



Historical climate-change influences modularity and nestedness of pollination networks

Bo Dalsgaard, Kristian Trøjelsgaard, Ana M. Martín González, David Nogués-Bravo, Jeff Ollerton, Theodora Petanidou, Brody Sandel, Matthias Schleuning, Zhiheng Wang, Carsten Rahbek, William J. Sutherland, Jens-Christian Svenning and Jens M. Olesen

B. Dalsgaard (bo.dalsgaard@bio.ku.dk), D. Nogués-Bravo, Z. Wang, and C. Rahbek, Center for Macroecology, Evolution and Climate, Univ. of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. – K. Trøjelsgaard, B. Sandel, J.-C. Svenning and J. M. Olesen, Dept of Bioscience, Aarhus Univ., Ny Munkegade 114, DK-8000 Aarhus C, Denmark. – A. M. Martín González, Pacific Ecoinformatics and Computational Ecology Lab, Berkeley, CA 94703, USA and Center for Macroecology, Evolution and Climate, Univ. of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark. – J. Ollerton, Landscape and Biodiversity Research Group, School of Science and Technology, Univ. of Northampton, Northampton, NN2 6JD, UK. – T. Petanidou, Lab. of Biogeography and Ecology, Dept of Geography, Univ. of the Aegean, University Hill, GR-81100 Mytilene, Greece. – M. Schleuning, Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, 60325 Frankfurt (Main), Germany. – W. J. Sutherland, Conservation Science Group, Dept of Zoology, Univ. of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK.

The structure of species interaction networks is important for species coexistence, community stability and exposure of species to extinctions. Two widespread structures in ecological networks are modularity, i.e. weakly connected subgroups of species that are internally highly interlinked, and nestedness, i.e. specialist species that interact with a subset of those species with which generalist species also interact. Modularity and nestedness are often interpreted as evolutionary ecological structures that may have relevance for community persistence and resilience against perturbations, such as climate-change. Therefore, historical climatic fluctuations could influence modularity and nestedness, but this possibility remains untested. This lack of research is in sharp contrast to the considerable efforts to disentangle the role of historical climate-change and contemporary climate on species distributions, richness and community composition patterns. Here, we use a global database of pollination networks to show that historical climate-change is at least as important as contemporary climate in shaping modularity and nestedness of pollination networks. Specifically, on the mainland we found a relatively strong negative association between Quaternary climate-change and modularity, whereas nestedness was most prominent in areas having experienced high Quaternary climate-change. On islands, Quaternary climate-change had weak effects on modularity and no effects on nestedness. Hence, for both modularity and nestedness, historical climate-change has left imprints on the network structure of mainland communities, but had comparably little effect on island communities. Our findings highlight a need to integrate historical climate fluctuations into eco-evolutionary hypotheses of network structures, such as modularity and nestedness, and then test these against empirical data. We propose that historical climate-change may have left imprints in the structural organisation of species interactions in an array of systems important for maintaining biological diversity.

There is no universal consensus on the causes of biogeographical variation in species richness (Rahbek et al. 2007, Nogués-Bravo et al. 2008, Sutherland et al. 2013). One issue of current debate is the extent to which historical climate-change offers a complementary explanation to contemporary climate in explaining contemporary patterns of species richness and community composition (Fjeldså et al. 1999, Dynesius and Jansson 2000, Jetz et al. 2004, Rahbek et al. 2007, Svenning and Skov 2007, Araújo et al. 2008, Hortal et al. 2011, Sandel et al. 2011). Species, however, are not only affected by environmental conditions, they

also evolve entangled in networks of interactions with other species (Bascompte and Jordano 2007, Olesen et al. 2007). Therefore, understanding how structures of species interaction networks are shaped and persist under fluctuating climates is crucial for predicting the consequences of environmental perturbations on ecological communities (Ings et al. 2009).

Modularity and nestedness are two network structures that may be important for community stability and biodiversity maintenance. Modularity describes whether a network is partitioned into weakly linked subgroups of species that are internally highly interlinked (Newman 2004, Olesen et al. 2007, Thébault and Fontaine 2010, Tylianakis et al. 2010, Stouffer and Bascompte 2011). Nestedness describes

The review and decision to publish this paper has been taken by the above noted SE. The decision by the handling SE was shared by a second SE.

a structure where specialist species interact with a subset of those species with which generalist species also interact (Bascompte and Jordano 2007, Fortuna et al. 2010, Thébault and Fontaine 2010, Tylianakis et al. 2010). Both structures are hypothesized to be a consequence of the evolutionary and ecological processes that shape the interaction patterns among species (Bascompte and Jordano 2007, Olesen et al. 2007, Krasnov et al. 2012, Martín González et al. 2012). Modularity and nestedness are widespread structural features in ecological systems; for instance, modular and nested structures are found in bacteria–phage networks, food-webs, and antagonistic and mutualistic networks (Olesen et al. 2007, Fortuna et al. 2010, Tylianakis et al. 2010, Flores et al. 2011, Stouffer and Bascompte 2011, Krasnov et al. 2012, Martín González et al. 2012, Trøjelsgaard and Olesen 2013). Among mutualistic systems, pollination networks are particularly well studied and we now know that pollination networks often are modular and nested; specifically, modularity tends to prevail towards the tropics and in areas of high contemporary precipitation, whereas nestedness is especially pronounced in drier habitats (Olesen et al. 2007, Dupont et al. 2009, Fortuna et al. 2010, Trøjelsgaard and Olesen 2013). Despite its potential importance, and in contrast to research into the causes of species richness and biotic specialization (Dynesius and Jansson 2000, Jetz et al. 2004, Rahbek et al. 2007, Svenning and Skov 2007, Araújo et al. 2008, Dalsgaard et al. 2011, Hortal et al. 2011, Sandel et al. 2011, Schleuning et al. 2012), it is unknown whether historical climate-change affects modularity and nestedness of pollination networks.

Why may historical climate-change offer an alternative, or complementary, hypothesis to contemporary climate in predicting the level of modularity and nestedness? Species may respond differently to climate-change, which, at a given locality, might disrupt species interactions through changed phenology and geographical distributions of species (Memmott et al. 2007, Tylianakis et al. 2008, Devoto et al. 2009, Martín González et al. 2009, Amano et al. 2010, Gilman et al. 2010, Lorenzen et al. 2011). Although these changes may occur over many different timescales – ranging from short-term intra-annually variation to deep historical timescales – the strongest and most important climatic shifts in the Quaternary (last 2.6 million yr) are the repeated oscillations between glacial cold maxima and warm interglacials. The most recent is that between Last Glacial Maximum (LGM; 21 000 yr ago) and the present, one of the strongest oscillations but with similar spatial pattern to the preceding oscillations (Ruddiman 2001, Jansson 2003). This recent glacial-interglacial shift has, for instance, been shown to affect range-size dynamics and associated biogeographical patterns of species endemism for an array of taxa (Jansson 2003, Araújo et al. 2008, Hortal et al. 2011, Sandel et al. 2011). Arguably, species assemblages in areas having experienced vast historical climate fluctuations may therefore be expected to have experienced a large turnover in species composition, phenological shifts and species interactions. Thus, in areas climatically unstable since the LGM, species assemblages often consist of widespread species that may have co-occurred for a shorter time. In accordance with this, strong Quaternary climate-change has been shown to decrease specificity in plant–hummingbird networks

(Dalsgaard et al. 2011, although see Schleuning et al. 2012 for pollination networks), but the consequences for modularity and nestedness are unknown. As the modular structure of pollination networks may partly reflect aggregates of co-evolutionary units of plant and animal species specializing upon each other (Olesen et al. 2007, Martín González et al. 2012), we propose that modularity may diminish in assemblages having experienced considerable Quaternary climate-change. Specifically, we hypothesize that modularity either decreases linearly with increasing historical climate-change or only decreases at high historical climate-change values as a certain threshold might be needed before an effect is detectable in modularity level. In contrast, we anticipate that nestedness shows opposite geographical patterns to modularity (Trøjelsgaard and Olesen 2013), especially with respect to historical climate-change, as the consequence of modularity and nestedness on community stability are inversely related (Thébault and Fontaine 2010). Accordingly, we anticipate that nestedness may increase when the rate of Quaternary climate-change increases. As Quaternary climate-change has small effects on island assemblages compared to the stronger effects observed on mainland (Kissling et al. 2012) and because pollination network characteristics differ between mainland and island systems (Olesen and Jordano 2002), we hypothesize that Quaternary climate-change effects on modularity and nestedness may be pronounced in mainland networks but less so, or even non-existing, in island networks.

Our objective with this paper is to highlight the value of historical climate-change as a potentially important determinant of ecological network complexity, such as modularity and nestedness. Specifically, we link macroecology and network analysis to determine whether historical climate fluctuations may diminish the modularity and increase the nestedness of species interaction networks using a global database of pollination networks and simulations of past climatic conditions for the last 21 000 yr. We test this both for the global dataset while accounting for insularity, and separately for mainland and island networks. In all cases, we also accounted for variation in contemporary climate and species richness. We found a relatively strong negative association between Quaternary climate-change and modularity on the mainland, whereas Quaternary climate-change had less effect on modularity on islands. Nestedness was on the mainland most pronounced in areas having experienced high Quaternary climate-change, while on islands Quaternary climate-change had no effects on nestedness. We place our results in an evolutionary-ecological history context and discuss the implications to the stability and persistence of pollination networks. Finally, we discuss potential future directions for how such an interdisciplinary research approach can provide new insights into the understanding of historical legacies in network structures in an array of ecological systems important to the maintenance of biodiversity.

Methods

The proposed approach for linking macroecology and species interaction network analysis requires four steps: 1) construction of species interaction networks, 2) calculation of metrics describing network structure, in this instance level

of modularity and nestedness, 3) estimation of historical climate-change and contemporary climate variables for each study locality, and 4) use of conventional regression analysis and – if significant spatial autocorrelation remains in regression residuals – spatial regression analysis to examine the relationship between network structure and climate estimates. We applied this approach using the global database of flower visitation (hereafter ‘pollination’) networks as published in Olesen et al. (2007) and Trøjelsgaard and Olesen (2013). This database consists of 54 pollination networks each sampled within a given locality. The networks include all observed flower visitation events irrespectively of taxonomy, i.e. they are all community-wide pollination networks. Twenty-three networks have a mainland origin and thirty-one networks are from insular environments (Fig. 1). We classified Australia as an island in accordance with previous analysis examining effects of historical climate-change on contemporary patterns of community composition (Jansson 2003).

Species interaction networks

In pollination networks, a plant and a pollinator species are linked if flower visitation is observed. The resulting pollination network illustrates the interaction pattern of an entire assemblage of plants and their animal pollinators. This network may be analysed as a matrix of size $P \times A$, where P is number of plant species and A is number of animal species. For binary networks as used in this study, this matrix consists of $P \times A$ elements of 1 if an animal species and a plant species interact, and 0 if they do not interact.

Modularity and nestedness analysis

The level of modularity M of each pollination network was calculated using an algorithm based on simulated annealing as implemented in the software developed by Guimerà and Amaral (2005a, b), often termed the SA method (Olesen

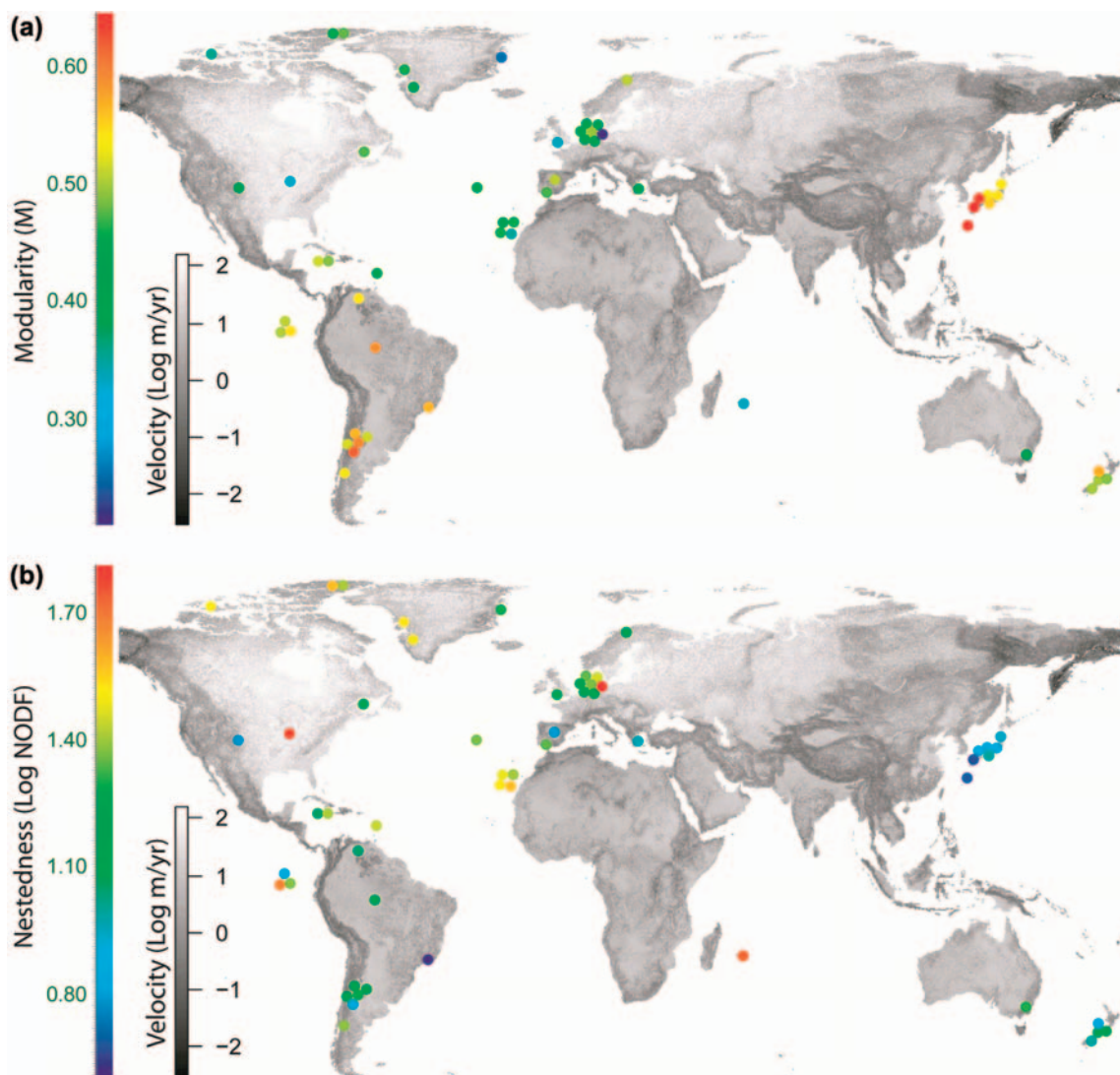


Figure 1. Global geographical patterns of (a) modularity and (b) nestedness in pollination networks and temperature-change velocity since the Last Glacial Maximum (21 kyr). The colours of filled circles illustrate the level of modularity and nestedness for each network (colour scale at the left). The grey-shading of the background illustrates temperature-change velocity; dark shading depicts climatically stable areas compared to light shaded high velocity areas (grey-shaded scale at the left). Note that the level of modularity overall is lowest in the climatically unstable North America and low-laying part of northern Europe as well as on islands (apart from the highly species-rich Japanese networks), whereas nestedness tends to show the opposite geographical pattern to modularity.

et al. 2007). This algorithm was designed for unipartite networks, and it identifies modules consisting of nodes (i.e. species) having most of their links within their own module and few links to species in other modules (Newman 2004, Olesen et al. 2007, Thébaud 2013). The level of modularity M ranges from 0 to 1; higher values indicate more distinct modules (for further explanation, see Guimerà and Amaral 2005a, b and Olesen et al. 2007). The level of nestedness NODF (nestedness based on overlap and decreasing fill) of each network was calculated using the software ANINHADO ver. 3.0.3 (Almeida-Neto et al. 2008). NODF ranges from 0 to 100; values increase with level of nestedness. All modularity and nestedness values included in our analysis originate from Olesen et al. (2007) and Trøjelsgaard and Olesen (2013). In all analyses, modularity M was untransformed and nestedness NODF was Log_{10} -transformed. Modularity M and nestedness NODF were inversely correlated ($R^2 = 0.44$, Dutilleul's $p < 0.05$).

Quaternary climate-change and contemporary climate

We tested the relationship between modularity/nestedness and two summaries of historical climate-change predictors: 1) velocity of mean annual temperature and mean annual precipitation between the LGM and the present; and 2) the maximum velocity of mean annual temperature and mean annual precipitation of 1000 yr time intervals from LGM to the present, i.e. maximum velocity of 21 time intervals. For the estimates of velocity between the LGM and the present, mean annual temperature and mean annual precipitation estimates at the LGM were obtained from the CCSM3 model, which we statistically down-scaled to a 2.5 arc-minute resolution (Collins et al. 2006, Otto-Bliesner et al. 2006). Then, for each study locality and at a 30 arc-second grid cell resolution, a temporal climate gradient was calculated as the average annual rate of change in mean annual temperature or mean annual precipitation since the LGM, and a measure of the spatial gradient was calculated as the slope of the current mean annual temperature or mean annual precipitation surface at all cells as obtained from the WorldClim 30 arc-second climate products (Hijmans et al. 2005). Dividing the temporal gradient by the spatial gradient gives the climate-change velocity since the LGM (Fig. 1). To calculate the maximum velocity of 1000 yr time intervals, 22 data layers of paleo-climate with a spatial resolution of $1^\circ \times 1^\circ$ were obtained from the Hadley Centre model, representing the projected paleo-climate at 1000 yr time intervals since 21 000 yr ago. The temperature and precipitation velocity of a grid cell was then calculated between every two time points (i.e. 21, 20, 19, ..., 0 kya) by dividing the temporal gradients of climate by the spatial gradients, and the maximum values of velocity were identified for each cell. Finally, as contemporary climatic predictors, we included mean annual temperature (MAT) and precipitation (MAP) estimates as extracted for each study locality by Trøjelsgaard and Olesen (2013). For all analyses, velocities were Log_{10} -transformed and contemporary mean annual precipitation was square-root transformed.

Statistical analysis

Sampling bias and species richness

Modularity M and nestedness NODF are some of the network structures which seem to be least affected by sampling bias (Rivera-Hutinel et al. 2012). However, to ensure that any potential relationships between modularity/nestedness and climate predictors (historical climate-change and contemporary climate) were not caused by differences in sampling along the climate gradients, we tested whether sampling extent (observational area), and sampling effort (number of observation days and hours) changed significantly along the climate gradients (for details about sampling, see Trøjelsgaard and Olesen 2013). Neither sampling extent nor effort correlated significantly ($p > 0.05$) with any climate gradients, so sampling bias could not have driven any detected relationship between climate and modularity/nestedness. On the other hand, modularity M was positively related to species richness ($p < 0.05$) and nestedness NODF was negatively related to species richness ($p < 0.05$), and species richness was therefore included as a predictor of modularity M and nestedness NODF. In all analyses, species richness was Log_{10} -transformed.

Historical climate-change and modularity/nestedness

To test our hypothesis that either modularity M decreases linearly with increasing historical climate-change or only decreases at high historical climate-change values, for each of the four historical climate predictors we conducted the model selection analyses based on information theory outlined in Diniz-Filho et al. (2008). First, we used $\Delta\text{AIC}_c < 2$ to identify minimum adequate models (MAMs) among all possible model combinations of the included explanatory variables, i.e. velocity, velocity², contemporary precipitation, contemporary temperature, species richness and insularity (Table 1). We identified MAMs both for the global dataset ($n = 54$), and separately for the mainland networks ($n = 23$) and the island networks ($n = 31$). Insularity was only included as an explanatory variable in the first case, whereas species richness and contemporary climate (temperature and precipitation) were considered in all cases. Therefore, for the global dataset we tested which of 63 alternative models were performing the best, and for the analysis of mainland and island networks separately we tested which of 31 alternative models were best (Table 1–2). The standardized regression coefficients are reported for both ordinary least squares (OLS) regression and spatial eigenvector mapping (SEVM) modelling, and reported for both an averaged model based on weighted w_i and minimum adequate models (MAMs) (Diniz-Filho et al. 2008). We tested whether significant positive spatial autocorrelation remained in model residuals (i.e. whether $p < 0.05$ in all distance classes, tested using 10 distance classes and applying a permutation test with 10 000 iterations). For each MAM, partial regression analysis based on OLS and SEVM modelling was used to partition the variation explained by historical climate-change versus contemporary climate (temperature and precipitation), species richness and insularity (Rangel et al. 2010). We conducted the same analyses for nestedness NODF, testing whether nestedness NODF increases linearly with increasing historical climate-change or only increases at high historical climate-change values. All analyses were conducted using the

Table 1. Models containing temperature-change velocity between the LGM and the present, contemporary climate, species richness and insularity as predictors of modularity in pollination networks. The standardized regression coefficients are reported for ordinary least squares (OLS) regression and spatial eigenvector mapping (SEVM) modelling, and reported for both an averaged model based on weighted w_i and minimum adequate models (MAMs) (Diniz-Filho et al. 2008). We also give AIC_c , Moran's I, and coefficients of determination (R^2) from partial regression models separating the effect of temperature-change velocity from the effect of the other predictors (Rangel et al. 2010). $R^2_{total\ velocity}$ describes total variation explained by velocity, and $R^2_{only\ velocity}$ reflects the unique variation explained by velocity. The analysis was conducted both for the global dataset ($n = 54$), and separately for mainland ($n = 23$) and island networks ($n = 31$).

	Global				Mainland				Islands			
	OLS		SEVM		OLS		SEVM		OLS		SEVM	
	Averaged	MAM [†]	Averaged	MAM	Averaged	MAM	Averaged	MAM [§]	Averaged	MAM [‡]	Averaged	MAM [¶]
Velocity	-0.24	-	+0.05	-	-0.68	-0.71*	-0.39	-	+0.23	-	+0.22	-
Velocity ²	-0.39	-0.44*	-0.11	-	-0.21	-	-0.35	-0.36*	-0.37	-0.33*	-0.39	-0.34*
MAP	+0.33	+0.33*	+0.02	-	+0.35	+0.35*	+0.17	-	+0.20	-	+0.24	-
MAT	+0.05	-	+0.03	-	+0.02	-	-0.00	-	+0.33	+0.30*	+0.33	+0.29*
Richness	+0.26	+0.21 ^{NS}	+0.30	+0.31*	-0.12	-	+0.07	-	+0.54	+0.57*	+0.61	+0.60*
Insularity	-0.28	-0.29*	-0.11	-								
AIC_c		-117.87		-138.37		-51.65		-51.22		-72.83		-69.76
Moran's I		$\leq 0.24^*$		$\leq 0.03^{NS}$		$\leq 0.07^{NS}$		$\leq 0.06^{NS}$		$\leq 0.17^{NS}$		$\leq 0.16^{NS}$
R^2		0.38		0.53		0.52		0.51		0.54		0.54
$R^2_{total\ velocity}$		0.15		0.00		0.40		0.30		0.15		0.15
$R^2_{only\ velocity}$		0.15		0.00		0.40		0.11		0.11		0.10

* $p < 0.05$, ^{NS} $p > 0.05$. [†]Two models were equally fit (i.e. $\Delta AIC_c \leq 2$) containing the following variables: 1) velocity², MAP, insularity; 2) velocity, velocity², MAP, species richness, insularity. [§]One other model had $\Delta AIC_c \leq 2$: velocity, spatial filter. [‡]One other model had $\Delta AIC_c \leq 2$: velocity, velocity², MAT, species richness. [¶]Three other models had $\Delta AIC_c \leq 2$: 1) velocity, velocity², MAT, species richness, spatial filter; 2) velocity², MAP, species richness, spatial filter; 3) velocity², species richness, spatial filter.

software Spatial Analysis in Macroecology, SAM 4.0 (Rangel et al. 2010).

Results

For modularity M, temperature-change velocity between the LGM and the present was more important than contemporary climate in all averaged models and was included in all MAMs except in the global SEVM model where only species richness

and spatial filters were included (Table 1). In both the global and the island models, temperature-change velocity related weakly and quadratically to modularity M, whereas for mainland networks temperature-change velocity was strongly negatively linearly related to modularity M (Table 1; Fig. 2). In all but the global SEVM partial regression model, temperature-change velocity explained a substantial amount of the spatial variation in modularity M ($0.15 < R^2 < 0.40$; Table 1).

For nestedness NODE, temperature-change velocity between the LGM and the present was as important as

Table 2. Models containing temperature-change velocity between the LGM and the present, contemporary climate, species richness and insularity as predictors of nestedness in pollination networks. The standardized regression coefficients are reported for ordinary least squares (OLS) regression and spatial eigenvector mapping (SEVM) modelling, and reported for both an averaged model based on weighted w_i and minimum adequate models (MAMs) (Diniz-Filho et al. 2008). We also give AIC_c , Moran's I, and coefficients of determination (R^2) from partial regression models separating the effect of temperature-change velocity from the effect of the other predictors (Rangel et al. 2010). $R^2_{total\ velocity}$ describes total variation explained by velocity, and $R^2_{only\ velocity}$ reflects the unique variation explained by velocity. The analysis was conducted both for the global dataset ($n = 54$), and separately for mainland ($n = 23$) and island networks ($n = 31$).

	Global				Mainland				Islands			
	OLS		SEVM		OLS		SEVM		OLS		SEVM	
	Averaged	MAM [†]	Averaged	MAM [§]	Averaged	MAM [‡]	Averaged	MAM	Averaged	MAM	Averaged	MAM
Velocity	+0.17	-	-0.02	-	+0.43	+0.45*	+0.04	-	-0.05	-	-0.05	-
Velocity ²	+0.23	+0.28*	+0.07	-	+0.23	-	+0.14	-	+0.11	-	+0.09	-
MAP	-0.27	-0.28*	-0.11	-	-0.30	-0.30*	-0.11	-	-0.34	-0.34*	-0.33	-0.34*
MAT	+0.01	-	+0.02	-	+0.08	-	+0.08	-	-0.05	-	-0.15	-
Richness	-0.63	-0.60*	-0.72	-0.73*	-0.61	-0.63*	-0.81	-0.82*	-0.63	-0.61*	-0.56	-0.54*
Insularity	+0.22	+0.24*	+0.06	-								
AIC_c		-20.88		-28.42		-5.414		-9.38		-10.46		-7.92
Moran's I		$\leq 0.10^{NS}$		$\leq 0.04^{NS}$		$\leq 0.17^{NS}$		$\leq 0.10^{NS}$		$\leq 0.05^{NS}$		$\leq 0.04^{NS}$
R^2		0.63		0.65		0.66		0.67		0.65		0.65
$R^2_{total\ velocity}$		0.08		0.00		0.24		0.00		0.00		0.00
$R^2_{only\ velocity}$		0.06		0.00		0.19		0.00		0.00		0.00

* $p < 0.05$, ^{NS} $p > 0.05$. [†]One model was equally fit (i.e. $\Delta AIC_c \leq 2$) containing the following variables: velocity, MAP, species richness, insularity. [§]One other model had $\Delta AIC_c \leq 2$: MAP, species richness, spatial filter. [‡]One other model had $\Delta AIC_c \leq 2$: velocity, species richness.

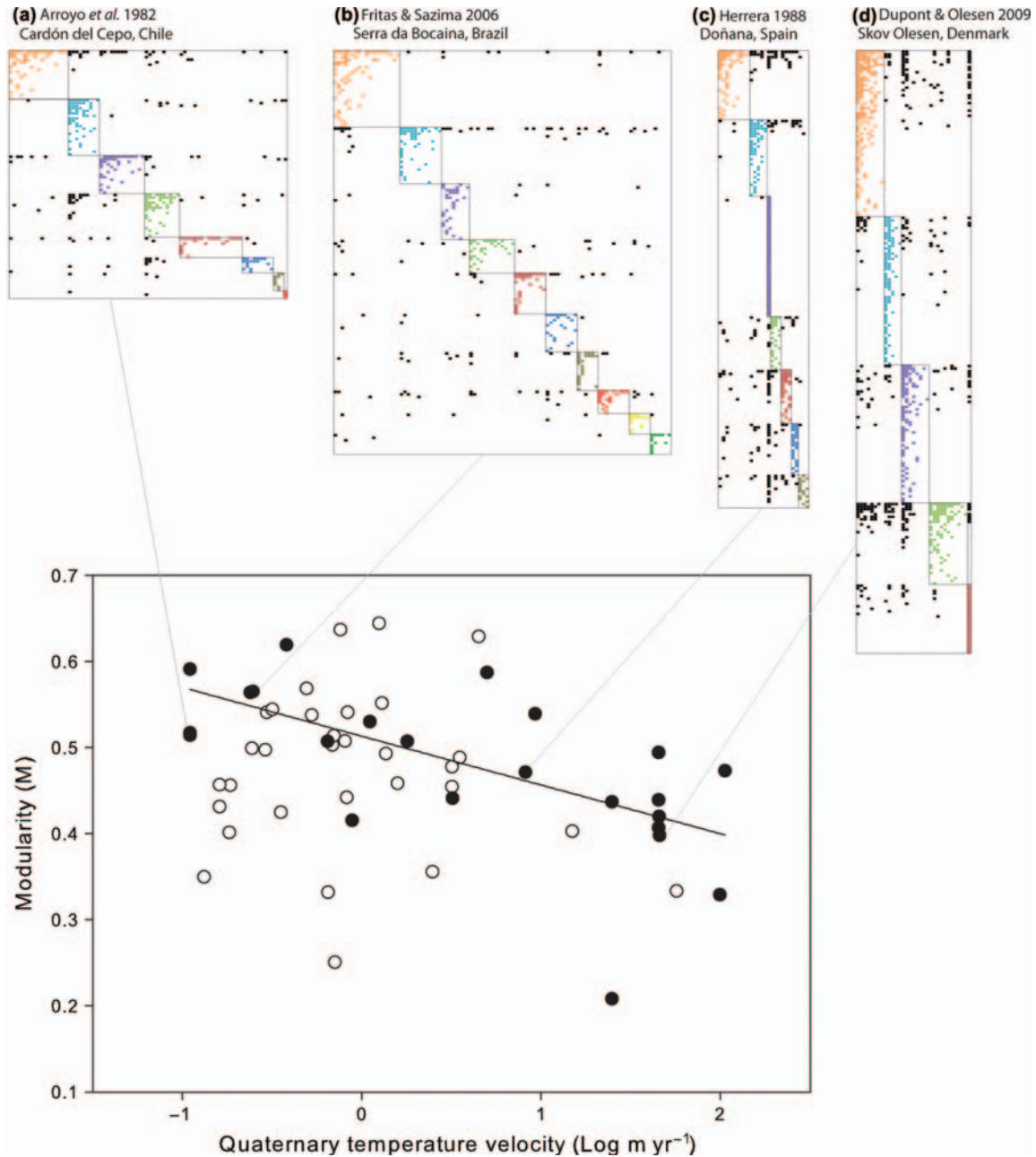


Figure 2. Linear relationship between Quaternary temperature-change velocity and modularity in pollination networks on the mainland. Each filled black symbol represents one mainland pollination network ($n = 23$). To illustrate the global dataset, we also plotted island networks ($n = 31$) as open symbols. The shown fit is based on ordinary least squares (OLS) regression and a linear relationship between temperature-change velocity and modularity in mainland pollination networks ($R^2 = 0.40$, $p < 0.05$, $n = 23$; Table 1). The depicted modular matrix versions of the networks have plant species in columns and pollinator species in rows and a filled cell signifies an interaction between a given plant and pollinator species; links within modules are delimited in boxes and are color-coded, whereas black cells are links gluing modules together into one large coherent network. The example matrices illustrate how modularity on the mainland is affected by temperature-change velocity and contemporary precipitation: (a) low temperature-change velocity (0.11 m yr^{-1}) and low contemporary precipitation (475 mm) lead to an intermediate level of modularity, (b) slightly higher temperature-change velocity (0.25 m yr^{-1}), but much higher contemporary precipitation (1693 mm) lead to an increased modularity, (c) intermediate velocity (8.17 m yr^{-1}) and lower contemporary precipitation (563 mm) lead to a decreased modularity, and (d) high velocity (45.72 m yr^{-1}) and low to intermediate precipitation (762 mm) lead to low modularity in pollination networks. Notice how the proportion of interactions outside the coloured modules increases as modularity decreases.

contemporary climate in all averaged models except in the models focusing on islands, where velocity was virtually unrelated to nestedness NODF (Table 2). In the global OLS MAM, temperature-change velocity related

weakly and quadratically to nestedness NODF, whereas for mainland networks temperature-change velocity was positively linearly related to nestedness NODF (Table 2; Fig. 3). However, velocity was neither included in the

global nor the mainland SEVM MAMs, which only contained species richness and spatial filters. Temperature-change velocity was also not included in OLS and SEVM MAMs focusing on islands. Hence, only in the

global and mainland OLS partial regression models, did temperature-change velocity explain a significant amount of the spatial variation in nestedness NODF ($0.08 < R^2 < 0.24$; Table 2).

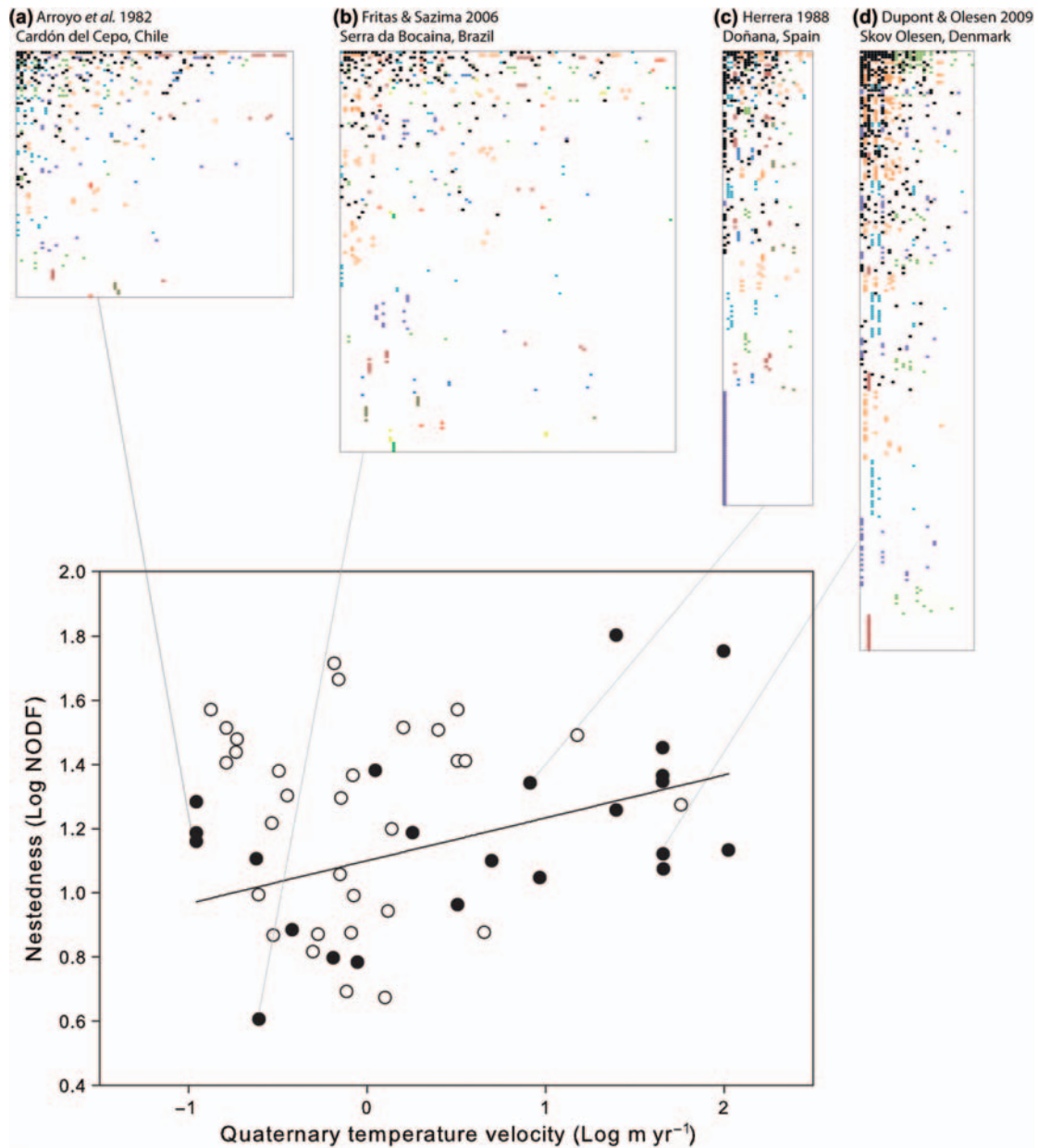


Figure 3. Linear relationship between Quaternary temperature-change velocity and nestedness in pollination networks on the mainland. Each filled black symbol represents one mainland pollination network ($n = 23$). To illustrate the global dataset, we also plotted island networks ($n = 31$) as open symbols. The shown fit is based on ordinary least squares (OLS) regression and a linear relationship between temperature-change velocity and nestedness in mainland pollination networks ($R^2 = 0.24$, $p < 0.05$, $n = 23$; Table 2). The depicted networks are the nested matrix versions of the same networks as in Fig. 2. They have plant species in columns and pollinator species in rows and a filled colored or black cell signifies an interaction between a given plant and pollinator species; species are sorted from upper left corner according to decreasing number of links. The example matrices illustrate how nestedness on the mainland is affected by temperature-change velocity, contemporary precipitation and species richness: (a) low temperature-change velocity (0.11 m yr^{-1}), low contemporary precipitation (475 mm) and low species richness (107 species) lead to an intermediate level of nestedness, (b) slightly higher temperature-change velocity (0.25 m yr^{-1}), but much higher contemporary precipitation (1693 mm) and species richness (273 species) lead to a drastic decreased nestedness, (c) intermediate velocity (8.17 m yr^{-1}), lower contemporary precipitation (563 mm) and species richness (205) all lead to a drastic increased nestedness, and (d) high velocity (45.72 m yr^{-1}) but low to intermediate precipitation (762 mm) and similar species richness (209 species) lead to slightly lower nestedness in pollination networks. Notice that nestedness is less associated with Quaternary temperature-change velocity than modularity is (Fig. 2).

For both modularity M and nestedness $NODF$, spatial autocorrelation was weak and Moran's I values were non-significant in all but the global OLS model for modularity, hence, we in the discussion focus mainly on the results from OLS models (Table 1–2). Precipitation-change velocity between the LGM and the present was virtually unrelated to modularity M ($0.00 < R^2 < 0.04$; Supplementary material Appendix 1, Table A1) and to nestedness $NODF$ ($0.00 < R^2 < 0.01$; Supplementary material Appendix 1, Table A4). We obtained qualitatively similar results when summarizing historical climate-change as the maximum velocity of 1000 yr time intervals (Supplementary material Appendix 1, Table A2–A3 and Table A5–A6).

Discussion

We have shown that high velocity of Quaternary climate-change is associated with reduced modularity and, to some extent, increased nestedness in pollination networks (Table 1–2; Fig. 2–3). This is especially evident within a mainland setting, for instance, when comparing the modularity and nestedness of pollination networks within climatically unstable North America with the modularity and nestedness of pollination networks in climatically more stable South America (Fig. 1). On islands Quaternary climate-change had weak effects on modularity and no effects on nestedness. This holds after incorporating contemporary climate, which in mainland pollination networks shows a weaker link to modularity and nestedness than historical climate-change, and species richness (Table 1–2), and is unrelated to sampling extent and effort (Methods; Trøjelsgaard and Olesen 2013). Also, although there was no effect of Quaternary climate-change on nestedness in SEVM models, while negative effects of high Quaternary climate-change on modularity were weaker in SEVM models they were still significant in both the mainland and on islands (Table 1–2). In plant–hummingbird interaction networks, specificity, measured as the degree of interspecific niche partitioning, has previously been shown to decrease in areas having experienced large historical climate-change, for example, specificity is particularly low in North American plant–hummingbird networks (Dalsgaard et al. 2011). A recent meta-analysis reports that specificity in pollination networks as a whole is not associated with historical climate-change but more with modern plant species richness (Schleuning et al. 2012). At least for mainland networks, the current study illustrates that the separation of interacting species into distinct modules tends to be less clear-cut in areas having experienced large historical climate-change (Fig. 2). Modules of pollination networks may reflect subgroups of species specializing upon each other and having somewhat similar traits, i.e. possibly reflecting ‘pollination syndromes’ (Olesen et al. 2007, Danielli-Silva et al. 2012, Martín González et al. 2012), such as trait convergence between large-sized hummingbirds and their floral plants or bees and their floral plants (Olesen et al. 2007, Ollerton et al. 2009, Dalsgaard et al. 2012, Danielli-Silva et al. 2012). Our results therefore suggest that large historical climate fluctuations have increased nestedness and partially broken down the otherwise distinct separation into modules of plants and their animal pollinators with

similar ‘pollination syndrome’. This may result from either phenological shifts or range-size dynamics associated with climate-change between the LGM and the present (Price 2003, Memmott et al. 2007, Araújo et al. 2008, Tylianakis et al. 2008, Devoto et al. 2009, Amano et al. 2010, Nogués-Bravo et al. 2010, Sandel et al. 2011), possibly increasing the proportion of super-generalist ‘network hub’ or ‘connector’ species gluing the network together and blurring the borders between modules (Fig. 2) while increasing nestedness (Fig. 3). The apparent disagreement with the study by Schleuning et al. (2012), showing no trends in specificity in relation to historical climate-change, could be explained by a higher between-module generalization level coupled with a higher within-module specificity in areas having experienced large historical climate-change. This may be the case if in climatically unstable areas, within-module specialists have specialized further within their module, for instance, caused by local extinction of co-evolutionary partners. In contrast, in climatically stable areas, species may show higher between-module specificity while generalizing within their historically stable co-evolved module.

Depending on the nature of interaction, the modular and nested network structures may either decrease or increase community stability (Thébault and Fontaine 2010, Tylianakis et al. 2010, Stouffer and Bascompte 2011). Specifically for pollination and other mutualistic networks, however, studies show that high modularity reduces community persistence (Thébault and Fontaine 2010), for instance, by decreasing functional redundancy of species and thereby increasing the likelihood of secondary extinctions (Tylianakis et al. 2010), while nestedness increases the resilience of the network (Thébault and Fontaine 2010). If indeed modularity decreases community persistence and nestedness increases resilience in pollination networks, the finding that pollination networks in climatically unstable North America and low-laying part of northern Europe have a low level of modularity and often relatively high level of nestedness (Fig. 1), corroborates suggestions that those communities that have experienced the greatest historical climate-change today are rich in widespread species resistant to future climate-change (Sandel et al. 2011). In light of the current anthropogenic climate-change and the global decline of pollinators and possible interlinked plant declines (Biesmeijer et al. 2006, Devoto et al. 2009), more research is clearly needed to address in detail the processes beneath the relationship between historical climate-change, modularity, nestedness and stability of pollination networks. For instance, future research should quantify to what extent effects of climate-change on modularity and nestedness arise from an effect of climate-change on species distribution independently of their interaction pattern, or directly influence the interaction pattern of species and subsequently modularity and nestedness.

Beyond pollination networks there is also an urgent need to understand the impact of climate-change on species interactions more generally and thereby on the assembly and functioning of biotic communities (Ings et al. 2009). Integration of network analysis and macroecology provides a powerful, but as yet under-explored tool for such assessments (Araújo et al. 2008, Ings et al. 2009, Dalsgaard et al. 2011, Carstensen et al. 2012, Thébault 2013, Trøjelsgaard and Olesen 2013). We hope that our contribution will

stimulate studies of how historical climate fluctuations may affect network structure in a wide range of systems important for the maintenance of biodiversity; for instance, testing to what extent our results from pollination networks may be generalised to networks of seed dispersal, predation, parasitism, and to entire food-webs.

Acknowledgements – Thanks to Marie N. Sorivelle, Nathan J. Sanders, and Subject Editor Dominique Gravel for constructive comments improving an earlier version of this manuscript. BD was supported by the Carlsberg Foundation, KT by Aarhus Univ. Research Foundation, AMMG by the Spanish Ministry of Education through the postdoctoral grant BVA-2010-0845, TP by the EU FP7 project STEP (244090-STEP-CP-FP), and BS was supported in part by MADALGO – Center for Massive Data Algorithmics, a Center of the Danish National Research Foundation and in part by funding from the Aarhus Univ. Research Foundation via the Center for Interdisciplinary Geospatial Informatics Research (CIGIR). DN-B and CR thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution and Climate. MS was supported by the research funding programme ‘LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz’ of Hesse’s Ministry of Higher Education, Research, and the Arts. WJS was funded by Arcadia. J-CS acknowledges his contribution as an outcome of the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by Aarhus Univ. and Aarhus Univ. Research Foundation under the AU IDEAS program. JMO was funded by the Danish National Research Foundation.

References

- Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – *Oikos* 117: 1227–1239.
- Amano, T. et al. 2010. A 250-year index of first flowering dates and its response to temperature changes. – *Proc. R. Soc. B* 277: 2451–2457.
- Araújo, M. B. et al. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. – *Ecography* 31: 8–15.
- Bascompte, J. and Jordano, P. 2007. Plant–animal mutualistic networks: the architecture of biodiversity. – *Annu. Rev. Ecol. Evol. Syst.* 38: 567–593.
- Biesmeijer, J. C. et al. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. – *Science* 313: 351–354.
- Carstensen, D. W. et al. 2012. Biogeographical modules and island roles: a comparison of Wallacea and the West Indies. – *J. Biogeogr.* 39: 739–749.
- Collins, W. D. et al. 2006. The community climate system model version 3 (CCSM3). – *J. Clim.* 19: 2122–2143.
- Dalsgaard, B. et al. 2011. Specialization in plant–hummingbird network is associated with species richness, contemporary precipitation and quaternary climate-change velocity. – *PLoS One* 6: e25891.
- Dalsgaard, B. et al. 2012. *Heliconia*–hummingbird interactions in the Lesser Antilles: a geographic mosaic? – *Caribb. J. Sci.* 46: 328–331.
- Danieli-Silva, A. et al. 2012. Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? – *Oikos* 121: 35–43.
- Devoto, M. et al. 2009. Patterns of species turnover in plant–pollinator communities along a precipitation gradient in Patagonia (Argentina). – *Austral Ecol.* 34: 848–857.
- Diniz-Filho, J. A. L. et al. 2008. Model selection and information theory in geographical ecology. – *Global Ecol. Biogeogr.* 17: 479–488.
- Dupont, Y. L. et al. 2009. Spatio-temporal variation in the structure of pollination networks. – *Oikos* 118: 1261–1269.
- Dynesius, M. and Jansson, R. 2000. Evolutionary consequences of changes in species’ geographical distributions driven by Milankovitch climate oscillations. – *Proc. Natl Acad. Sci. USA* 97: 9115–9120.
- Fjeldså, J. et al. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. – *Ecography* 22: 63–78.
- Flores, C. O. et al. 2011. Statistical structure of host–pathogen interactions. – *Proc. Natl Acad. Sci. USA* 108: E288–E297.
- Fortuna, M. A. et al. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? – *J. Anim. Ecol.* 78: 811–817.
- Gilman, S. E. et al. 2010. A framework for community interactions under climate change. – *Trends Ecol. Evol.* 25: 325–331.
- Guimerà, R. and Amaral, L. A. N. 2005a. Cartography of complex networks: modules and universal roles. – *J. Stat. Mech. Theor. Exp.*: P02001.
- Guimerà, R. and Amaral, L. A. N. 2005b. Functional cartography of complex metabolic networks. – *Nature* 433: 895–900.
- Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – *Int. J. Climatol.* 25: 1965–1978.
- Hortal, J. et al. 2011. Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. – *Ecol. Lett.* 14: 741–748.
- Ings, T. et al. 2009. Ecological networks – beyond food webs. – *J. Anim. Ecol.* 78: 253–269.
- Jansson, R. 2003. Global patterns in endemism explained by past climatic change. – *Proc. R. Soc. B* 270: 583–590.
- Jetz, W. et al. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. – *Ecol. Lett.* 7: 1180–1191.
- Kissling, D. W. et al. 2012. Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. – *Global Ecol. Biogeogr.* 21: 909–921.
- Krasnov, B. R. et al. 2012. Phylogenetic signal in module composition and species connectivity in compartmentalized host–parasite networks. – *Am. Nat.* 179: 501–511.
- Lorenzen, E. D. et al. 2011. Species-specific responses of late quaternary megafauna to climate and humans. – *Nature* 479: 359–364.
- Martín González, A. M. et al. 2009. Effects of climate on pollination networks in the West Indies. – *J. Trop. Ecol.* 25: 493–506.
- Martín González, A. M. et al. 2012. Drivers of compartmentalization in a Mediterranean pollination network. – *Oikos* 121: 2001–2013.
- Memmott, J. et al. 2007. Global warming and the disruption of plant–pollinator interactions. – *Ecol. Lett.* 10: 710–717.
- Newman, M. E. J. 2004. Detecting community structure in networks. – *Eur. Phys. J. B* 38: 321–330.
- Nogués-Bravo, D. et al. 2008. Scale effects and human impact on the elevational species richness gradients. – *Nature* 453: 216–219.
- Nogués-Bravo, D. et al. 2010. Climate predictors of late quaternary extinctions. – *Evolution* 64: 2442–2449.
- Olesen, J. M. and Jordano, P. 2002. Geographic patterns in plant–pollinator mutualistic networks. – *Ecology* 83: 2416–2424.
- Olesen, J. M. et al. 2007. The modularity of pollination networks. – *Proc. Natl Acad. Sci. USA* 104: 19891–19896.

- Ollerton, J. et al. 2009. A global test of the pollination syndrome hypothesis. – *Ann. Bot.* 103: 1471–1480.
- Otto-Bliesner, B. L. et al. 2006. Last Glacial Maximum and Holocene climate in CCSM3. – *J. Clim.* 19: 2526–2544.
- Price, P. W. 2003. Macroevolutionary theory on macroecological Patterns. – Cambridge Univ. Press.
- Rahbek, C. et al. 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. – *Proc. R. Soc. B* 274: 165–174.
- Rangel, T. F. et al. 2010. SAM: a comprehensive application for spatial analysis in macroecology. – *Ecography* 33: 46–50.
- Rivera-Hutinel, A. et al. 2012. Effects of sampling completeness on the structure of plant–pollinator networks. – *Ecology* 93: 1593–1603.
- Ruddiman, W. F. 2001. Earth's climate: past and future. – W. H. Freeman.
- Sandel, B. et al. 2011. The influence of late Quaternary climate-change velocity on species endemism. – *Science* 334: 660–664.
- Schleuning, M. et al. 2012. Specialization of mutualistic interaction networks decreases towards tropical latitudes. – *Curr. Biol.* 22: 1925–1931.
- Stouffer, D. B. and Bascompte, J. 2011. Compartmentalization increases food-web persistence. – *Proc. Natl Acad. Sci. USA* 108: 3648–3652.
- Svenning, C. J. and Skov, F. 2007. Ice age legacies in the geographical distribution of tree species richness in Europe. – *Global Ecol. Biogeogr.* 16: 234–245.
- Sutherland, W. J. et al. 2013. Identification of 100 fundamental ecological questions. – *J. Ecol.* 101: 58–67.
- Thébault, E. 2013. Identifying compartments in presence–absence matrices and bipartite networks: insights into modularity measures. – *J. Biogeogr.* doi: 10.1111/jbi.12015
- Thébault, E. and Fontaine, C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. – *Science* 329: 853–856.
- Trøjelsgaard, K. and Olesen, J. M. 2013. Macroecology of pollination networks. – *Global Ecol. Biogeogr.* 22: 149–162.
- Tylianakis, J. M. et al. 2008. Global change and species interactions in terrestrial ecosystems. – *Ecol. Lett.* 11: 1351–1363.
- Tylianakis, J. M. et al. 2010. Conservation of species interactions networks. – *Biol. Conserv.* 143: 2270–2279.

Supplementary material (Appendix ECOG-00201 at <www.oikosoffice.lu.se/appendix>). Appendix 1.