

Using life-history traits to explain bird population responses to changing weather variability

Running head: Explaining population responses with bird life-history traits

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Abstract

It is expected that bird population dynamics will change in response to increased weather variability, an expression of climate change. The extent to which species are sensitive to effects of weather on survival and reproduction depends on their life-history traits. We investigated how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated population dynamics. We developed and applied the linear trait-environment method (LTE) which is a modified version of the fourth-corner method. Despite our focus on single traits, two strategies - combinations of several traits - stand out. As expected, breeding populations of waterfowl species that often breed at ground or water level, feed on plant material, are precocial, and are generally short distance or partial migrants are negatively impacted by severe winters directly preceding territory monitoring, probably due to increased adult mortality. Furthermore, a decline in population growth rates of insectivorous long-distance migrants due to mild winters and warm springs in the year before territory monitoring was found, which may be caused by reduced reproduction due to trophic mismatches. If we extrapolate these correlations to the future, we are able to point out species that are expected to show most significant responses to changing weather variability - assuming that our conclusions are based on causal relationships, and that the way species, weather variables, and the nature of habitat types interact will not alter. As species traits play an important role in constructing functional groups that are relevant to the provisioning of ecosystem services, our study allows to incorporate the vulnerability of ecosystems to climate change into such functional approaches.

Keywords

life-history trait; bird population dynamics; climate change; Linear Trait-Environment method (LTE); weather variability

INTRODUCTION

Climate change is likely to be manifested by changes in the variance of weather with an increased frequency of extreme weather (IPCC 2001, 2007). Population dynamics of many bird species are changing in response to increased weather variability (Bolger et al. 2005, Jiguet et al. 2006, Robinson et al. 2007), presumably through impacts of weather on variation in adult survival and reproduction success (including first year survival, Robinson et al. 2007). The extent to which species are sensitive to effects of weather on survival and reproduction has been shown to depend on life-history traits (Van Turnhout et al. 2010). Considering resident birds, in several recent studies, relationships were found between adult survival and (extreme) weather circumstances during the preceding non-breeding season (temperature and snowfall, e.g. Brown & Brown 1998, Sæther et al. 2000, Both & Visser 2001, Sparks et al. 2002, Jones et al. 2003, Robinson et al. 2007). Mild winters and early, warm springs were on the other hand found to have negative effects on reproduction of insectivorous migrants, because of increased probability of mismatches between the timing of reproduction and the main food supply, i.e. organisms at lower levels in the food chain (Brown & Brown 1998, Both & Visser 2001, 2005, Both et al. 2006, Both et al. 2009). This is especially pronounced in habitats with a seasonal food peak, such as forests (Both et al. 2010). Furthermore, population growth rates of altricial ground nesting species have been shown to be negatively impacted by a dry heat wave (Jiguet et al. 2006), while Sæther et al. (2004) reported negative effects of extreme rainfall and wind events year-round on adult survival and reproduction success of altricial species. Most of the cited studies are focused on only one or a few species and traits, and responses in

population dynamics to (extreme) weather vary amongst the species, habitats, and geographical locations considered in the different studies. However, Van Turnhout et al. (2010) found that population trends of 170 Dutch breeding bird species in 1990-2005 were strongly correlated with amongst others migration strategy, and that declines were associated with late arrival on the breeding grounds in migratory birds (see also Møller et al. 2008), suggesting climate change to be an important driver of population changes.

Impacts of enhanced weather variability on population dynamics may interfere with aims set in nature conservation programmes, which are often described in terms of the presence and abundance of target species in protected areas. In response to the emerging understanding of the impacts of climate change, researchers and policy makers (e.g. EU 2009 White paper Adapting to climate change) have called for adaptive measures to mitigate the effects of climate change on population dynamics. Therefore, there is a need for more insight into the impacts of weather variability on a broad spectrum of species. Because nature conservation is generally not based on species-specific measures, such adaptive measures demand a generalized view on responses of species (Dolédec et al. 1999). An approach that allows for the generalization and extrapolation of predictions on future performance of species (Keddy 1992), is to investigate which specific combination of life-history traits makes species sensitive to specific weather events (c.f. Dolédec et al. 1999). In this paper, we aim to investigate this by examining how breeding bird species can be grouped, based on their life-history traits and according to weather-correlated population dynamics.

The interaction between weather and life-history traits could be influenced by habitat characteristics (Karlsson & Wiklund 2005) due to the way weather affects specific habitats. The same species may therefore show different responses in different ecosystem types (Karlsson & Van Dyck 2005, Both et al. 2010). Therefore, we analyze possible differences between habitat types by comparing growth rate data of a broad selection of specialist and generalist species breeding in two ecosystem types in the Netherlands: marshlands (i.e. a mosaic of open water, reed marshes and marshland shrubs) and deciduous forests. These ecosystem types are important from a nature conservation point of view. About 16% of the Netherlands has been classified as international key marshland area (Wolff 1993), and this area is of importance for marshland species in Europe. Moreover, we expect marshlands and forests to differ in the way weather affects these systems. Water levels in marshlands can highly fluctuate with precipitation amount, and can freeze over during severe winters, whereas forests are relatively buffered against extreme weather (Stoutjesdijk & Barkman 1992). On the other hand, forests show a more pronounced seasonal food peak, especially to insectivorous species, than marshlands, due to simultaneous leaf unfolding over the whole habitat area during spring (Both et al. 2010). This might result in higher sensitivity to mismatches in the food chain.

In exploring the relationship between population dynamics and weather, we studied changes in abundances after the occurrence of specific weather circumstances. We tested the relationships between typical nest location, diet, offspring development, and migration strategy of selected bird species - traits that were shown to correlate with weather conditions in other studies - and weather variables. Further argumentations for using these specific traits are indicated in more detail in Table 1. We analyzed data on annual changes in bird abundances, above mentioned traits, and values of weather variables simultaneously. As the analyzed species experienced the same weather conditions, we hypothesize that differences in their response could be attributed to different trait combinations.

Instead of looking at linear population trends (cf. Both et al. 2010, Van Turnhout et al. 2010), we analyzed year-to-year changes in abundances in response to weather conditions. We developed and applied the linear trait-environment method (LTE) which is a modified version of the fourth-corner method (Legendre et al. 1997, Dray & Legendre 2008). Subsequently, we compared changes in the occurrence of the significant weather variables between the present climate and several climate change scenarios. This comparison gives an indication which combination of traits and corresponding species might benefit or suffer from future weather circumstances in terms of population growth.

METHODS

Deriving yearly population indices

We selected 77 species that annually breed in the Netherlands, of which 43 species breed in marshland areas and 53 species breed in forest areas; from these 77 species, 19 breed in both marshland and forest areas (Appendix 1). Since 1984, monitoring of breeding birds in the Netherlands, organized by SOVON Dutch Centre for Field Ornithology and Statistics Netherlands, is based on the method of territory mapping in fixed study plots (Bibby et al. 1997, Van Turnhout et al. 2010). Between March and July study plots (10-500 hectares each) are visited 5-10 times. Size of study plots, as well as number, timing and duration of visits depend on habitat type and species selection. All birds with behaviour indicative of a territory (e.g. song, pair bond, display, alarm, nests) are recorded on field maps. Species-specific interpretation criteria are used to determine the number of territories at the end of the season. Fieldwork and interpretation methods are standardized and are described in detail in manuals (Van Dijk 2004, Van Dijk et al. 2004). For the selected species, abundances per habitat type are presented as yearly indices; for each of the 19 species that breed in both marshland and forest areas, 2 indices are available. Indices are calculated using TRIM-software (Pannekoek & Van Strien 2005), based on loglinear Poisson regression. Indices are presented using 1990 as a base year (index=100). Logratios of subsequent yearly values of indices ($\ln[\text{index}_{\text{species}_i, \text{year}_t} / \text{index}_{\text{species}_i, \text{year}_{t-1}}]$) are used in our analyses and correspond to yearly population growth rates of the species on log scale. Since weather influences population growth via reproduction and mortality rates, population growth rate is a proper index to describe population dynamics. We used index values from 1984-2005.

Deriving weather variables

The Royal Netherlands Meteorological Institute (KNMI) acquires weather data according to the global standards of the World Meteorological Organization. The KNMI administers ca. 35 weather stations and 54 wind stations evenly distributed over the Netherlands, of which the station in De Bilt is located in the centre of the country. Weather data acquired from this station are representative for the mean climate conditions in the Netherlands (Van Oldenborgh & Van Ulden 2003), except for wind speeds that differ too much spatially (generally higher wind speeds along the North Sea coast). We obtained data on mean daily temperatures and wind speeds, as well as total daily precipitation, precipitation duration, snowfall, and occurrence of thunderstorms from KNMI for the period 1984-2005. From these we calculated 12 weather variables, that describe the weather in the breeding season and in the non-breeding season (Table 2). For wind speeds, values were derived

from data from all meteorological stations in the Netherlands; remaining weather variable values were derived from the De Bilt meteorological station.

Weather variables that impact population dynamics due to adult mortality will change numbers of territories immediately. Changes in population dynamics due to a weather event affecting recruitment rates (reflecting reproductive success and first winter survival) will become noticeable in territory numbers one year after the occurrence of the weather event, especially for species that are able to reproduce one year since their hatching. Therefore, we derived values for weather variables that occurred during the non-breeding or winter season ('NB'; from October to March) and the breeding season ('B'; from April to August); see Appendix 2. We related weather variable values of current years ('t') and previous years ('t-1'; one year before territory monitoring) to population growth rates (Figure 1). Weather in the non-breeding season of the previous year ('NBt-1') can affect species condition and eventually the reproduction success (carry-over effects, Norris & Taylor 2006). Reproduction success in the breeding season of the previous year (Bt-1) will lead to altered population numbers in the breeding season of the current year (Bt). Adult mortality in the non-breeding and breeding season of the current year (NBt and Bt) will also lead to altered population numbers in the breeding season of the current year (Bt).

Weather variables indicating winter severity (IJnsen, mean temperature of the coldest month, longest duration of consecutive frost days) are strongly correlated (see Appendix 3). Mild winters are often rainy - relatively high winter temperatures and precipitation are supplied by west winds from the North Sea (Van Oldenborgh & Van Ulden 2003) - and are frequently followed by a warm spring and breeding season (Vandendool & Nap 1981). Moreover, in the period 1984-2005 warm breeding seasons were often followed by mild winters, and a rainy winter was frequently followed by another rainy (but not necessarily a mild) winter. The number of days comprising a heat wave is positively correlated to the mean temperature of the breeding season. Correlations between weather variables will not affect the analysis because each weather variable is tested separately. However, it may affect the interpretation of the results and hamper inferences (see Discussion).

Selecting traits

We selected 4 traits that have been demonstrated to correlate with population dynamics in response to weather circumstances in literature. For each species, the following categorical traits are considered: (1) nest location (at water table, along water banks or in holes in the ground (low elevations) vs. higher elevations), (2) main diet type (food during breeding season consists of plant material vs. insects vs. fish vs. mammals), (3) offspring development (altricial vs. precocial), and (4) migration strategy (resident vs. partial migrant vs. long-distance migrant). These traits are used in the analysis with the LTE method (see below). Data sources for trait values, classifications, and references are indicated in Table 1.

The linear trait-environment method (LTE)

LTE relates a species trait (z) to an environmental variable (x) via data on (change in) abundance of the set of species in a set of sites. Here, sites are years, the environmental variable is an annual weather variable, and year-to-year change in abundance or growth rate is derived for the selection of Dutch breeding birds. To introduce LTE we start with a two-step analysis. In the first step regressions per

species of the growth rate values to each weather variable give a species specific regression coefficient b_k . In the second step, these regression coefficients are correlated to each trait. LTE integrates both steps in a single model (see Figure 2 for a schematic overview). LTE, described in detail in Appendix 4, achieves this integration on the basis of a linear model with main effects for the weather variable and the trait and their interaction. The interaction between trait and weather variable in this model captures the trait-weather relationship, in particular the trait-dependent effect of weather on the population growth rate. We tested the significance of this interaction by a permutation test. In Appendix 4, we compare LTE and permutation test with fourth-corner analysis (Legendre et al. 1997, Dray & Legendre 2008) which is a method of trait-environment analysis designed primarily for presence-absence data. We performed separate analyses for marshland birds and for forest birds and we report correlation coefficients R , statistics on the b_k , and the results of the significance tests, obtained from the LTE function that we wrote in R 2.9.0 software (Ihaka & Gentleman 1996).

To obtain first insight into the clustering of species against their traits, we performed a separate ordination of the traits (Z matrix) next to the LTE analyses. This principal component analysis (PCA) was conducted with CANOCO (Ter Braak & Šmilauer 2002), providing an optimal ordination of species and traits.

RESULTS

The PCA and LTE analyses show that in marshland birds one distinct group of species, that share a specific combination of traits, stands out: waterfowl species that often breed at ground or water level, feed on plant material, are precocial and do generally not migrate over long distances. These traits are correlated (see Figure 3a and Appendix 5a). As expected, these waterfowl are negatively impacted by severe winters directly preceding territory monitoring during the breeding season, and benefit from mild, rainy winters (see Table 3a for results marshland birds). Moreover, the analyses show a decline in population growth rates of altricial marshland species that do not breed at ground level and feed on other sources than plant material (especially insects) that is correlated with warm springs in the year preceding territory monitoring. Our results do not indicate a relationship between growth rates of altricial species and heat waves or rain storm events. Beside our expectations, we found a few other correlations between life-history traits and weather-correlated variation in growth rate. Migratory marshland species that do not breed at ground level and are often altricial benefit from severe winters. Waterfowl species are negatively impacted by long snow cover duration in the year preceding territory monitoring. Furthermore, waterfowl species benefit from a warm spring in the year before territory monitoring (April-May), while residential marshland species benefit from a warm breeding season.

In forest birds, also one distinct group of species stands out: long-distance migrants that are often insectivorous, or feed insects to their juveniles (see Figure 3b and Appendix 5b for results forest birds). These insectivorous migrants show an increase in population growth rates following severe winters and cold springs (April-May), and a decline in population growth rates following mild winters and warm springs in the year before territory monitoring (Table 3b). Our results do not indicate a negative impact of cold and snowy winters. Neither can we distinguish a negative impact of heat waves or rain storm events on growth rates of altricial (low nesting) species. However, also for forest species we found a few other correlations between life-history traits and weather-correlated variation in growth rates.

Carnivorous and residential species show a decline in population growth rates that is correlated with severe, dry winters in the year before territory monitoring. Partial or short-distance migrants are negatively impacted by severe winters directly preceding territory monitoring and by high precipitation sums over the breeding season when territories are counted. Partial migrants profit from rainy breeding seasons in the year before territory monitoring, while carnivorous and other non-insectivorous species are negatively impacted by high precipitation sums over the breeding seasons. Migrants, however, profit from these weather circumstances.

DISCUSSION

We investigated how bird species can be grouped according to weather-correlated population dynamics, based on their life-history traits. Despite our focus on single traits, two strategies (traits that jointly appear in bird species) stand out. We have shown that waterfowl that often breed at ground or water level, feed on plant material, are precocial, and do not migrate over long distances in general, are negatively impacted by severe winters directly preceding territory monitoring. This is probably due to increased adult mortality (e.g. Bibby 1981). Furthermore, a decline in population growth rates of insectivorous long-distance migrants due to mild winters and warm springs in the year before territory monitoring may be caused by a reduced reproduction success. When these species arrive relatively late from the wintering grounds after mild winters, mismatches can occur between the timing of reproduction and the food supply to the juveniles. Competition with residents who survived the mild winter in high numbers could be another cause for reduced reproductive success of migrants.

As we interpret our data, juvenile survival in year $t-1$ and adult survival in year t of residential marshland and waterfowl species increase due to a warm spring and breeding season. This can probably be explained by increased food availability during a warm spring. However, increased chance for juveniles to survive their first year until the next breeding season - the moment of territory monitoring -, can also be caused by a mild winter, often following a warm breeding season (Morgan & Glue 1977, Besbeas et al. 2002).

We see remarkable differences as well as similarities in comparing the results between marshland and forest species (Tables 3a and b). Both marshland and forest species respond to winter severity. Nest location and offspring development are important traits for marshland species in this respect, but not for forest species. This is probably caused by the fact that almost all forest species breed in trees and are altricial. Hence, the variation amongst traits nest location and offspring development is relatively low (see also Figure 3b), and these traits do not affect the sensitivity to winter severity in forest birds.

Marshland and forest long-distance migrants differ in their response to winter severity and spring temperature considering timing (t and $t-1$, respectively). Our findings on long-distance migrants in forests that are negatively impacted by mild winters and warm springs in the year before territory monitoring are in agreement with the findings of Both and Visser (2001, 2005) and Both et al. (2006, 2010). Both et al. (2010) show mismatches between timing of food requirements and food availability for long-distance migrants, but only in habitats with a seasonal food peak, like forests. The correlations Both et al. used were based on linear trends over a 20-year time span. We analyzed population trend data in a different way, looking at year-to-year variation, using the (positive or negative) population growth

rate between subsequent years. In addition to the long-term trend analyses of Both et al. we showed that the impact on population dynamics of long-distance migrants is not immediate but delayed by one year. This indicates clearly, as hypothesized by Both et al., that early springs result in a low breeding success, consequently followed by a lower population size one year later. This is in further support of the mismatch hypothesis. It is remarkable that, in contrast to Both et al., we also found an effect of winter severity, which is strongly correlated to spring temperatures, on long-distance migrants in marshland habitat. This is difficult to interpret however. Winter conditions are correlated with population size in the following breeding season, suggesting an immediate response. This indicates effects on survival, e.g. lower survival rates for long-distance migrants after mild winters. But this seems quite unlikely, since these migrants are in their distant winter quarters. One can only speculate about the true causal relationship. It might result from impact on food resources or interspecific competition pressures. After a severe winter, the population size of sedentary species is low thus allowing a higher population size of migrants to settle (Lemoine et al. 2007). Clearly this needs further study. In contrast with the forest bird community in which most of the migrants are passerines and insectivores, the migrant marshland bird community is more diverse. This and the year-to-year approach could explain the difference with the findings of Both et al. that are based on long-term trend estimates and deals with a restricted species set (only passerines).

For long-distance migrants, there might be other constraints en route or on the wintering grounds that could additionally impact population fluctuations (Newton 2004, Sanderson et al. 2006), which are not taken into account by considering only Dutch weather variables. Especially species wintering in the Sahel have shown strong declines in breeding population numbers during severe droughts there in the 1970s and 1980s (Foppen et al. 1999, Zwarts et al. 2009). However, most likely these effects do not change our results considering responses to weather on the breeding grounds. Conditions during the breeding season in the Netherlands - which the Dutch populations of long-distance migrants share - correlate unambiguously to population fluctuations of most of these species and their responses adequately match the expectations we formulated in Table 1 on basis of recent literature.

Marshland species respond to snow cover duration, while forest species do not. This difference can be attributed to the fact that marshland systems are open and can become totally covered with snow. Especially in combination with temperatures below the freezing point, long-lasting snow cover can be detrimental to waterfowl species, foraging on terrestrial plant material (e.g. agricultural managed grasslands) which is then covered with snow (see also Figure 3a; waterfowl clustered near trait main diet type of plants).

Neither marshland nor forest species respond to heat waves and dry periods. This is in contrast to the results of Jiguet et al. (2006), who found a response in population growth rates to the 2003 French heat wave, a 6-month exceptionally hot and dry period. In the Netherlands, only 9 heat waves occurred over the period 1984-2005, with an average duration of 9 days. Probably, these heat waves were not experienced as harmful by the species. Moreover, the longest duration of dry days during the breeding season over the period 1984-2005 was 28 days, which occurred in both 1995 and 2003. Again, these dry periods were probably not experienced as exceptionally long by the species. Furthermore, events such as droughts, heavy rain, and squalls often occur at a local scale, and effects of these events on population dynamics can be leveled off in national population trends.

The main assumption in our study is that species differ in their responses to weather, and that these responses could be attributed to different trait combinations. We used a dataset on a large number of species counted in the same (biogeographical) region over the same set of years. Population changes may be correlated to other causal factors operating in the same years and region, that are not covered by our explanatory variables. However, we expect that on such temporal and spatial scales, weather will be an important explanatory factor in year-to-year population changes, taking into account the numerous studies that found evidence for the impact of weather on bird vital rates (e.g. Sæther et al. 2004, Both et al. 2006).

We chose not to explicitly take account of differences in accuracy in the index values (derived from TRIM), except by taking logarithms and by excluding rare species, of which the indices are likely to be more error prone. By trying to take account of differences in accuracy, the simplicity of the method would be lost. We believe the permutation approach to be quite robust to any differences. Moreover, if the errors associated with the LTE model are large compared those in the (log) indices, not taking account of differences in accuracy is close to optimal.

Autocorrelation in time series may lead to spurious cross-correlations and a standard cure is pre-whitening. We diminished the autocorrelation in yearly indices by analysing the logratio of subsequent values. The resulting lag-1 autocorrelations are mostly slightly negative (in absolute value 75% is smaller than 0.3 and the maximum is 0.55). The lag-1 autocorrelations in the weather variables are even smaller in size. The values are too small to invalidate our analysis and the series are too short to account in a more elaborate way for autocorrelation. Ranta et al. (2000) warn that it can be very hard to detect environmental forcing of population dynamics if the dynamics is not stable. However, they argue that slowly growing species such as birds show mostly stable dynamics and “are likely to respond to climatic variability in a straightforward way”. By consequence, the method of our paper works for birds, as we showed, but may fail to detect environmental forcing for rapidly multiplying organisms.

Implications of future weather conditions

We extrapolated the observed correlations to future weather conditions predicted by climate change models. By doing so, we assume that these correlations are based on causal relationships, and that the way species, weather variables, and the nature of habitat types interact will not alter in the future. This enables us to point out species that are expected to show most outspoken responses to weather circumstances under climate change. From KNMI data on future daily temperatures and precipitation sums (http://climexp.knmi.nl/Scenarios_monthly/), we could calculate future values for weather variables affecting species population dynamics (Figure 4). We used KNMI scenarios W and W⁺, which implies for both scenarios an average global temperature rise of 2 °C from 1990 till 2050, and an increased occurrence of mild wet winters and warm dry summers for the W⁺ scenario (see http://www.knmi.nl/research/climate_services/). Climate change is likely to be manifested by fewer cold and frost days (IPCC 2001, 2007), and hence by more frequent occurrence of mild winters (Figure 4a), as well as warm springs (Figure 4c). Based on our results, we can hypothesize that in general more frequent occurrence of mild winters and warm springs is expected to be detrimental to insectivorous long-distance migrants (marshland and forest species) in the Netherlands. Waterfowl species in the Netherlands are expected to profit from the more frequent occurrence of mild winters. It is unclear how the precipitation sum

over the non-breeding season and over the breeding season will alter in the future climate (Figure 4b and d). For the non-breeding season, the precipitation sum might increase, but this increase is only significant in 2100 under the W^+ scenario. Under the W^+ scenario the precipitation sum in the breeding season will decrease from present to 2100, while under the W scenario the precipitation sum in 2100 will remain similar to the present sum (no significant difference). Subsequently, it is unclear if species will be harmed by future precipitation.

Based on species specific regression coefficients b_k resulting from the LTE analyses (Appendix 6) we can point out the species that are expected to respond positively or negatively to a more frequent occurrence of mild winters. Most of the species that are expected to respond positively to climate change or a more frequent occurrence of mild winters based on their b_k 's (listed in Table 4a) can indeed be characterized as waterfowl (Figure 3a; a.o. Teal *Anas crecca* and Mute swan *Cygnus olor*). Most of the species that are expected to respond negatively to climate change (listed in Table 4b) can be characterized as insectivorous long-distance migrants (Figure 3b; a.o. Icterine warbler *Hippolais icterina* and Golden oriole *Oriolus oriolus*).

Our results show that impacts of climate change on species dynamics may interfere with aims set in nature conservation programmes, which often concern the presence and abundance of specific target species in protected areas. In recent literature on ecosystem resilience it is argued that future nature conservation programmes should focus on the functioning of ecosystems and the distribution of functional groups of species over ecosystems, rather than setting conservation targets on specific rare or declining species (Turner et al. 2007). Species traits play an important role in constructing functional groups that help to understand the relationship between biodiversity and ecosystem functioning. In addition, our study shows that trait analysis also helps to gain insight into the responses to climate change which could be linked to these functional groups. In this way, our approach presents a generalized view on the responses of species to weather variability.

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Table 1 - Traits, used for analysis in Z matrix

<i>trait (data source)</i>	<i>abbreviation</i>	<i>explanation (classification)</i>	<i>reasoning</i>
nest location (Cramp and Simmons (1977-1994))	lownest	Nest location at water table, along water banks or in holes in the ground (1; low elevations), in contrast to nest locations higher in elevation (0)	Low precipitation in non- and pre-breeding season leads to low water tables, which is most negative for species breeding on or just above water and ground level, because of low nest site availability and high predation pressure (Newton 1998). Extreme wind may destroy nests located higher in elevation (trees and reed vegetation) (Wunderle et al. 1992). A dry heat wave might negatively impact ground nesting species (Jiguet et al. 2006).
main diet type (Cramp and Simmons (1977-1994))	fdpl	Main food during breeding season: plants (vegetative and generative parts) (1; herbivorous), in contrast to other diets (0)	When temperature drops below 5 °C, plant growth stops leading to reduced food availability for herbivores. Temperatures below 0 °C are negative for piscivorous species (frozen water bodies) (Morgan & Glue 1977, Besbeas et al. 2002), as well as for insectivorous species (Newton 1998). Snow cover is negative for ground feeders (insectivorous species and herbivores) (Peach et al. 1995). Both low water tables during non-breeding and breeding seasons are negative to piscivorous species (Den Held 1981). Warmth in spring and summer is positive for insectivorous species, because of high insect abundance (Birch 1953). But in combination with drought, warmth is expected to negatively affect herbivorous species through food shortages (Newton 1998).
	fdinvert	Main food during breeding season: insects (1; insectivorous), in contrast to other diets (0)	
	fdpisci	Main food during breeding season: fish (1; piscivorous), in contrast to other diets (0) - <i>trait occurs only for marshland species</i>	
	fdmeat	Main food during breeding season: small mammals (1; raptors), in contrast to other diets (0)	
offspring development (Cramp and Simmons (1977-1994))	altr	Altricial species (1) that are nidicolous and hatched without feathers, in contrast to precocial species (0) that are nidifugous and hatched with feathers	Extreme rainfall and wind events during the breeding season is most negative for precocial species that often lack shelter of a nest, in contrast to altricial species (Sæther et al. 2004). A dry heat wave might negatively impact altricial species (Jiguet et al. 2006).
migration strategy (Speek and Speek (1984), Wernham et al. (2002))	resid	Migration strategy: resident (1) during winter time, in contrast to other migration strategies (0)	Mild winters are most beneficial for sedentary birds, because of high winter survival. For long-distant migrants mild winters will have either neutral effect, because they are away on the wintering grounds, or even negative due to the competition with residents for the resources and occurrence of mismatches (Newton 1998). Early warm spring temperatures are negative to (long-distance) migrants due to the increased probability for a food mismatches (Both & Visser 2001, 2005, Both et al. 2006).
	pmigr	Migration strategy: partial migrant/short-distance migrant (1) during winter time, in contrast to other migration strategies (0)	
	migr	Migration strategy: long distance migrant (1) during winter time, in contrast to other migration strategies (0)	

Table 2 - Weather variables, used for analysis in X matrix

<i>abbreviation</i>	<i>explanation (units)</i>
<i>Weather variables during the non-breeding season ("NB")</i>	
NB_IJnsen	IJnsen value (IJnsen 1981) ranging from 0 to 60 (-), expressing winter severity; the higher the value, the more severe the winter. Calculation: $(v^2/363) + (2y/3) + (10z/9)$, where v, y and z stand for the number of 24 h periods with a minimum temperature below 0°C, with a maximum temperature below 0°C and with a maximum temperature below -10°C, respectively, during the period November-March.
NB_tempcoldmonth	Mean temperature of the coldest month (°C). For each year, the mean temperature of each month from October to March was calculated and the coldest monthly average was taken.
NB_frostdays	Longest duration of consecutive days (-) with daily mean temperature below 0°C.
NB_rain	Total precipitation sum over non-breeding season (mm)
NB_snowdays	Longest duration of consecutive days (-) with snow cover more than or equal to 2 cm
<i>Weather variables during the breeding season ("B")</i>	
B_temp	Mean temperature (°C)
B_tempaprmay	Mean temperature (°C) from 16 April to 15 May
B_rain	Total precipitation sum over breeding season (mm)
B_heavyraindays	Longest duration of consecutive days (-) with daily average precipitation sum exceeding 3mm
B_drydays	Longest duration of consecutive days (-) with daily precipitation sum less than 1mm (Robinson et al. 2007)
B_squall	Total number of squalls (-) (wind speed exceeding 22 knots (11.31m/s) and lasting for at least one minute (MANMAR).
B_heatwave	Number of days comprising a heat wave (-). For the Netherlands, a heat wave is defined as a period of at least 5 consecutive days in which the maximum temperature at De Bilt exceeds 25°C, provided that on at least 3 days in this period the maximum temperature at De Bilt exceeds 30°C (Meehl & Tebaldi 2004).

NB: non-breeding season; B: breeding season. For B_squall, values were derived from data from all meteorological stations in the Netherlands; remaining weather variable values were derived from the De Bilt meteorological station. All weather variable values were log transformed ($\ln(x+1)$, and $\ln(x+5)$ for NB_tempcoldmonth), except values for B_temp and B_tempaprmay

Table 3 - Relations between traits and weather variables expressed by significance (P), traits-weather correlation (R) and mean species-specific regression coefficients b_k resulting from the LTE analysis for different trait categories.
a: marshland species

trait	abbreviation (n trait 0; n trait 1)	weather variable	P	R	b_k mean (trait=0)	b_k 25-75% (trait=0)	b_k mean (trait=1)	b_k 25-75% (trait=1)
nest location	lowest (28;15)	NB_IJnsen	0.042	-0.348	0.019	-0.016 - 0.071	-0.036	-0.083 - 0.014
		NB_tempcoldmonth	0.013	0.407	-0.035	-0.085 - 0.02	0.065	-0.019 - 0.136
		NB_frostdays	0.043	-0.384	0.017	-0.007 - 0.057	-0.032	-0.082 - 0.012
		NB_rain	0.023	0.335	-0.066	-0.173 - -0.01	0.123	-0.041 - 0.21
		NB_snowdays t-1	0.011	-0.628	0.023	0.002 - 0.052	-0.043	-0.088 - -0.005
		B_tempaprmay t-1	0.005	0.628	-0.012	-0.026 - -0.001	0.023	0.005 - 0.042
main diet type	fdpl (35;8)	NB_snowdays t-1	0.035	-0.421	0.010	-0.011 - 0.039	-0.045	-0.096 - 0.008
		B_tempaprmay t-1	0.044	0.392	-0.005	-0.018 - 0.009	0.022	0 - 0.054
offspring development	altr (10;33)	NB_IJnsen	0.035	0.380	-0.052	-0.085 - 0.005	0.016	-0.027 - 0.059
		NB_tempcoldmonth	0.010	-0.447	0.094	-0.01 - 0.165	-0.029	-0.079 - 0.027
		NB_frostdays	0.047	0.430	-0.048	-0.085 - 0	0.014	-0.013 - 0.055
		NB_rain	0.040	-0.305	0.149	-0.009 - 0.212	-0.045	-0.164 - 0.022
		NB_snowdays t-1	0.009	0.683	-0.063	-0.098 - -0.026	0.019	0 - 0.046
		B_tempaprmay t-1	0.010	-0.678	0.033	0.017 - 0.052	-0.010	-0.019 - 0.004
migration strategy	resid (31;12)	B_temp t-1	0.037	0.373	-0.016	-0.035 - 0.015	0.042	0.022 - 0.082
		B_tempaprmay	0.040	0.308	-0.007	-0.017 - 0.004	0.018	-0.001 - 0.037
	migr (25;18)	NB_tempcoldmonth	0.026	-0.351	0.035	-0.036 - 0.108	-0.048	-0.089 - -0.002
		NB_frostdays	0.044	0.366	-0.019	-0.07 - 0.02	0.026	-0.004 - 0.056

b: forest species

trait	abbreviation (n trait 0; n trait 1)	weather variable	P	R	b_k mean (trait=0)	b_k 25-75% (trait=0)	b_k mean (trait=1)	b_k 25-75% (trait=1)
main diet type	fdinvert (50;3)	NB_IJnsen t-1	0.014	0.380	-0.029	-0.054 - 0.009	0.011	-0.022 - 0.046
		NB_tempcoldmonth t-1	0.027	-0.369	0.038	0.009 - 0.06	-0.015	-0.042 - 0.032
		NB_frostdays t-1	0.030	0.379	-0.023	-0.053 - 0	0.009	-0.014 - 0.033
		B_rain	0.016	0.359	-0.088	-0.138 - 0	0.035	-0.051 - 0.113
	fdmeat (48;5)	NB_IJnsen t-1	0.006	-0.557	0.009	-0.022 - 0.038	-0.082	-0.078 - -0.058
		NB_frostdays t-1	0.015	-0.591	0.007	-0.014 - 0.033	-0.070	-0.073 - -0.059
		NB_rain t-1	0.017	0.511	-0.022	-0.082 - 0.038	0.211	0.086 - 0.37
		B_rain	0.008	-0.539	0.027	-0.057 - 0.089	-0.257	-0.366 - -0.157
migration strategy	resid (29;24)	NB_IJnsen t-1	0.019	-0.332	0.014	0.005 - 0.047	-0.017	-0.032 - 0.001
		NB_tempcoldmonth t-1	0.027	0.331	-0.020	-0.054 - 0.021	0.024	0.008 - 0.049
		NB_frostdays t-1	0.019	-0.348	0.012	-0.005 - 0.047	-0.015	-0.031 - 0.005
	pmigr (39;14)	NB_IJnsen	0.007	-0.403	0.015	-0.002 - 0.05	-0.041	-0.088 - 0.011
		NB_tempcoldmonth	0.003	0.412	-0.022	-0.068 - 0.012	0.061	-0.011 - 0.114
		NB_frostdays	0.012	-0.344	0.011	-0.009 - 0.044	-0.032	-0.066 - 0.009
		B_rain t-1	0.032	0.328	-0.031	-0.107 - 0.024	0.088	-0.034 - 0.186
		B_rain	0.042	-0.323	0.030	-0.061 - 0.121	-0.083	-0.067 - 0.011
	migr (38;15)	NB_IJnsen t-1	0.001	0.579	-0.017	-0.033 - 0.008	0.044	0.023 - 0.058
		NB_tempcoldmonth t-1	0.003	-0.524	0.022	-0.008 - 0.042	-0.055	-0.089 - -0.011
		NB_frostdays t-1	0.001	0.611	-0.015	-0.028 - 0.007	0.037	0.03 - 0.052
		NB_rain t-1	0.018	-0.412	0.034	-0.03 - 0.058	-0.087	-0.149 - -0.036
		B_tempaprmay t-1	0.040	-0.358	0.005	-0.002 - 0.013	-0.013	-0.024 - 0.007
		B_rain	0.005	0.462	-0.045	-0.104 - 0.025	0.113	0.013 - 0.205

Significant relationships are shown; n: number of species; P: statistical significance for trait-environment relationship; R: Pearson correlation between the trait z and the species-specific regression coefficients b_k , obtained from regressions per species of population growth rate values on indicated weather variables; b_k mean: mean of b_k values of species that do not hold the trait (trait 0) or hold the trait (1); b_k 25-75%: 25th and 75th percentile of b_k values of species that do not hold the trait (trait 0) or hold the trait (1)

1 Table 4 - Species expected to respond most positively (a) and negatively (b) to the
 2 expected increased occurrence of mild winters, which can be expected from their
 3 species specific regression coefficient (b_k) values. For abbreviations of traits, see
 4 Table 1.

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 6 a: species expected to respond most positively

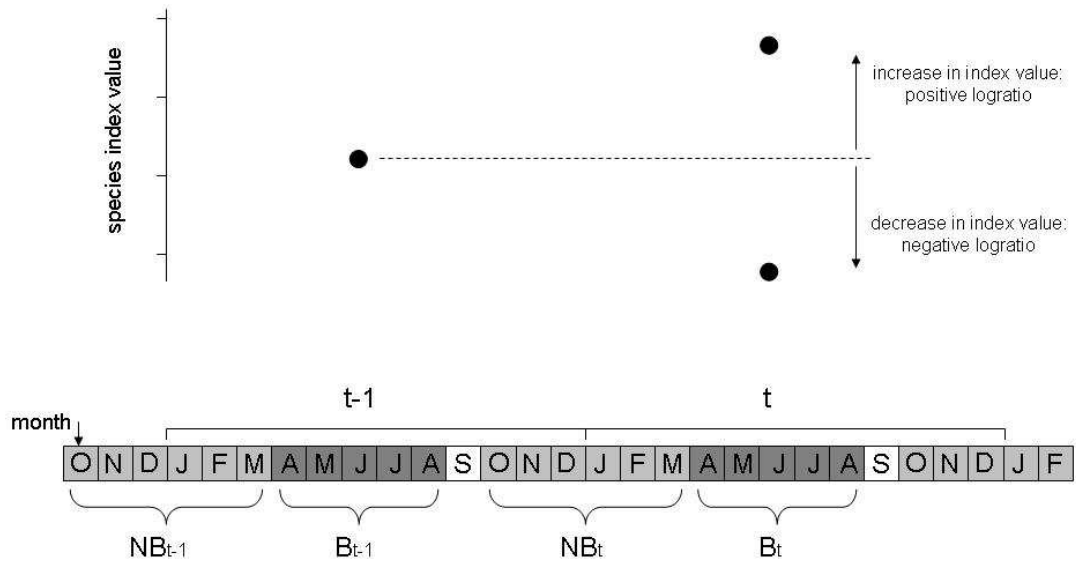
abbreviation	scientific name	English name	lownest	fdpl	altr	resid	habitat (marshland species (M); forest species (F); both (M&F))
ACAU	<i>Aegithalos caudatus</i>	Long-tailed tit	0	0	1	1	M&F
ACRE	<i>Anas crecca</i>	Teal	1	1	0	0	M
ASTR	<i>Anas strepera</i>	Gadwall	1	1	0	0	M
BSTE	<i>Botaurus stellaris</i>	Bittern	1	0	1	1	M
COLO	<i>Cygnus olor</i>	Mute swan	1	1	0	1	M
GCHL	<i>Gallinula chloropus</i>	Moorhen	1	0	0	1	M
LMEG	<i>Luscinia megarhynchos</i>	Nightingale	0	0	1	0	M&F
RAQU	<i>Rallus aquaticus</i>	Water rail	1	0	0	0	M
SATR	<i>Sylvia atricapilla</i>	Blackcap	0	0	1	0	M&F
TRUF	<i>Tachybaptus ruficollis</i>	Little grebe	1	0	0	0	M

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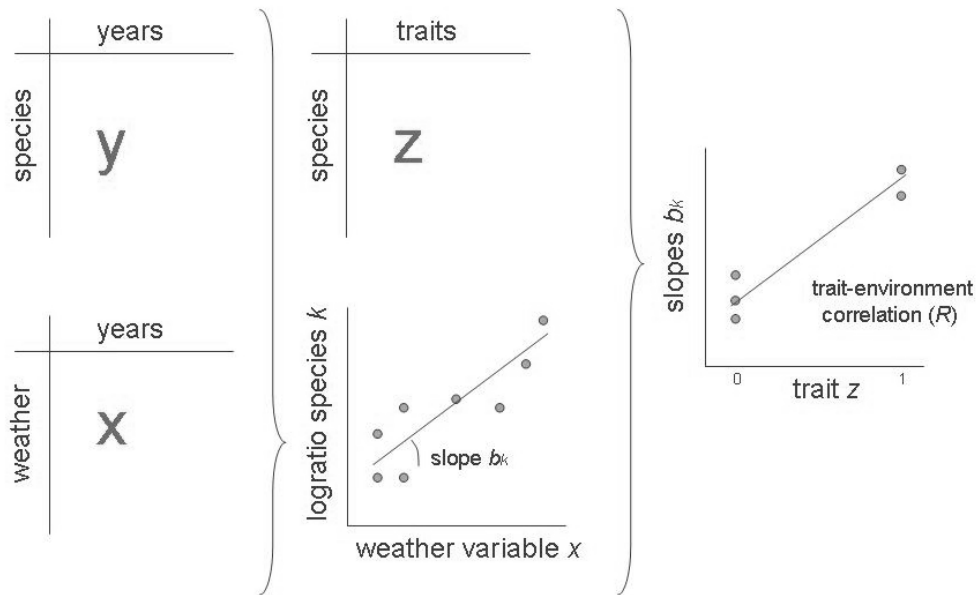
8 b: species expected to respond most negatively

abbreviation	scientific name	English name	fdinvert	migr	habitat (marshland species (M); forest species (F); both (M&F))
ECIT	<i>Emberiza citrinella</i>	Yellowhammer	1	0	F
FSUB	<i>Falco subbuteo</i>	Hobby	1	1	F
HICT	<i>Hippolais icterina</i>	Icterine warbler	1	1	F
OORI	<i>Oriolus oriolus</i>	Golden oriole	1	1	F
PCOLL	<i>Phylloscopus collybita</i>	Chiffchaff	1	1	M&F
PSIB	<i>Phylloscopus sibilatrix</i>	Wood warbler	1	1	F
RIGN	<i>Regulus ignicapillus</i>	Firecrest	1	0	F
SATR	<i>Sylvia atricapilla</i>	Blackcap	1	1	M&F
SBOR	<i>Sylvia borin</i>	Garden warbler	1	1	M&F
SCOM	<i>Sylvia communis</i>	Whitethroat	1	1	M&F
STUR	<i>Streptopelia turtur</i>	Turtle dove	0	1	M&F
TTRO	<i>Troglodytes troglodytes</i>	Winter wren	1	0	M&F
TVIS	<i>Turdus viscivorus</i>	Mistle thrush	1	0	F

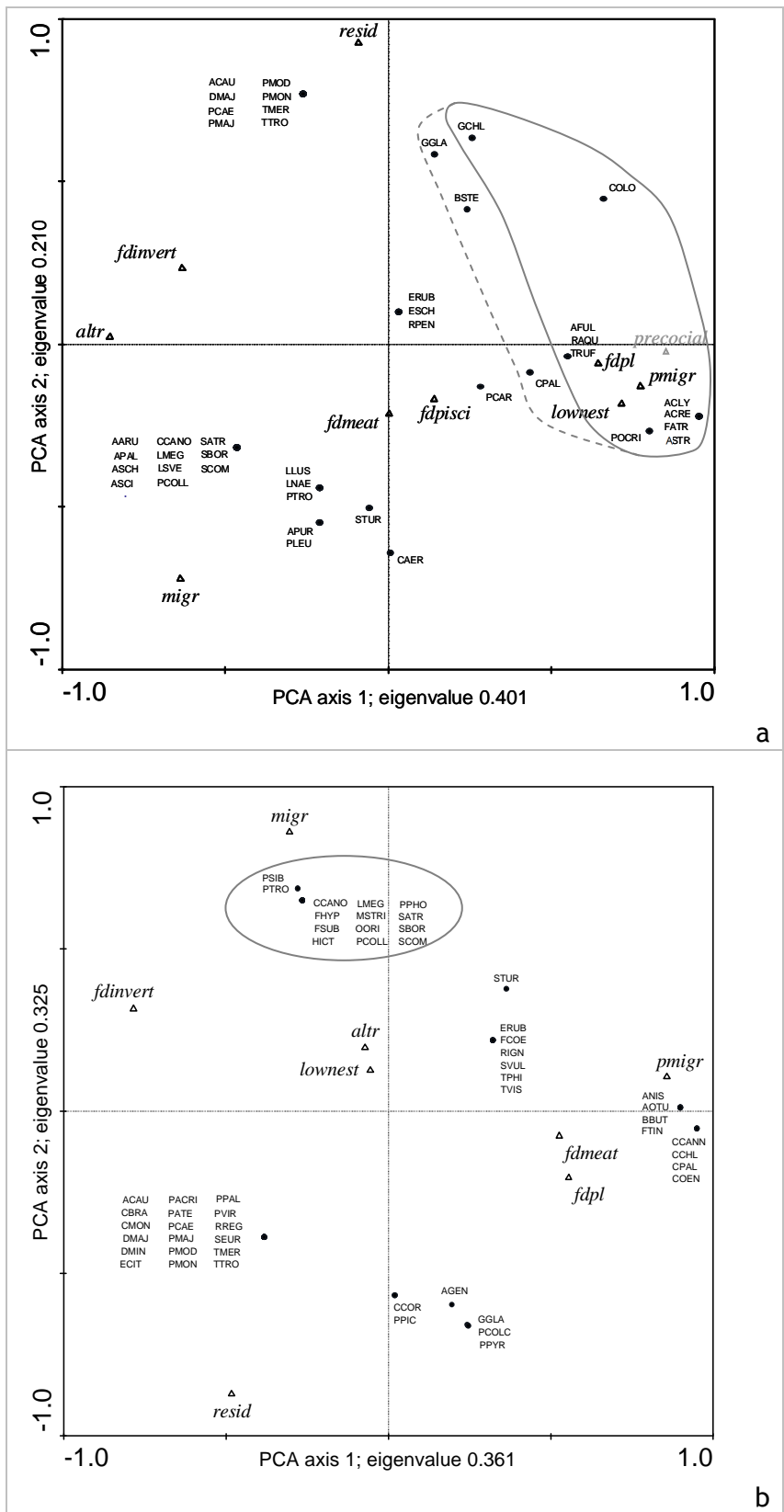
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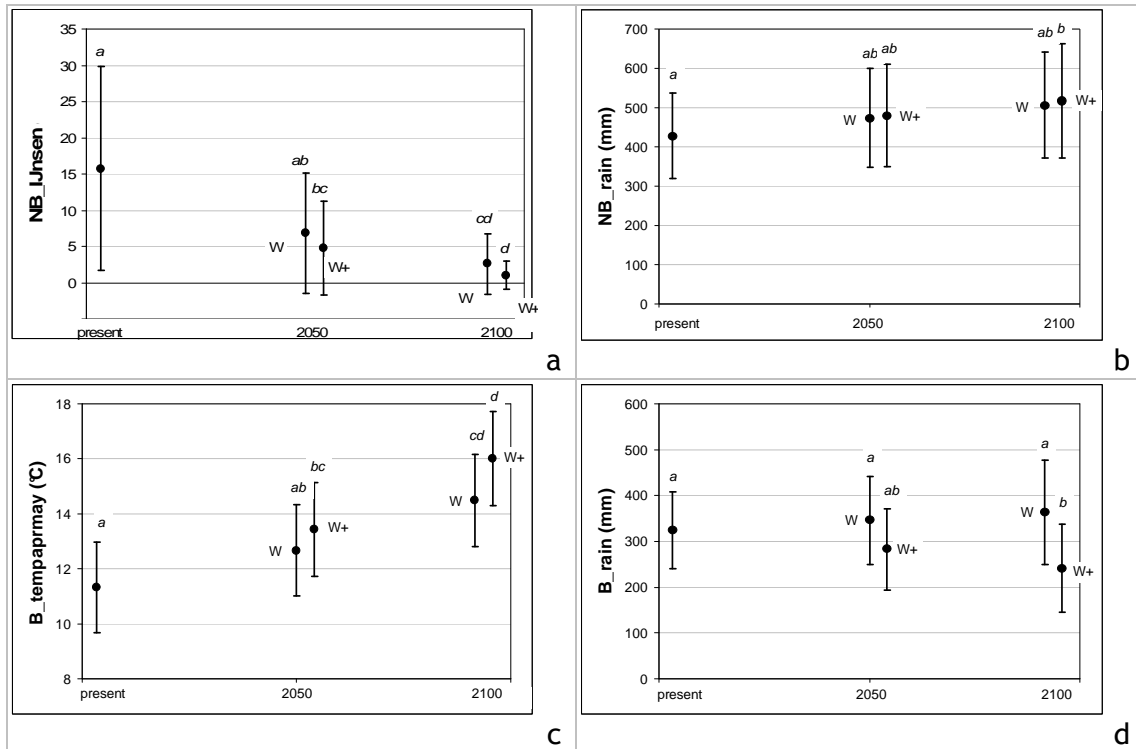
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 12 Figure 1 - Timing of territory monitoring (•) and periods of occurrence of weather
 13 variables in two subsequent years, t-1 and t. Increase in index value between t-1
 14 and t results in positive population growth rate, and vice versa. NB: non-breeding
 15 season, from October to March; B: breeding season, from April to August
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17
 18 Figure 2 - Schematic overview of LTE analysis procedure. Species-specific
 19 regression coefficients (b_k) are obtained from regressions per species of the
 20 population growth rate values (Y matrix) on to each weather variable (X matrix).
 21 Subsequently, the species-specific regression coefficients are correlated to each
 22 trait z (Z matrix). R is the Pearson correlation between the trait z and the species-
 23 specific regression coefficients b_k , with R^2 being the fraction of the environmentally
 24 structured variation that can be explained by the trait. When both regressions
 25 (regression population growth rates - weather variable and regression b_k 's - trait)
 26 are significant, we report a trait-environment relationship.



27
 28 Figure 3 - Ordination of marshland (a) and forest (b) species and traits, resulting
 29 from PCA. Encircled are waterfowl s.s. (dashed: s.l.; Jay, Bittern and Wood pigeon
 30 can strictly not be classified as waterfowl, but share most traits and responses) (a)
 31 and insectivorous long-distance migrants (b). For abbreviations of species names,
 32 see Appendix 1; for abbreviations of traits, see Table 1.



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Figure 4 - Weather variable values and SDs for present (1984-2004), 2050 (range 2037-2065), and 2100 (range 2087-2115) for IJnsen (a), total precipitation sum over non-breeding season (b), mean temperature from 16 April to 15 May (c), and total precipitation sum over breeding season (d); expectation based on data KNMI scenarios W and W⁺ (http://climexp.knmi.nl/Scenarios_monthly/; for explanation on scenarios, see http://www.knmi.nl/research/climate_services/). Within each weather variable, bars sharing the same letter are not significantly different (P > 0.05). For abbreviations of weather variables, see Table 2.

43 APPENDIX

44 Appendix 1

45 Species, used for analysis in Y and Z matrix, and their traits (1: species holds trait;

46 0: species does not hold trait). For abbreviations of traits, see Table 1

abbreviation	scientific name	English name	lownest	fdpl	fainvert	fdpisci	fdmeat	altr	resid	pmigr	migr	habitat (marshland species (M); forest species (F); both (M&F))
AARU	<i>Acrocephalus arundinaceus</i>	Great reed warbler	0	0	1	0	0	1	0	0	1	M
ACAU	<i>Aegithalos caudatus</i>	Long-tailed tit	0	0	1	0	0	1	1	0	0	M&F
ACLY	<i>Anas clypeata</i>	Northern shoveler	1	1	0	0	0	0	0	1	0	M
ACRE	<i>Anas crecca</i>	Teal	1	1	0	0	0	0	0	1	0	M
AFUL	<i>Aythya fuligula</i>	Tufted duck	1	0	1	0	0	0	0	1	0	M
AGEN	<i>Accipiter gentilis</i>	Goshawk	0	0	0	0	1	1	1	0	0	F
ANIS	<i>Accipiter nisus</i>	Sparrowhawk	0	0	0	0	1	1	0	1	0	F
AOTU	<i>Asio otus</i>	Long-eared owl	0	0	0	0	1	1	0	1	0	F
APAL	<i>Acrocephalus palustris</i>	Marsh warbler	0	0	1	0	0	1	0	0	1	M
APUR	<i>Ardea purpurea</i>	Purple heron	0	0	0	1	0	1	0	0	1	M
ASCH	<i>Acrocephalus schoenobaenus</i>	Sedge warbler	0	0	1	0	0	1	0	0	1	M
ASCI	<i>Acrocephalus scirpaceus</i>	Reed warbler	0	0	1	0	0	1	0	0	1	M
ASTR	<i>Anas strepera</i>	Gadwall	1	1	0	0	0	0	0	1	0	M
BBUT	<i>Buteo buteo</i>	Buzzard	0	0	0	0	1	1	0	1	0	F
BSTE	<i>Botaurus stellaris</i>	Bittern	1	0	0	1	0	1	1	0	0	M
CAER	<i>Circus aeruginosus</i>	Western marsh harrier	1	0	0	0	1	1	0	0	1	M
CBRA	<i>Certhia brachydactyla</i>	Short-toed treecreeper	0	0	1	0	0	1	1	0	0	F
CCANN	<i>Carduelis cannabina</i>	Linnet	0	1	0	0	0	1	0	1	0	F
CCANO	<i>Cuculus canorus</i>	Cuckoo	0	0	1	0	0	1	0	0	1	M&F
CCHL	<i>Chloris chloris</i>	Greenfinch	0	1	0	0	0	1	0	1	0	F
CCOR	<i>Corvus corone</i>	Carrion crow	0	0	0	0	0	1	1	0	0	F
CMON	<i>Corvus monedula</i>	Jackdaw	0	0	1	0	0	1	1	0	0	F
COEN	<i>Columba oenas</i>	Stock pigeon	0	1	0	0	0	1	0	1	0	F
COLO	<i>Cygnus olor</i>	Mute swan	1	1	0	0	0	0	1	0	0	M
CPAL	<i>Columba palumbus</i>	Wood pigeon	0	1	0	0	0	1	0	1	0	M&F
DMAJ	<i>Dendrocopos major</i>	Great spotted woodpecker	0	0	1	0	0	1	1	0	0	M&F
DMIN	<i>Dendrocopos minor</i>	Lesser spotted woodpecker	0	0	1	0	0	1	1	0	0	F
ECIT	<i>Emberiza citrinella</i>	Yellowhammer	0	0	1	0	0	1	1	0	0	F
ERUB	<i>Erithacus rubecula</i>	Robin	0	0	1	0	0	1	0	1	0	M&F
ESCH	<i>Emberiza schoeniclus</i>	Reed bunting	0	0	1	0	0	1	0	1	0	M
FATR	<i>Fulica atra</i>	Coot	1	1	0	0	0	0	0	1	0	M
FCOE	<i>Fringilla coelebs</i>	Chaffinch	0	0	1	0	0	1	0	1	0	F
FHYP	<i>Ficedula hypoleuca</i>	Pied flycatcher	0	0	1	0	0	1	0	0	1	F
FSUB	<i>Falco subbuteo</i>	Hobby	0	0	1	0	0	1	0	0	1	F

FTIN	<i>Falco tinnunculus</i>	Kestrel	0	0	0	0	1	1	0	1	0	F
GCHL	<i>Gallinula chloropus</i>	Moorhen	1	0	1	0	0	0	1	0	0	M
GGLA	<i>Garrulus glandarius</i>	Jay	0	1	0	0	0	1	1	0	0	M&F
HICT	<i>Hippolais icterina</i>	Icterine warbler	0	0	1	0	0	1	0	0	1	F
LLUS	<i>Locustella luscinioides</i>	Savi's warbler	1	0	1	0	0	1	0	0	1	M
LMEG	<i>Luscinia megarhynchos</i>	Nightingale	0	0	1	0	0	1	0	0	1	M&F
LNAE	<i>Locustella naevia</i>	Grasshopper warbler	1	0	1	0	0	1	0	0	1	M
LSVE	<i>Luscinia svecica</i>	Bluethroat	0	0	1	0	0	1	0	0	1	M
MSTR	<i>Muscicapa striata</i>	Spotted flycatcher	0	0	1	0	0	1	0	0	1	F
OORI	<i>Oriolus oriolus</i>	Golden oriole	0	0	1	0	0	1	0	0	1	F
PACRI	<i>Parus cristatus</i>	Crested tit	0	0	1	0	0	1	1	0	0	F
PATE	<i>Parus ater</i>	Coal tit	0	0	1	0	0	1	1	0	0	F
PCAE	<i>Parus caeruleus</i>	Blue tit	0	0	1	0	0	1	1	0	0	M&F
PCAR	<i>Phalacrocorax carbo</i>	Cormorant	0	0	0	1	0	1	0	1	0	M
PCOLC	<i>Phasianus colchicus</i>	Pheasant	1	1	0	0	0	0	1	0	0	F
PCOLL	<i>Phylloscopus collybita</i>	Chiffchaff	0	0	1	0	0	1	0	0	1	M&F
PLEU	<i>Platalea leucorodia</i>	Spoonbill	0	0	0	1	0	1	0	0	1	M
PMAJ	<i>Parus major</i>	Great tit	0	0	1	0	0	1	1	0	0	M&F
PMOD	<i>Prunella modularis</i>	Dunnoek	0	0	1	0	0	1	1	0	0	M&F
PMON	<i>Parus montanus</i>	Willow tit	0	0	1	0	0	1	1	0	0	M&F
POCRI	<i>Podiceps cristatus</i>	Great crested grebe	1	0	0	1	0	0	0	1	0	M
PPAL	<i>Parus palustris</i>	Marsh tit	0	0	1	0	0	1	1	0	0	F
PPHO	<i>Phoenicurus phoenicurus</i>	Redstart	0	0	1	0	0	1	0	0	1	F
PPIC	<i>Pica pica</i>	Magpie	0	0	0	0	0	1	1	0	0	F
PPYR	<i>Pyrrhula pyrrhula</i>	Bullfinch	0	1	0	0	0	1	1	0	0	F
PSIB	<i>Phylloscopus sibilatrix</i>	Wood warbler	1	0	1	0	0	1	0	0	1	F
PTRO	<i>Phylloscopus trochilus</i>	Willow warbler	1	0	1	0	0	1	0	0	1	M&F
PVIR	<i>Picus viridis</i>	Green woodpecker	0	0	1	0	0	1	1	0	0	F
RAQU	<i>Rallus aquaticus</i>	Water rail	1	0	1	0	0	0	0	1	0	M
RIGN	<i>Regulus ignicapillus</i>	Firecrest	0	0	1	0	0	1	0	1	0	F
RPEN	<i>Remiz pendulinus</i>	Penduline tit	0	0	1	0	0	1	0	1	0	M
RREG	<i>Regulus regulus</i>	Goldcrest	0	0	1	0	0	1	1	0	0	F
SATR	<i>Sylvia atricapilla</i>	Blackcap	0	0	1	0	0	1	0	0	1	M&F
SBOR	<i>Sylvia borin</i>	Garden warbler	0	0	1	0	0	1	0	0	1	M&F
SCOM	<i>Sylvia communis</i>	Whitethroat	0	0	1	0	0	1	0	0	1	M&F
SEUR	<i>Sitta europaea</i>	Nuthatch	0	0	1	0	0	1	1	0	0	F
STUR	<i>Streptopelia turtur</i>	Turtle dove	0	1	0	0	0	1	0	0	1	M&F
SVUL	<i>Sturnus vulgaris</i>	Starling	0	0	1	0	0	1	0	1	0	F
TMER	<i>Turdus merula</i>	Blackbird	0	0	1	0	0	1	1	0	0	M&F
TPHI	<i>Turdus philomelos</i>	Song thrush	0	0	1	0	0	1	0	1	0	F
TRUF	<i>Tachybaptus ruficollis</i>	Little grebe	1	0	1	0	0	0	0	1	0	M
TTRO	<i>Troglodytes troglodytes</i>	Winter wren	0	0	1	0	0	1	1	0	0	M&F
TVIS	<i>Turdus viscivorus</i>	Mistle thrush	0	0	1	0	0	1	0	1	0	F

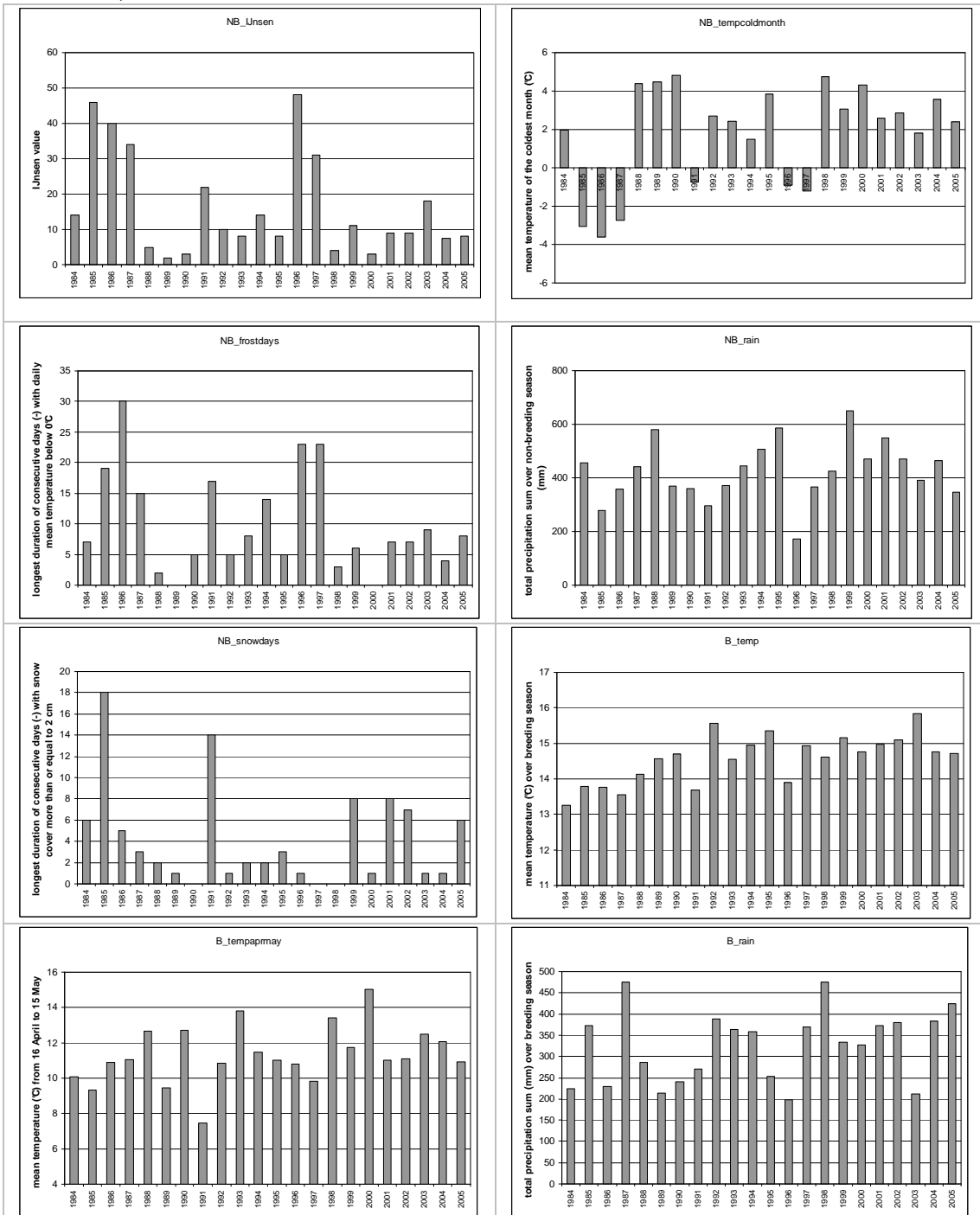
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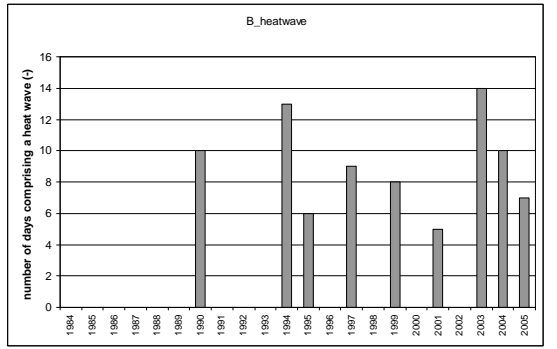
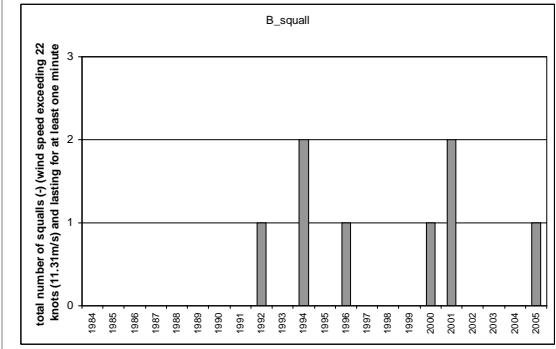
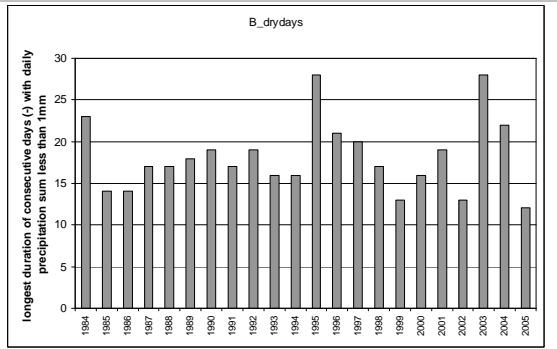
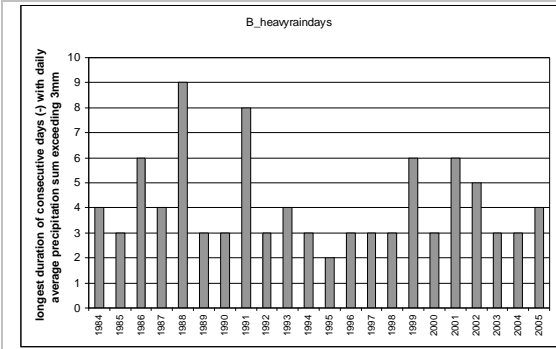
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Appendix 2

Occurrence of weather variables in 1984-2005. For abbreviations of weather variables, see Table 2





52 Appendix 3 Correlations between weather variables; grey shading: relatively high Pearson score. For abbreviations of weather variables, see Table 2

	NB_IJnsen	NB_IJnsen t-1	NB_tempcoldmonth	NB_tempcoldmonth t-1	NB_frostdays	NB_frostdays t-1	NB_rain	NB_rain t-1	NB_snowdays	NB_snowdays t-1	B_temp	B_temp t-1	B_tempaprmay	B_tempaprmay t-1	B_rain	B_rain t-1	B_heavyraindays	B_heavyraindays t-1	B_drydays	B_drydays t-1	B_squall	B_squall t-1	B_heatwave	B_heatwave t-1
NB_IJnsen	-	0.31	-0.87	-0.29	0.90	0.37	-0.49	-0.35	0.38	0.27	-0.41	-0.29	-0.50	-0.13	-0.04	-0.30	-0.25	0.04	-0.02	0.17	-0.02	-0.04	-0.07	-0.17
NB_IJnsen t-1	0.31	-	-0.41	-0.86	0.18	0.90	0.05	-0.50	-0.27	0.40	-0.19	-0.39	0.12	-0.51	0.31	-0.03	0.19	-0.28	0.04	-0.04	-0.26	0.00	-0.28	-0.06
NB_tempcoldmonth	-0.87	-0.41	-	0.48	-0.74	-0.37	0.46	0.39	-0.39	-0.39	0.64	0.50	0.47	0.25	0.03	0.34	0.34	0.12	0.22	0.00	0.15	0.16	0.28	0.26
NB_tempcoldmonth t-1	-0.29	-0.86	0.48	-	-0.20	-0.75	-0.13	0.48	0.14	-0.40	0.38	0.55	-0.07	0.46	-0.25	-0.01	-0.18	0.38	0.06	0.28	0.27	0.13	0.35	0.26
NB_frostdays	0.90	0.18	-0.74	-0.20	-	0.22	-0.42	-0.49	0.33	0.07	-0.32	-0.19	-0.46	-0.13	0.02	-0.25	-0.21	-0.05	-0.07	0.23	-0.01	0.08	0.12	-0.17
NB_frostdays t-1	0.37	0.90	-0.37	-0.75	0.22	-	0.03	-0.42	-0.16	0.33	-0.14	-0.29	0.00	-0.46	0.29	0.02	0.25	-0.20	0.06	-0.06	-0.29	-0.02	-0.29	0.11
NB_rain	-0.49	0.05	0.46	-0.13	-0.42	0.03	-	0.04	0.04	-0.15	0.45	0.05	0.41	0.36	0.34	0.55	0.23	0.05	-0.03	-0.49	-0.05	0.32	0.31	-0.12
NB_rain t-1	-0.35	-0.50	0.39	0.48	-0.49	-0.42	0.04	-	0.22	0.08	0.06	0.38	0.22	0.39	-0.26	0.35	-0.05	0.22	-0.02	-0.06	0.27	-0.03	-0.13	0.33
NB_snowdays	0.38	-0.27	-0.39	0.14	0.33	-0.16	0.04	0.22	-	0.04	-0.30	-0.20	-0.50	0.34	0.12	0.19	-0.33	0.22	-0.49	-0.01	0.03	0.12	-0.17	0.02
NB_snowdays t-1	0.27	0.40	-0.39	-0.40	0.07	0.33	-0.15	0.08	0.04	-	0.00	-0.36	0.07	-0.51	-0.17	0.02	-0.20	-0.26	-0.01	-0.38	0.09	-0.04	-0.35	-0.25
B_temp	-0.41	-0.19	0.64	0.38	-0.32	-0.14	0.45	0.06	-0.30	0.00	-	0.31	0.31	0.07	0.03	0.30	0.26	0.10	0.37	-0.22	0.19	0.34	0.58	-0.01
B_temp t-1	-0.29	-0.39	0.50	0.55	-0.19	-0.29	0.05	0.38	-0.20	-0.36	0.31	-	0.42	0.35	-0.08	0.14	0.05	0.19	0.27	0.25	0.12	0.22	0.27	0.59
B_tempaprmay	-0.50	0.12	0.47	-0.07	-0.46	0.00	0.41	0.22	-0.50	0.07	0.31	0.42	-	-0.12	0.15	0.43	0.19	0.05	0.05	-0.26	0.09	-0.03	0.08	0.04
B_tempaprmay t-1	-0.13	-0.51	0.25	0.46	-0.13	-0.46	0.36	0.39	0.34	-0.51	0.07	0.35	-0.12	-	0.02	0.21	-0.12	0.15	-0.04	-0.02	0.34	0.12	0.40	0.12
B_rain	-0.04	0.31	0.03	-0.25	0.02	0.29	0.34	-0.26	0.12	-0.17	0.03	-0.08	0.15	0.02	-	-0.02	0.17	-0.03	-0.42	0.13	0.15	0.11	-0.03	0.08
B_rain t-1	-0.30	-0.03	0.34	-0.01	-0.25	0.02	0.55	0.35	0.19	0.02	0.30	0.14	0.43	0.21	-0.02	-	0.21	0.19	-0.27	-0.41	0.09	0.12	-0.01	-0.04
B_heavyraindays	-0.25	0.19	0.34	-0.18	-0.21	0.25	0.23	-0.05	-0.33	-0.20	0.26	0.05	0.19	-0.12	0.17	0.21	-	-0.12	0.28	-0.07	0.13	0.05	-0.06	0.21
B_heavyraindays t-1	0.04	-0.28	0.12	0.38	-0.05	-0.20	0.05	0.22	0.22	-0.26	0.10	0.19	0.05	0.15	-0.03	0.19	-0.12	-	-0.22	0.23	-0.22	0.19	-0.05	-0.03
B_drydays	-0.02	0.04	0.22	0.06	-0.07	0.06	-0.03	-0.02	-0.49	-0.01	0.37	0.27	0.05	-0.04	-0.42	-0.27	0.28	-0.22	-	-0.06	-0.08	0.17	0.34	0.09
B_drydays t-1	0.17	-0.04	0.00	0.28	0.23	-0.06	-0.49	-0.06	-0.01	-0.38	-0.22	0.25	-0.26	-0.02	0.13	-0.41	-0.07	0.23	-0.06	-	-0.05	-0.01	0.01	0.40
B_squall	-0.02	-0.26	0.15	0.27	-0.01	-0.29	-0.05	0.27	0.03	0.09	0.19	0.12	0.09	0.34	0.15	0.09	0.13	-0.22	-0.08	-0.05	-	-0.08	0.16	0.02
B_squall t-1	-0.04	0.00	0.16	0.13	0.08	-0.02	0.32	-0.03	0.12	-0.04	0.34	0.22	-0.03	0.12	0.11	0.12	0.05	0.19	0.17	-0.01	-0.08	-	0.09	0.13
B_heatwave	-0.07	-0.28	0.28	0.35	0.12	-0.29	0.31	-0.13	-0.17	-0.35	0.58	0.27	0.08	0.40	-0.03	-0.01	-0.06	-0.05	0.34	0.01	0.16	0.09	-	-0.05
B_heatwave t-1	-0.17	-0.06	0.26	0.26	-0.17	0.11	-0.12	0.33	0.02	-0.25	-0.01	0.59	0.04	0.12	0.08	-0.04	0.21	-0.03	0.09	0.40	0.02	0.13	-0.05	-

53 *Appendix 4*

54 In this appendix we describe the linear trait-environment (LTE) method, which is
55 the linear counter part of the fourth-corner method of Dray and Legendre (2008).
56 See below for a detailed comparison. The LTE method relates the quantitative
57 environmental variable x to the quantitative species trait z via the species-site
58 data y . It differs from the fourth-corner method by using multivariate linear
59 regression model for the species-site data, thus allowing negative values y . In our
60 application, sites are years and $y_{ik} = \ln[\text{index}_{\text{year}_i, \text{species}_k} / \text{index}_{\text{year}_i-1, \text{species}_k}]$.

61 *Notation:* Denote the value of environmental variable x at site i by x_i , the value of
62 the trait z of species k by z_k , and the population growth rate y of species k in site i
63 by y_{ik} ($i = 1, \dots, n$, $k = 1, \dots, m$). All these values are interval scaled taking values on
64 the real line.

65 *Model:* The LTE method starts from a multivariate linear regression of the species-
66 site data using a single predictor variable x . This regression can be expressed as m
67 separate simple linear regressions, one for each species,

68
$$y_{ik} = a_k + b_k x_i + \varepsilon_{ik}, \quad (1)$$

69 where a_k and b_k are the intercept and slope for species k with respect to
70 environmental variable x and ε_{ik} is a noise variable with mean 0 and a species-
71 specific variance. This models the environmentally structured variation in the
72 species-site data. We define the amount of environmentally structured variation by
73 the sum across species of the regression sum of squares, say SS_x . We now relate this
74 variation to the species trait z by a simple regression of the species-specific slopes
75 (b_k) on to the trait z , that is

76
$$b_k = c + dz_k + \delta_k,$$

77 where c and d are the intercept and slope for trait z and δ_k is species specific noise
78 variable with mean 0. By inserting this equation in the previous we obtain one
79 regression model for all $n \times m$ data points

80
$$y_{ik} = a_k + cx_i + dz_k x_i + \varepsilon_{ik}^* \quad (2)$$

81 with $\varepsilon_{ik}^* = \varepsilon_{ik} + \delta_k x_i$, an error term with mean zero. Note that the errors are no
82 longer independent. The trait-environment relation is represented by the
83 coefficient d and the amount of trait-environment variation is expressed as the sum
84 of squares, say SS_{xz} , associated with the term $z_k x_i$. Equation (2) could also be
85 expressed as a linear mixed model, but we do not do so because we estimate
86 parameters by least-squares and perform statistical tests by Monte Carlo
87 permutation.

88 *Fitting the model:* The least-squares estimate, \hat{d} , of the coefficient d can be
89 calculated most easily by subtracting the mean of x and of z from x_i and z_k and by
90 continuing with the centered versions, denoted by the vectors \mathbf{x} and \mathbf{z} . With $\mathbf{Y} =$
91 $[\mathbf{y}_{ik}]$, the matrix with species-site data, we then have (see also Takane et al. 1991,
92 Takane & Hunter 2001)

93 $\hat{d} = (\mathbf{x}^T \mathbf{x})^{-1} \mathbf{x}^T \mathbf{Y} \mathbf{z} (\mathbf{z}^T \mathbf{z})^{-1}$ and $SS_{xz} = \hat{d}^2 \sum_{i,k} (x_i z_k)^2$ (3)

94 These results can be derived by noting that the term $z_k x_i$ is orthogonal to all terms
 95 a_k and x_i , e.g. for the latter

96 $\sum_{i,k} z_k x_i^2 = 0,$

97 so that \hat{d} can be obtained by regressing a response with elements y_{ik} on the single
 98 predictor with elements $x_i z_k$ using all $n \times m$ data points and by re-expressing the
 99 least-squares estimate in terms of the vectors \mathbf{x} and \mathbf{z} and matrix \mathbf{Y} .

100 *Testing statistical significance:* Dray and Legendre (2008) evaluated six
 101 permutation-based significance tests for testing the trait-environment relationship,
 102 but none faithfully controlled the type I error. This means that these tests may
 103 more frequently indicate a trait-environment relationship than the nominal
 104 significance level (e.g. 0.05) in the case no such relationship exists. Ter Braak et al.
 105 (in prep.) showed that their sixth method (the combined method) can be
 106 transformed into a sequential test that does control the type I error. The new test
 107 is carried out as follows.

108 (1) Select a test statistic that is sensitive to the strength of the trait-environment
 109 relationship, for which we use SS_{xz} , and compute its value for the data, yielding F_0 .

110 (2) Randomly permute the values in \mathbf{x} and compute the statistic using the permuted
 111 \mathbf{x} , yielding F_1 . Repeat this operation so as to yield the additional values F_2, \dots, F_K ,
 112 with K the number of permutations. We used $K = 999$.

113 (3) Compute the Monte Carlo significance level, i.e. compute the number of values
 114 F_0, F_1, \dots, F_K that is greater than or equal to F_0 (this number is thus at least 1), and
 115 divide by $K+1$. Denote the result by a_1 .

116 (4) Randomly permute the values in \mathbf{z} and compute the statistic using the permuted
 117 \mathbf{z} , yielding G_1 . Repeat this operation so as to yield the additional values G_2, \dots, G_K ,
 118 with K the number of permutations.

119 (3) Compute the Monte Carlo significance level, i.e. compute the number of values
 120 F_0, G_1, \dots, G_K that is greater than or equal to F_0 (this number is thus at least 1), and
 121 divide by $K+1$. Denote the result by a_2 .

122 (4) The final Monte Carlo significance level, a , is the maximum of the two
 123 significance levels, i.e. $a = \max(a_1, a_2)$.

124 *Trait-environment correlation:* The fourth-corner problem linking two quantitative
 125 variables yields an easy to interpret correlation (Dray & Legendre 2008). For the
 126 LTE method we define the trait-environment correlation (R) as the Pearson
 127 correlation between the species-specific slopes (b_k) and the trait \mathbf{z} . It can be shown
 128 that R^2 is the fraction of the environmentally structured variation that can be
 129 explained by the trait, i.e. $R^2 = SS_{xz}/SS_x$. Note the caveat in the interpretation of R
 130 that R can be high even when the environmentally structured variation is small. For
 131 this reason, the squared correlation is less suited for testing.

132 *Discussion:* One may wonder why we use the simple test statistic SS_{xz} instead of an
 133 F-type statistic which compares the regression mean square to the error mean

134 square as is optimal in permutation tests for testing the significance of one or more
 135 regression terms in the presence of other (so called nuisance) terms (Anderson &
 136 Legendre 1999, Anderson & Robinson 2001, Ter Braak & Šmilauer 2002). The reason
 137 is that the other models than model (2) can be formulated that are equally
 138 appealing but that yield another error mean square. For example, by also
 139 expressing a_k as a linear function of z we obtain a standard model with main
 140 effects for x and z and the interaction between x and z , that is

$$141 \quad y_{ik} = c_0 + c_1 x_i + c_2 z_k + c_3 x_i z_k + \varepsilon_{ik}^{**} . \quad (4)$$

142 One can verify that the least-squares estimates of d in model (2) and of c_3 in model
 143 (4) are equal. The amounts of trait-
 144 environment variation are equal as well. A third model with the same interaction
 145 parameter and the same amount of trait-environment variation is a model with
 146 free parameters for sites (rows) and species (species) and an interaction term
 147 between x and z , that is

$$148 \quad y_{ik} = r_i + c_k + dx_i z_k + \varepsilon_{ik}^{***} . \quad (5)$$

149 This model can simply be expressed as

$$150 \quad \tilde{y}_{ik} = dx_i z_k + \varepsilon_{ik}^{***} . \quad (6)$$

151 with \tilde{y}_{ik} the double centered version of y_{ik} , *i.e.* $\tilde{y}_{ik} = y_{ik} - y_{i+} / m - y_{+k} / n + y_{++} / nm$,
 152 where we use the notation that a '+' replacing an index means the sum over the
 153 index. So, only one term remains, making it unnecessary to use an F -type statistic.
 154 The proposed permutation test is thus based on a model with all variation that is
 155 either environmentally structured or trait-structured but not both removed. Here
 156 'all' means not only variation related to our specific x or to z , but to any
 157 environmental variable or trait.

158 *Comparison of LTE with the fourth-corner method:* The fourth-corner method
 159 (Dray & Legendre 2008) calculates a weighted Pearson correlation between the
 160 trait and the environmental variable by using all species-site combinations as cases,
 161 the measure of abundance as a weight and by assigning to each case the trait and
 162 the environmental value of the combination. This generates a weighted data set of
 163 $n \times m$ cases with two variables. As zero abundance implies zero weight, the
 164 standard fourth-corner method calculates the correlation between trait and
 165 environmental variable for the species-site combinations with positive abundance.
 166 The method thus has particular appeal for presence/absence data for which it was
 167 originally developed (Legendre et al. 1997) and for abundance data with many
 168 zeroes. As weights must be non-negative, the method cannot be used with a
 169 measure of (change in) abundance that can be negative, for example, when an
 170 index value decreases from one year to the next.

171 Whereas the standard fourth-corner method relates to doubly constrained
 172 correspondence analysis and the method of weighted averaging (that is, methods
 173 that have appeal for unimodal relationships in niche studies, Ter Braak & Prentice
 174 1988), the LTE method relates similarly to doubly constrained principal component
 175 analysis and linear regression. This relationship to linear methods may appear a
 176 step in the wrong direction in terms of model complexity. However, because we
 177 apply the method to log-ratios or population growth rates, the method is well
 178 suited to analyze unimodal data, as shown in section 3.9 of Ter Braak and Šmilauer
 179 (2002).

180 *Appendix 5*

181 Correlations between traits; grey shading: relatively high Pearson score. For
 182 abbreviations of traits, see Table 1

183

184 a: marshland species

	lownest	fdpl	fdinvert	fdpisci	fdmeat	altr	resid	pmigr	migr
lownest	-	0.28	-0.32	0.04	0.21	-0.75	-0.13	0.37	-0.23
fdpl	0.28	-	-0.69	-0.17	-0.07	-0.44	-0.03	0.34	-0.28
fdinvert	-0.32	-0.69	-	-0.52	-0.22	0.32	0.10	-0.30	0.19
fdpisci	0.04	-0.17	-0.52	-	-0.06	0.03	-0.06	0.08	-0.01
fdmeat	0.21	-0.07	-0.22	-0.06	-	0.08	-0.10	-0.10	0.18
altr	-0.75	-0.44	0.32	0.03	0.08	-	0.10	-0.60	0.47
resid	-0.13	-0.03	0.10	-0.06	-0.10	0.10	-	-0.41	-0.53
pmigr	0.37	0.34	-0.30	0.08	-0.10	-0.60	-0.41	-	-0.56
migr	-0.23	-0.28	0.19	-0.01	0.18	0.47	-0.53	-0.56	-

185

186

187

b: forest species

	lownest	fdpl	fdinvert	fdmeat	altr	resid	pmigr	migr
lownest	-	0.12	-0.03	-0.08	-0.57	-0.06	-0.15	0.21
fdpl	0.12	-	-0.67	-0.14	-0.33	-0.07	0.23	-0.15
fdinvert	-0.03	-0.67	-	-0.51	0.22	0.07	-0.38	0.30
fdmeat	-0.08	-0.14	-0.51	-	0.04	-0.16	0.39	-0.20
altr	-0.57	-0.33	0.22	0.04	-	-0.15	0.08	0.09
resid	-0.06	-0.07	0.07	-0.16	-0.15	-	-0.55	-0.57
pmigr	-0.15	0.23	-0.38	0.39	0.08	-0.55	-	-0.38
migr	0.21	-0.15	0.30	-0.20	0.09	-0.57	-0.38	-

188

189 Appendix 6

190 Species specific regression coefficients b_k resulting from the LTE analyses. For abbreviations of species names, see Appendix 1; for
 191 abbreviations of weather variables, see Table 2

192 a: marshland species

abbreviation	NB_Jnsen	NB_Jnsen t-1	NB_tempcoldmonth	NB_tempcoldmonth t-1	NB_frostdays	NB_frostdays t-1	NB_rain	NB_rain t-1	NB_snowdays	NB_snowdays t-1	B_temp	B_temp t-1	B_tempaprrmay	B_tempaprrmay t-1	B_rain	B_rain t-1	B_heavyraindays	B_heavyraindays t-1	B_drydays	B_drydays t-1	B_squall	B_squall t-1	B_heatwave	B_heatwave t-1
AARU	0.08	0.06	-0.13	-0.13	0.07	0.05	0.02	-0.08	0.05	0.02	-0.09	0.00	0.00	0.01	0.11	0.10	0.04	-0.08	-0.12	-0.14	0.08	-0.01	-0.03	0.00
ACAU	-0.05	-0.09	0.14	0.08	-0.04	-0.05	-0.10	0.21	-0.06	-0.06	0.00	0.14	0.01	0.03	-0.02	-0.17	0.21	-0.02	0.26	0.08	0.17	0.07	-0.02	0.07
ACLY	0.00	-0.01	-0.01	0.01	0.00	-0.02	-0.10	0.04	0.05	-0.08	-0.09	-0.06	-0.04	0.02	0.17	0.02	-0.06	0.12	-0.37	0.42	-0.03	-0.04	-0.02	0.00
ACRE	-0.01	-0.08	0.05	0.16	-0.05	-0.06	-0.09	0.29	0.11	-0.09	-0.08	0.00	-0.02	0.05	-0.12	0.39	-0.26	0.71	-0.39	0.25	-0.12	0.07	-0.09	-0.04
AFUL	0.01	0.00	-0.03	0.01	0.00	0.01	-0.01	-0.01	0.03	0.01	0.00	-0.05	-0.02	0.01	0.13	-0.03	-0.10	-0.03	-0.18	0.01	0.05	-0.07	0.00	-0.01
APAL	0.07	0.01	-0.09	-0.01	0.06	-0.01	-0.11	0.06	0.05	0.05	-0.06	-0.01	0.00	-0.01	-0.06	-0.02	-0.11	0.07	-0.09	0.17	0.07	0.06	-0.01	0.00
APUR	0.02	0.03	-0.01	-0.01	0.02	0.04	0.00	-0.01	0.01	0.04	0.05	0.02	0.01	-0.02	0.12	0.05	0.22	-0.03	-0.03	0.06	0.09	-0.02	0.00	0.04
ASCH	0.02	0.06	-0.04	-0.09	0.00	0.07	0.07	0.06	0.00	0.06	-0.03	0.03	0.01	-0.01	-0.02	0.04	0.19	-0.08	0.15	-0.06	0.03	0.06	-0.03	0.04
ASCI	0.05	0.01	-0.08	-0.01	0.04	0.01	-0.05	-0.05	0.04	0.06	0.03	-0.03	-0.02	-0.02	-0.03	0.00	-0.01	0.00	-0.04	-0.06	0.05	0.03	0.01	0.00
ASTR	-0.09	-0.12	0.16	0.19	-0.09	-0.07	0.03	0.24	-0.02	-0.10	0.06	0.09	-0.02	0.06	-0.06	-0.11	-0.02	0.15	0.13	0.08	0.07	-0.06	0.04	0.04
BSTE	-0.09	0.04	0.11	-0.06	-0.09	0.04	0.35	-0.02	-0.01	-0.01	0.10	-0.05	0.02	0.01	0.21	0.32	0.23	0.06	-0.12	-0.33	-0.06	0.08	-0.02	-0.02
CAER	0.02	0.01	-0.03	-0.03	0.02	0.00	0.05	-0.05	0.01	0.01	-0.03	-0.02	0.00	0.01	-0.09	0.09	-0.01	-0.11	-0.06	-0.10	0.06	-0.01	0.01	0.00
CCANO	0.05	0.00	-0.06	0.04	0.03	0.01	-0.15	0.04	0.04	0.02	-0.02	0.01	-0.01	-0.01	-0.03	-0.07	-0.08	0.13	0.00	0.16	0.02	0.01	-0.01	0.02
COLO	-0.08	-0.09	0.17	0.09	-0.08	-0.03	0.18	0.14	-0.03	-0.14	0.04	0.10	-0.02	0.07	0.08	-0.16	-0.05	0.10	0.32	-0.08	-0.06	0.09	0.04	0.04
CPAL	0.03	-0.01	-0.02	0.03	0.02	-0.01	-0.06	0.06	0.01	0.03	0.02	0.01	0.00	0.00	-0.19	0.03	0.02	-0.05	0.12	-0.01	0.02	-0.06	0.02	0.00
DMAJ	0.04	-0.04	-0.06	0.08	0.06	-0.05	-0.17	0.03	0.06	0.01	-0.07	0.03	0.01	-0.01	-0.07	0.06	-0.08	-0.02	-0.27	0.24	0.06	0.00	-0.02	0.01
ERUB	-0.09	-0.02	0.07	0.04	-0.07	-0.03	-0.04	-0.08	-0.09	0.03	0.10	0.05	0.00	-0.02	-0.35	0.15	0.10	-0.08	0.08	-0.24	-0.04	-0.01	-0.01	0.00

ESCH	0.03	-0.01	-0.01	0.02	0.03	0.00	-0.01	-0.01	0.04	-0.01	0.00	0.02	-0.01	0.01	0.02	0.10	-0.05	0.05	-0.10	0.07	0.03	0.02	0.01	0.01
FATR	0.04	-0.02	-0.04	0.03	0.05	-0.01	-0.01	-0.07	0.05	0.00	0.03	-0.03	-0.02	0.00	0.01	-0.04	0.01	0.01	-0.02	-0.02	-0.01	-0.02	0.02	-0.01
GCHL	-0.13	-0.04	0.18	0.05	-0.10	-0.04	0.22	0.16	-0.06	-0.05	0.07	0.09	0.04	0.02	0.13	0.11	0.22	0.04	-0.03	-0.01	0.08	-0.01	0.01	0.03
GGLA	0.08	0.00	-0.07	-0.05	0.03	0.05	-0.17	0.13	0.03	-0.03	-0.14	0.03	-0.02	0.02	0.21	-0.33	-0.03	0.00	0.19	0.03	-0.01	-0.12	-0.06	0.03
LLUS	-0.03	0.03	0.03	-0.05	-0.02	0.01	0.20	0.01	-0.02	0.00	0.03	0.01	0.03	0.00	0.05	0.16	0.10	0.02	-0.05	-0.10	0.00	0.03	0.02	-0.01
LMEG	-0.07	-0.07	0.02	0.18	-0.06	-0.08	-0.34	0.06	-0.01	0.00	-0.03	0.04	-0.06	0.02	-0.76	0.21	-0.24	-0.05	-0.15	0.25	0.01	-0.03	-0.04	0.02
LNAE	0.03	0.01	-0.01	-0.01	0.02	0.01	-0.16	0.08	-0.04	-0.01	-0.07	0.07	0.02	-0.01	-0.11	-0.14	-0.09	-0.10	0.23	0.31	-0.01	-0.13	0.02	0.05
LSVE	0.09	0.02	-0.13	-0.04	0.08	0.03	-0.07	-0.09	0.05	0.05	-0.05	-0.03	-0.01	-0.01	-0.10	-0.05	-0.08	-0.11	0.07	-0.08	-0.07	-0.01	0.00	-0.01
PCAE	0.03	0.00	-0.01	-0.02	0.01	-0.01	-0.15	0.18	-0.02	0.07	-0.01	0.01	0.03	-0.02	-0.05	0.02	0.08	0.03	-0.01	0.07	0.17	-0.12	-0.02	0.00
PCAR	0.02	0.01	-0.06	-0.02	0.02	0.00	-0.16	0.01	0.01	0.05	-0.05	0.00	0.00	-0.04	-0.28	-0.05	0.05	0.00	0.14	0.01	-0.16	0.02	-0.04	0.02
PCOLL	0.05	0.07	-0.06	-0.06	0.05	0.04	-0.13	-0.21	-0.07	0.07	0.05	-0.01	0.00	-0.05	-0.06	-0.32	0.06	-0.19	0.51	0.00	-0.10	0.14	0.01	-0.02
PLEU	-0.07	0.13	0.00	-0.12	-0.02	0.07	0.76	-0.63	0.01	0.00	0.17	-0.16	-0.01	0.01	0.45	-0.11	-0.13	-0.35	-0.10	-0.48	-0.30	0.51	0.10	-0.06
PMAJ	0.08	0.01	-0.09	-0.02	0.07	0.00	-0.27	0.03	0.01	0.04	-0.05	0.03	0.00	-0.03	-0.06	-0.10	-0.05	0.04	0.05	0.12	0.03	-0.05	-0.01	0.02
PMOD	-0.04	0.01	0.05	-0.01	-0.02	-0.01	-0.05	0.01	-0.09	0.03	0.05	0.08	0.05	-0.03	-0.10	0.04	0.02	-0.04	0.16	-0.04	0.04	-0.04	0.01	0.01
PMON	0.00	0.00	-0.06	-0.01	-0.01	0.01	-0.17	0.05	0.00	0.01	-0.07	0.03	-0.01	-0.01	-0.15	0.01	0.17	-0.08	-0.07	-0.11	0.00	-0.01	-0.05	0.05
POCRI	0.01	-0.04	-0.01	0.03	0.00	-0.03	0.02	0.15	0.06	-0.02	-0.07	-0.05	-0.01	0.03	0.09	-0.01	-0.10	-0.08	-0.26	-0.02	0.11	-0.13	0.01	0.01
PTRO	0.06	0.01	-0.08	0.00	0.05	0.01	-0.07	-0.05	0.03	-0.01	-0.04	-0.01	-0.01	0.00	-0.03	-0.03	-0.15	0.00	-0.01	0.10	-0.05	-0.04	0.02	-0.01
RAQU	-0.05	0.03	0.05	-0.05	-0.03	0.04	0.32	-0.12	-0.01	-0.05	0.06	-0.05	0.02	0.02	0.22	0.35	0.12	-0.01	-0.20	-0.34	-0.06	-0.06	0.02	-0.06
RPEN	0.17	-0.05	-0.30	-0.08	0.12	-0.05	-0.56	-0.26	0.09	-0.05	-0.31	-0.32	-0.14	-0.03	0.10	-1.00	-0.48	0.06	-0.07	0.29	-0.26	-0.26	-0.06	-0.13
SATR	-0.01	0.02	0.04	-0.02	0.00	0.00	0.03	-0.04	-0.01	-0.02	-0.01	0.01	0.03	-0.02	0.12	-0.05	-0.06	0.03	0.06	0.11	-0.07	0.03	0.00	0.01
SBOR	0.10	0.01	-0.11	0.00	0.09	0.01	-0.15	-0.04	0.07	0.01	-0.06	-0.01	-0.03	0.00	0.09	-0.18	-0.12	-0.02	-0.04	0.23	0.04	0.01	0.01	0.02
SCOM	0.08	0.04	-0.16	-0.03	0.06	0.03	-0.27	-0.06	0.01	0.09	-0.06	-0.04	-0.01	-0.03	-0.03	-0.21	-0.23	-0.08	-0.06	0.08	0.05	-0.10	-0.02	-0.02
STUR	-0.03	0.02	0.03	0.05	-0.01	-0.01	-0.23	-0.11	-0.09	0.05	0.07	-0.05	0.00	-0.04	-0.03	-0.24	-0.01	-0.37	0.06	0.20	0.15	-0.14	0.03	0.00
TMER	-0.01	0.03	0.03	-0.06	0.01	0.01	0.07	-0.02	-0.06	0.02	0.03	0.03	0.04	-0.01	-0.13	0.26	0.10	-0.03	0.06	-0.13	0.04	0.00	0.02	-0.02
TRUF	-0.23	-0.04	0.43	0.08	-0.19	-0.03	0.93	0.20	-0.09	-0.10	0.34	0.05	0.11	0.05	0.29	0.59	0.35	0.49	0.20	-0.38	0.04	0.24	0.12	-0.06
TTRO	-0.18	0.08	0.21	-0.16	-0.14	0.04	0.62	-0.21	-0.13	0.00	0.20	-0.01	0.09	-0.03	0.29	0.34	0.30	-0.09	0.07	-0.64	-0.14	0.10	0.03	-0.05

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194 b: forest species

abbreviation	NB_Unsen	NB_Unsen t-1	NB_tempcoldmonth	NB_tempcoldmonth t-1	NB_frostdays	NB_frostdays t-1	NB_rain	NB_rain t-1	NB_snowdays	NB_snowdays t-1	B_temp	B_temp t-1	B_tempaprrmay	B_tempaprrmay t-1	B_rain	B_rain t-1	B_heavyraindays	B_heavyraindays t-1	B_drydays	B_drydays t-1	B_squall	B_squall t-1	B_heatwave	B_heatwave t-1
ACAU	0.01	0.00	-0.01	0.03	-0.01	0.00	-0.05	0.07	0.00	0.05	0.03	-0.03	0.00	0.00	-0.04	-0.05	0.01	-0.10	0.07	-0.11	0.10	-0.04	0.01	-0.02
AGEN	0.04	-0.06	-0.13	0.07	0.04	-0.06	-0.19	0.06	0.09	0.01	-0.11	-0.06	-0.04	-0.01	-0.16	-0.12	-0.16	0.05	-0.26	0.12	-0.10	-0.10	0.04	-0.01
ANIS	-0.07	-0.07	0.10	0.02	-0.06	-0.06	-0.02	0.09	-0.06	-0.04	0.01	-0.04	0.00	-0.01	-0.17	-0.17	-0.07	-0.04	0.28	-0.14	-0.10	-0.08	-0.07	-0.03
AOTU	-0.10	-0.08	0.15	0.09	-0.09	-0.07	-0.09	0.37	-0.01	-0.01	0.02	0.10	0.02	0.01	-0.58	0.58	-0.02	0.29	-0.06	-0.02	0.02	-0.07	-0.10	0.03
BBUT	0.02	-0.04	-0.05	0.03	0.02	-0.02	-0.05	0.09	0.07	0.01	-0.04	-0.06	-0.02	-0.01	-0.02	-0.02	-0.07	0.05	-0.13	-0.03	-0.01	-0.04	0.02	-0.01
CBRA	0.01	-0.03	0.01	0.04	0.01	-0.02	0.00	0.00	0.00	0.01	0.04	-0.01	-0.01	0.01	0.00	-0.05	-0.11	0.00	-0.01	-0.05	0.07	-0.01	0.01	-0.02
CCANN	-0.01	0.01	0.01	0.02	0.01	0.00	0.08	-0.08	-0.04	-0.02	0.04	0.09	0.02	0.02	0.00	-0.04	-0.02	-0.11	0.09	0.11	0.00	0.03	-0.01	0.01
CCANO	0.02	0.01	-0.02	0.00	0.04	0.00	0.07	-0.11	0.03	0.02	0.05	-0.02	0.00	-0.01	0.21	-0.02	-0.07	0.06	-0.10	0.07	0.04	0.14	0.02	-0.02
CCHL	-0.04	0.01	0.07	-0.01	-0.02	0.01	0.18	0.00	-0.02	-0.02	0.05	0.05	0.03	0.01	0.02	0.12	0.12	-0.14	0.18	-0.07	-0.07	0.03	-0.04	0.01
CCOR	0.04	-0.02	-0.07	0.05	0.01	-0.02	-0.04	-0.02	0.05	0.00	-0.03	-0.05	-0.04	0.01	0.06	-0.26	-0.14	0.11	-0.09	0.13	-0.01	0.00	0.04	-0.01
CMON	0.00	0.01	-0.02	-0.03	0.02	0.01	0.13	-0.10	0.04	-0.05	-0.02	-0.02	-0.02	0.01	0.19	-0.01	0.06	0.03	-0.10	0.04	-0.10	0.07	0.00	0.00
COEN	0.02	0.02	-0.02	0.00	0.01	0.03	-0.10	-0.03	-0.03	-0.01	-0.01	0.01	-0.01	-0.01	-0.06	-0.12	0.10	-0.08	0.22	0.07	-0.05	-0.03	0.02	0.02
CPAL	0.01	-0.02	0.00	0.04	0.00	-0.01	-0.04	0.05	0.03	-0.01	-0.01	0.01	-0.02	0.01	-0.03	0.00	0.00	0.04	-0.02	0.09	0.02	-0.01	0.01	0.02
DMAJ	0.02	0.01	-0.02	-0.02	0.02	0.01	0.06	-0.04	0.02	0.00	0.00	0.00	0.00	0.01	0.04	0.02	-0.03	0.04	-0.01	-0.04	0.00	0.06	0.02	0.00
DMIN	0.00	-0.03	0.03	0.04	0.03	-0.04	-0.08	0.02	-0.01	-0.05	-0.02	0.06	0.01	0.00	0.08	-0.07	-0.01	0.05	0.04	0.28	0.02	0.14	0.00	0.02
ECIT	0.03	0.05	-0.07	-0.10	0.05	0.02	-0.08	-0.22	-0.06	0.08	0.01	-0.06	0.02	-0.06	0.09	-0.10	-0.03	-0.15	-0.08	-0.08	0.05	-0.08	0.03	-0.07
ERUB	-0.09	0.00	0.10	-0.02	-0.07	-0.01	0.23	0.02	-0.01	-0.01	0.05	0.02	0.03	0.00	-0.03	0.30	0.14	0.06	-0.13	-0.18	-0.01	0.05	-0.09	0.00
FCOE	0.01	-0.03	-0.01	0.03	0.01	-0.02	-0.05	0.06	0.02	0.00	0.00	0.02	-0.02	0.01	-0.07	-0.03	0.03	0.01	0.00	-0.02	0.05	-0.01	0.01	0.02
FHYP	0.03	0.01	0.02	0.05	0.01	0.03	-0.02	-0.07	-0.03	-0.02	0.11	0.01	-0.03	0.01	0.12	-0.26	0.12	0.07	0.35	0.12	0.02	0.14	0.03	0.02
FSUB	0.14	0.04	-0.18	-0.20	0.15	0.06	-0.20	-0.31	0.06	0.03	-0.18	-0.23	-0.04	-0.06	0.25	-0.23	0.26	-0.41	-0.24	-0.17	0.07	-0.17	0.14	-0.04
FTIN	-0.09	-0.17	0.12	0.17	-0.06	-0.14	-0.25	0.45	-0.02	-0.08	-0.09	0.08	-0.01	0.06	-0.37	0.13	-0.25	-0.17	-0.19	0.03	0.20	-0.21	-0.09	0.03
GGLA	0.06	-0.03	-0.06	0.05	0.04	-0.01	-0.13	0.00	0.04	-0.01	-0.02	0.01	-0.04	0.02	-0.12	-0.08	-0.17	0.10	0.02	0.02	0.00	0.00	0.06	0.00
HICT	-0.07	0.04	0.10	-0.01	-0.07	0.04	0.06	0.08	-0.04	-0.03	0.02	0.15	0.04	0.00	0.31	-0.08	0.26	-0.27	0.14	0.22	0.01	-0.08	-0.07	0.11
LMEG	-0.01	0.07	-0.05	-0.09	0.00	0.06	0.16	-0.10	0.02	-0.03	-0.05	0.00	0.00	0.03	0.12	0.18	-0.09	-0.16	-0.20	-0.15	-0.06	0.04	-0.01	0.01

MSTR	-0.02	0.05	0.04	-0.01	-0.03	0.05	0.14	-0.13	-0.02	-0.01	0.08	-0.02	0.00	0.01	0.14	0.00	0.08	-0.06	0.10	-0.04	0.00	0.08	-0.02	0.00
OORI	0.05	0.05	-0.08	-0.09	0.05	0.05	0.01	-0.17	-0.01	0.02	-0.04	0.06	0.01	-0.01	0.35	-0.18	-0.10	0.02	-0.04	-0.05	0.03	0.10	0.05	0.00
PACRI	0.09	-0.02	-0.11	0.04	0.06	-0.02	-0.23	0.02	0.07	0.02	-0.08	-0.06	-0.03	-0.01	-0.06	-0.13	-0.10	0.17	-0.15	0.25	0.01	-0.08	0.09	-0.02
PATE	0.01	-0.05	0.00	0.11	0.00	-0.06	-0.14	0.04	0.00	0.00	0.00	0.05	0.00	0.00	-0.14	-0.16	-0.15	0.24	0.02	0.21	0.01	0.03	0.01	0.00
PCAE	0.05	-0.03	-0.03	0.03	0.04	-0.01	-0.15	0.08	0.04	-0.02	-0.07	0.04	-0.02	0.02	-0.09	0.02	-0.03	0.01	-0.02	0.11	0.04	-0.06	0.05	0.03
PCOLC	0.05	-0.01	-0.08	0.02	0.05	-0.01	-0.14	-0.03	0.05	0.00	-0.06	0.01	-0.03	0.01	-0.04	-0.01	-0.13	-0.05	-0.19	0.13	0.04	-0.08	0.05	0.01
PCOLL	0.00	0.09	0.00	-0.10	0.00	0.05	0.03	-0.21	-0.09	0.07	0.07	-0.07	0.00	-0.05	0.06	-0.23	0.17	-0.23	0.40	-0.05	-0.08	0.12	0.00	-0.05
PMAJ	0.05	-0.03	-0.04	0.02	0.06	-0.01	-0.17	0.03	0.02	0.00	-0.04	0.06	-0.01	0.01	-0.15	0.03	-0.01	-0.02	0.02	0.08	0.06	-0.01	0.05	0.03
PMOD	-0.02	0.00	0.03	0.01	-0.02	0.01	0.06	0.01	0.00	0.00	0.05	0.01	-0.01	0.01	-0.03	0.09	0.07	-0.07	0.04	-0.17	0.02	0.05	-0.02	0.01
PMON	0.06	-0.02	-0.08	0.04	0.06	-0.01	-0.19	-0.05	0.04	-0.01	-0.06	-0.03	-0.03	0.01	-0.11	-0.07	-0.22	-0.02	-0.10	0.13	0.02	-0.08	0.06	-0.01
PPAL	0.04	-0.06	-0.02	0.08	0.04	-0.04	-0.16	0.05	0.03	-0.03	-0.04	0.06	-0.01	0.00	-0.12	-0.11	-0.08	0.00	0.08	0.13	-0.01	0.00	0.04	0.03
PPHO	0.03	0.01	-0.06	-0.02	0.03	0.02	-0.10	-0.06	-0.02	-0.01	-0.05	0.03	0.00	0.01	0.00	-0.04	-0.10	-0.04	-0.07	-0.01	0.03	-0.02	0.03	0.00
PPIC	0.01	0.01	-0.03	-0.01	-0.02	0.01	-0.06	0.02	0.01	-0.01	-0.07	-0.02	-0.01	0.00	-0.07	-0.09	-0.10	0.07	-0.07	0.12	-0.09	-0.18	0.01	0.03
PPYR	0.03	-0.05	-0.03	0.10	0.02	-0.05	-0.17	0.13	0.04	-0.03	-0.05	-0.02	-0.02	0.02	0.00	-0.13	-0.23	0.08	-0.09	0.31	0.01	-0.05	0.03	-0.01
PSIB	0.00	0.08	-0.09	-0.14	-0.01	0.00	0.11	0.06	0.06	0.12	-0.10	-0.08	0.07	-0.07	-0.02	0.30	-0.21	0.28	-0.26	-0.09	-0.26	0.08	0.00	-0.08
PTRO	0.04	0.03	-0.05	-0.01	0.02	0.03	-0.02	-0.03	0.01	0.00	-0.01	-0.02	-0.02	0.01	-0.02	-0.02	-0.04	0.06	0.04	0.11	-0.03	-0.05	0.04	0.00
PVIR	-0.04	-0.03	0.02	0.04	-0.03	-0.03	0.09	0.01	0.02	0.00	0.03	0.00	-0.01	0.02	0.03	-0.04	-0.11	-0.04	-0.13	-0.11	0.04	-0.02	-0.04	0.01
RIGN	-0.18	0.10	0.28	-0.10	-0.15	0.05	0.49	0.04	-0.23	0.04	0.23	0.07	0.12	-0.05	-0.06	0.27	0.52	0.02	0.59	-0.19	0.02	0.15	-0.18	-0.01
RREG	-0.13	0.01	0.23	0.03	-0.16	-0.01	0.30	0.37	-0.12	-0.01	0.15	0.04	0.09	-0.01	-0.02	0.26	0.31	0.52	0.36	-0.13	-0.06	0.04	-0.13	-0.03
SATR	-0.02	0.05	0.02	-0.05	-0.02	0.03	0.12	-0.11	-0.02	0.03	0.06	-0.06	0.00	-0.01	0.15	-0.01	0.08	-0.10	0.00	-0.06	0.04	0.00	-0.02	-0.02
SBOR	0.06	0.02	-0.05	-0.03	0.05	0.03	-0.08	-0.05	0.03	0.01	-0.01	-0.01	-0.03	0.00	0.03	-0.06	0.01	-0.08	0.07	0.13	0.03	-0.01	0.06	0.01
SCOM	0.07	0.06	-0.13	-0.04	0.03	0.05	-0.22	0.08	0.01	0.08	-0.09	0.02	0.00	-0.01	-0.20	0.02	-0.06	0.03	-0.02	0.06	0.04	-0.12	0.07	0.02
SEUR	0.06	-0.07	-0.06	0.05	0.07	-0.04	-0.05	-0.01	0.06	-0.02	-0.04	0.05	-0.02	0.03	-0.13	0.05	-0.19	0.01	-0.12	-0.15	0.04	0.04	0.06	0.01
STUR	0.00	0.06	-0.02	-0.07	0.00	0.05	0.03	-0.19	0.02	0.01	0.05	-0.08	-0.02	-0.03	0.20	0.00	0.03	0.04	-0.04	-0.06	-0.10	0.14	0.00	0.00
SVUL	0.03	0.03	-0.06	-0.01	0.03	0.03	-0.03	-0.06	0.05	0.00	-0.02	-0.01	-0.02	0.00	0.04	0.10	-0.05	0.02	-0.17	0.08	0.01	0.01	0.03	0.03
TMER	-0.03	0.00	0.03	-0.01	-0.02	0.00	0.07	0.03	0.00	-0.01	0.01	-0.01	0.00	0.01	0.00	0.10	0.09	-0.02	-0.06	-0.10	0.01	0.02	-0.03	0.00
TPHI	-0.09	-0.02	0.15	0.02	-0.07	-0.01	0.20	0.11	-0.05	-0.05	0.06	0.05	0.03	0.02	0.09	0.21	0.20	0.02	-0.03	-0.11	0.08	0.03	-0.09	0.01
TTRO	-0.18	0.05	0.20	-0.10	-0.14	0.03	0.55	-0.11	-0.09	-0.03	0.15	-0.02	0.06	0.00	0.23	0.32	0.40	-0.13	-0.05	-0.51	-0.07	0.05	-0.18	-0.03
TVIS	-0.02	0.01	0.03	-0.04	-0.01	0.01	0.14	-0.14	-0.02	0.01	0.06	-0.03	0.00	-0.01	0.07	-0.09	0.08	-0.09	0.15	-0.20	-0.03	0.04	-0.02	-0.02

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