths of correlations among four groups of species divided by migratory classification and predatory status. Overall, this model shows significant differences among groups ($F = 6.69$, d.f. = 3, $P = 0.0014$) and contrasts among the groups show that the relationship between

Table 1 Pearson's correlation matrix of relationships between springtime (March–May) ENSO Precipitation Index (ESPI), North Atlantic Oscillation (NAOI), averaged annual (1992–2000) reproductive indices (RI) for groups of 16 neotropical- and 18 temperate-wintering birds that breed in forests of the Pacific Northwest of North America, Mexican weather variables averaged across five montane and seven coastal WBAN stations, and defoliation levels due to western spruce budworm and Douglas fir oak tussock moth among six National Forests of the Pacific Northwest (DEFOI). Statistically significant correlations ($P < 0.05$, 7 d.f., two-tailed) are shown in bold

	ESPI (March–May)	NAOI (March–May)	Neotropical RI	Temperate RI	Montane temperature	Coastal temperature	Montane precipitation	Coastal precipitation
NAOI (March–May)	0.16							
Neotropical RI	**0.73**	0.15						
Temperate RI	0.26	**0.69**	0.66					
Montane temperature	**−0.93**	−0.31	**−0.71**	−0.39				
Coastal temperature	−0.54	**−0.71**	−0.58	**−0.70**	0.55			
Montane precipitation	**0.70**	0.07	**0.76**	0.35	**−0.78**	−0.39		
Coastal precipitation	**0.74**	0.11	**0.85**	0.50	**−0.79**	−0.47	**0.86**	
Defoliation (DEFOI)	0.27	**0.90**	0.42	**0.79**	−0.36	**−0.89**	0.25	0.27

Table 2 Numbers of adults and young of 34 species captured during the breeding seasons of the 9-year period (1992–2000) at MAPS stations across six national forests of the Pacific Northwest region. The species are divided into groups of neotropical- and temperate-wintering species and identified by their common and scientific names and a four-character code supplied by the USGS Bird Banding Laboratory (BBL Code). Pearson correlation coefficients (r) between annual reproductive indices and seasonal (March to May) indices of both ENSO precipitation (ESPI) and North Atlantic Oscillation (NAOI) are given (*$P < 0.05$; **$P < 0.01$). Some species (KP) are recognized by the USDA Forest Service (Pacific Northwest Region) as avian predators of western spruce budworm larvae (B), Douglas fir tussock moth larvae (T), or both (BT). Summary results of generalized linear models (GLM) show the probabilities associated with each independent variable (P_{ESPI} and P_{NAOI}) and the overall model ($P_{overall}$)

Common name	Scientific name	BBL code	Nos. captured		ESPI *r*	NAOI *r*	KP	GLM summary		
			Adults	Young				P_{ESPI}	P_{NAOI}	$P_{overall}$
Neotropical wintering species										
Hammond's flycatcher	*Empidonax hammondii*	HAFL	483	115	0.51	0.77*	B	0.104	0.045	0.017
Dusky flycatcher	*E. oberholseri*	DUFL	548	63	0.63	0.47		0.089	0.233	0.101
'Western' flycatcher	*E. difficilis/occidentalis*	WEFL	620	86	0.56	−0.58		0.013	0.012	0.011
Warbling vireo	*Vireo gilvus*	WAVI	665	60	0.53	0.47	B	0.179	0.246	0.176
House wren	*Troglodytes aedon*	HOWR	97	77	0.61	−0.07	B	0.092	0.601	0.212
Swainson's thrush	*Catharus ustulatus*	SWTH	2524	322	0.52	0.13	B	0.195	0.889	0.382
Orange-crowned warbler	*Vermivora celata*	OCWA	239	625	0.66	0.08		0.078	0.933	0.183
Yellow warbler	*Dendroica petechia*	YWAR	122	42	0.88**	0.48	B	0.001	0.043	0.001
Townsend's warbler	*D. townsendi*	TOWA	521	537	0.42	−0.13	B	0.261	0.605	0.480
Hermit warbler	*D. occidentalis*	HEWA	262	100	−0.06	−0.14		0.930	0.750	0.936
Common yellowthroat	*Geothlypis trichas*	COYE	268	197	−0.38	0.08		0.322	0.722	0.577
MacGillivray's warbler	*Oporornis tolmiei*	MGWA	1397	810	0.79*	0.10	B	0.021	0.943	0.054
Wilson's warbler	*Wilsonia pusilla*	WIWA	933	263	0.78*	0.35	T	0.022	0.376	0.040
Western tanager	*Piranga ludoviciana*	WETA	280	38	0.78*	0.47	BT	0.014	0.143	0.018
Chipping sparrow	*Spizella passerina*	CHSP	269	73	0.29	0.51	BT	0.562	0.215	0.335
Lincoln's sparrow	*Melospiza lincolnii*	LISP	815	421	0.24	0.02	T	0.571	0.971	0.839
Average			10043	3829	0.73*	0.15		0.044	0.901	0.105
Temperate wintering species										
Red-naped sapsucker	*Sphyrapicus nuchalis*	RNSA	113	42	0.29	0.17		0.515	0.760	0.729
Red-breasted sapsucker	*S. ruber*	RBSA	182	65	−0.01	0.41		0.839	0.306	0.566
Hairy woodpecker	*Picoides villosus*	HAWO	111	80	0.33	0.11		0.447	0.891	0.706
Mountain chickadee	*Poecile gambeli*	MOCH	323	355	0.42	0.67*	BT	0.297	0.066	0.091
Chestnut-backed chickadee	*P. rufescens*	CBCH	408	266	0.49	0.56	T	0.215	0.145	0.138
Red-breasted nuthatch	*Sitta canadensis*	RBNU	207	183	−0.21	0.76*	BT	0.202	0.013	0.033
Brown creeper	*Certhia americana*	BRCR	167	142	0.33	0.43		0.470	0.326	0.417
Winter wren	*Troglodytes troglodytes*	WIWR	590	276	0.06	0.11		0.921	0.819	0.962
Golden-crowned kinglet	*Regulus satrapa*	GCKI	386	1203	−0.23	0.42	BT	0.400	0.230	0.396
Ruby-crowned kinglet	*R. calendula*	RCKI	311	135	0.31	0.81**	BT	0.458	0.015	0.031
Hermit thrush	*Catharus guttatus*	HETH	195	72	0.49	0.56		0.213	0.150	0.140
American robin	*Turdus migratorius*	AMRO	311	162	0.30	0.55	B	0.570	0.172	0.271
Varied thrush	*Ixoreus naevius*	VATH	191	99	0.49	0.45		0.231	0.286	0.234
Yellow-rumped warbler	*Dendroica coronata*	YRWA	801	668	0.28	0.63	BT	0.580	0.105	0.187
Song sparrow	*Melospiza melodia*	SOSP	483	478	0.70*	−0.03		0.048	0.626	0.121
White-crowned sparrow	*Zonotrichia leucophrys*	WCSP	137	101	0.03	0.39	T	0.927	0.333	0.601
Dark-eyed junco	*Junco hyemalis*	DEJU	1718	1622	0.61	0.56	BT	0.090	0.122	0.068
Pine siskin	*Carduelis pinus*	PISI	680	188	0.54	0.81**	BT	0.048	0.004	0.005
Average			7314	6137	0.26	0.69*		0.622	0.065	0.129

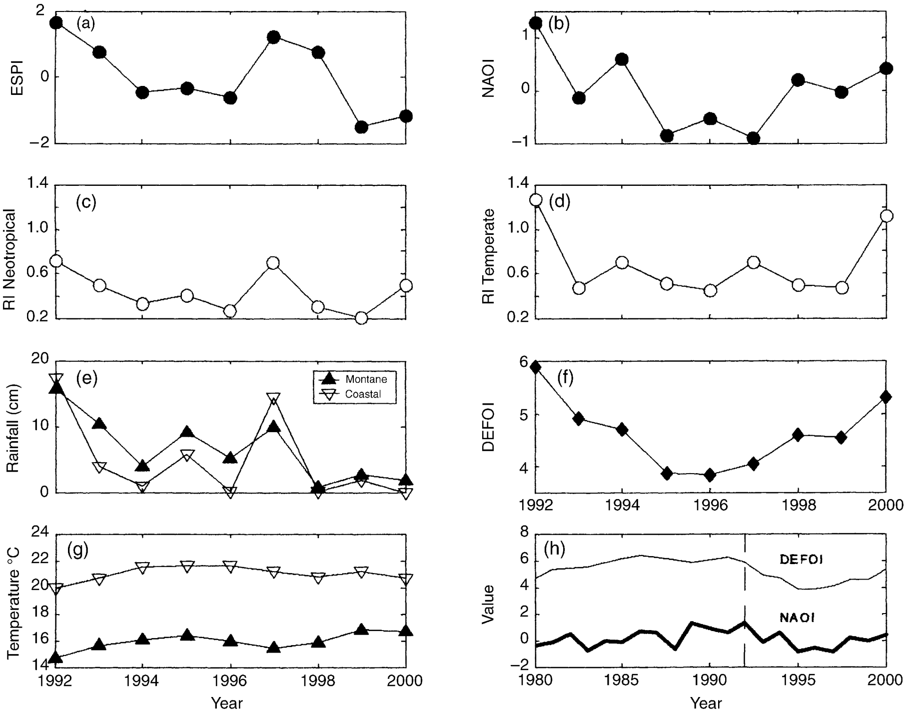

Fig. 2 Temporal patterns (1992–2000) of climate indices, reproductive success, precipitation, temperature and defoliation. (a) Mean monthly (March–May) ENSO precipitation index (ESPI). (b) Mean monthly (March–May) indices of the North Atlantic Oscillation (NAOI). For species that breed in the forests of the Pacific Northwest: (c) annual mean reproductive indices (RI) for neotropical wintering species and (d) annual mean reproductive indices for temperate-wintering species. Environmental conditions (February–April) in western Mexico: (e) mean monthly rainfall and (g) mean monthly temperature. (f) Index of defoliation (DEFOI) in national forests of the Pacific Northwest. (h) a longer-term (1980–2000) plot shows temporal covariation in values of NAOI and DEFOI for both the entire period (Pearson's correlation coefficient: $r = 0.55$, $P < 0.01$) and for the period 1992–2000 ($r = 0.90$, $P < 0.001$) to the right of the vertical dashed line.

reproductive success and NAOI among temperate-wintering species known to prey upon defoliating lepidopteran larvae was significantly different from those of the other groups ($F = 17.28$, d.f. = 1, $P < 0.001$). Highly significant correlations also exist between annual springtime NAOI and annual levels of defoliation (DEFOI), both for the period of this study ($r = 0.90$, $P < 0.001$) and for the longer-term period 1980–2000 ($r = 0.55$, $P < 0.01$).

Strong relationships exist between seasonal ESPI values and weather data from montane and coastal WBAN stations of western Mexico (Table 1), whereby precipitation significantly increases as a function of ESPI ($r = 0.70$, $P < 0.05$ and $r = 0.74$, $P < 0.05$, respectively), but temperature decreases ($r = -0.93$, $P < 0.01$ and $r = -0.54$, NS, respectively). Hence, low ESPI values are associated with decreased soil moisture (and high ESPI values are associated with increased soil moisture) throughout the Pacific slope of Mexico (Fig. 4a). The wetter springtime weather associated with El Niño conditions extends across the south-western United States and throughout California (Schonher & Nicholson, 1989; Kalnay *et al.*, 1996; NOAA-CIRES, 2001).

DISCUSSION

Multiple mechanisms may explain the effect of ENSO-driven weather patterns on the reproductive success of Pacific Northwestern landbirds wintering in the neotropics. Prey biomass on their wintering grounds in the relatively arid forests of north and central Mexico is probably greater in the wetter El Niño years, as it is in the forests of south-western North America (Swetnam & Betancourt, 1998), thereby enhancing the ability of individual birds to survive both the winter and the rigours of spring migration. Additionally, spring migration is favoured by light southerly winds associated with warm sectors of incoming low pressure systems (Richardson, 1990). Such winds are more prevalent throughout western North America between March and May of El Niño years (Fig. 3b). These factors may affect the physical condition of migrating birds, as well as the timing of their arrival on the breeding grounds and, consequently, the potential length of the breeding season. The cause of the difference between our results and those reported for black-throated blue warblers that winter in Jamaica and breed in New

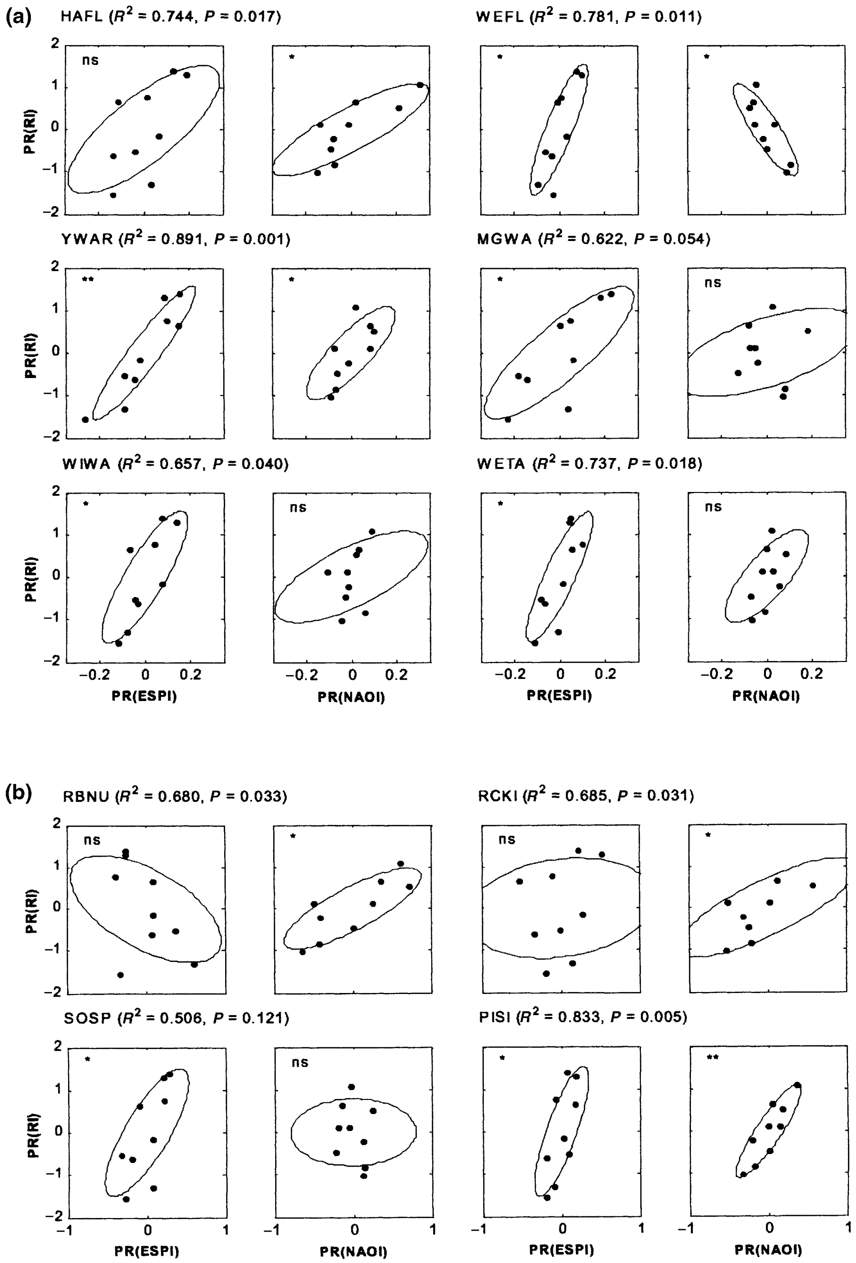

Fig. 3 Pairs of partial residual plots from multiple regressions of reproductive indices (RI), of species that breed in the forests of the Pacific Northwest of North America as functions of seasonal values of ESPI and NAOI. (a) Six neotropical wintering species (see Table 1 for species names). (b) Four temperate wintering species. Plots for each species show the relationships between the partial residuals for ESPI (PR(ESPI)) against the partial residuals for reproductive indices PR(RI) controlling for NAOI (left-hand plots), and for NAOI (PR(NAOI)) against PR(RI) controlling for ESPI (right-hand plots). Ellipses plotted around each dataset capture 95% of the variation in the data. Significance levels of each partial regression are denoted by *($P < 0.05$) and **($P < 0.01$) and adjusted R^2 and P-values of the multiple regression models are given above each pair of plots.

Hampshire may be that temperatures are cooler than average in Mexico, but warmer than average in Jamaica (Sillet *et al.*, 2000; NOAA-CIRES, 2001; NOAA, 2001) during the winter (November–February) and premigration (March–May) months of El Niño years. Furthermore, more westerly winds, associated with these years, extend from the Caribbean to northern Florida and may hamper migration into eastern North America (Fig. 4b).

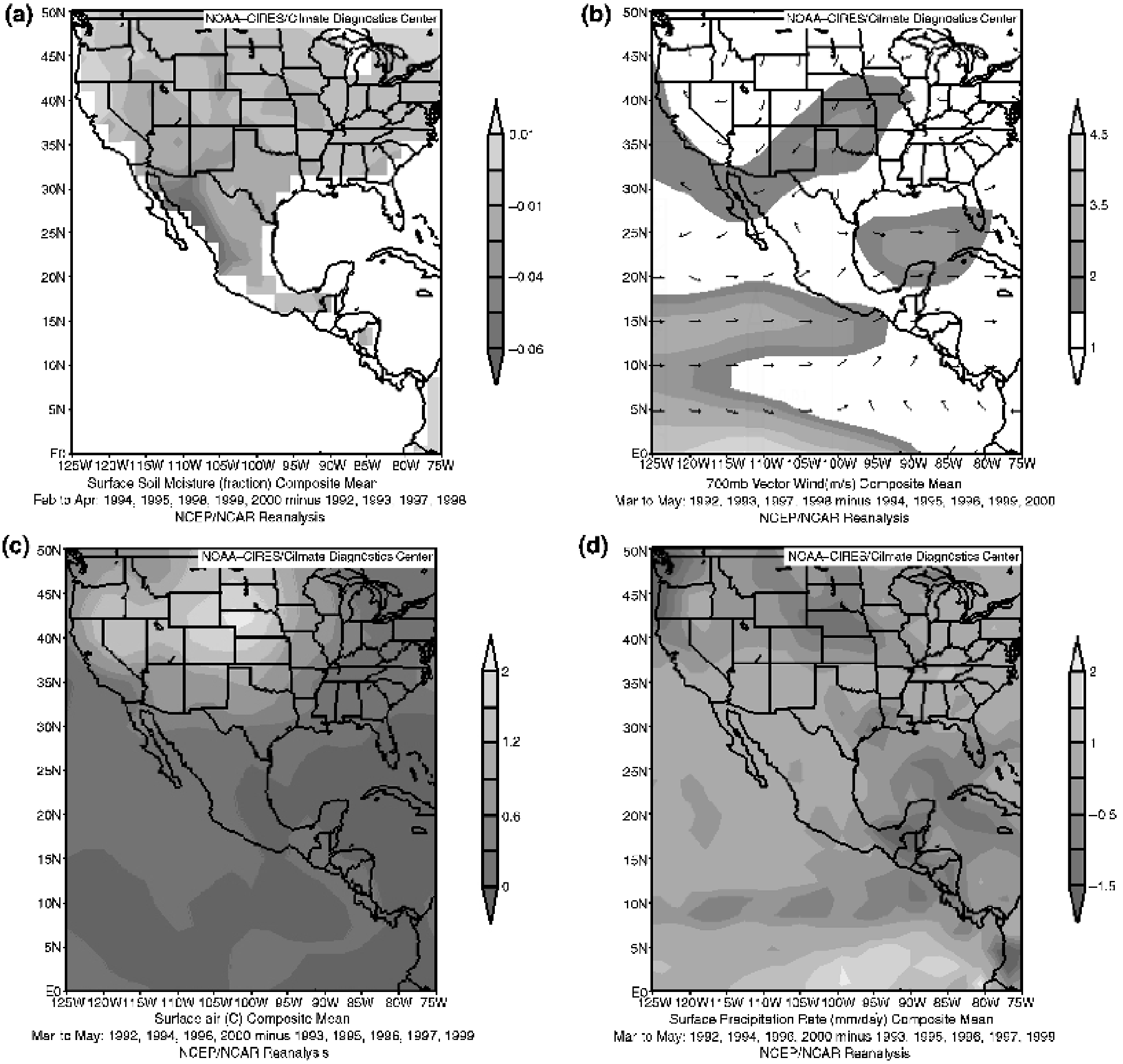

Fig. 4 Composite plots of seasonal differences in spatial patterns of weather variables between years with positive seasonal ESPI values (1992, 1993, 1997 and 1998) and years with negative seasonal ESPI values (1994, 1995, 1996, 1999 and 2000). (a) Surface soil moisture (reverse year sequences produces darker shading to indicate less soil moisture during ESPI negative years) prior to migration (February–April). (b) 700 mb (measured at an altitude of ~2.5 km) vector winds during migration months of March to May. Composite plots of seasonal (March–May) differences in spatial patterns of weather variables in the Pacific Northwest between years of warm phase NAO (1992, 1994, 1998, 2000) and years of cold phase NAO (1993, 1995, 1996, 1997, 1999): (c) temperature; (d) precipitation. Images provided by the NOAA-CIRES Climate Diagnostics Center, Boulder, Colorado from their website at http://www.cdc.noaa.gov/(April 2002).

In the Pacific Northwest, high positive values of NAOI (warm phase) are associated with warmer and drier (March–May) conditions during the late winter and springtime (Fig. 4c,d), whereas high negative values are associated with colder extremes during the winter (NOAA-CIRES, 2001; Thompson & Wallace, 2001). Previous research has suggested that ENSO influences insect outbreaks in north-western North America (Swetnam & Lynch, 1993). In this study,

Table 3 Multiple analysis of variance (MANOVA) of ENSO and NAO effects on reproductive success of groups of landbird species in forests of the Pacific Northwest of North America. The species are divided into groups of neotropical- and temperate-wintering species, and further divided into (*N*) species *known* and *not known* to be predators of the larval stages of Douglas fir tussock moth and western spruce budworm. Group means are given for correlation coefficients between annual reproductive indices (1992–2000) with ESPI (ENSO effect) and with NAOI (NAO effect)

Group	*N*	ENSO effect	NAO effect
Neotropical			
known	11	0.577	0.282
not known	5	0.282	−0.018
Temperate			
known	10	0.254	0.616
not known	8	0.335	0.276

however, we detected highly significant correlations between NAOI and defoliation for the period 1992–2000 and also for the longer period 1980–2000, whereby high levels of defoliation were associated with high values of springtime NAOI (Table 1; Fig. 2b, 2f,h). Incorporating ESPI as well as NAOI into a multiple regression model did not greatly increase the amount of variation explained; thus it appears that NAO, at least in recent history, has a stronger influence than ENSO on the population dynamics of these defoliating insects.

Although the reproductive success of the majority of species responded positively to NAO, Table 2 shows that the relationship was most pronounced among those temperate-wintering species known to prey upon western spruce budworm and/or Douglas fir tussock moth (Torgersen *et al.*, 1990). Temperate-wintering species are already present on their breeding grounds before neotropical-wintering species arrive, especially in years when the NAO induces warmer, drier conditions (Thompson & Wallace, 2001; Fig. 4c,d), and may be better able to take advantage of abundant early instars that occur during extensive insect outbreaks. In contrast, many neotropical-wintering species may not arrive early enough to take advantage of the increased defoliant biomass, because for many species migration is triggered by photoperiodicity (Richardson, 1990), which is unaffected by global climate phenomena (Both & Visser, 2001).

Understanding how landbird population dynamics respond to short-term climate variation is a crucial step in predicting the effects of longer-term global climate shifts on bird populations. Palaeoecological studies show that longer-term global climate change, such as that experienced since the late Pleistocene glacial maximum (18000 BP), drastically affected the composition and distribution of forest communities (e.g. Delcourt & Delcourt, 1988) upon which insects and birds depend. Because birds are vagile, it seems likely that their geographical ranges will also shift in response to changing spatial patterns of suitable breeding and wintering habitat. Some species with restricted geographical ranges may become extinct as critical habitat disappears entirely, and populations of more widespread species may become isolated as their ranges become disrupted. In recent years, researchers have made considerable advances in constructing predictive models of climate and vegetation/ecosystem change in response to anthropogenic factors such as land conversion and greenhouse gas emissions (Schimel *et al.*, 2000). By incorporating species–habitat and weather–demography relationships into such models we may begin to understand how a shifting climate will alter avian distribution and abundance.

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SUPPLEMENTARY MATERIAL

Supplementary information is available on IBP's world-wide web site http://www.birdpop.org/Results/PNW/suppdoc.htm.

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