

Community-wide changes in intertaxonomic temporal co-occurrence resulting from phenological shifts

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Abstract

Global climate change is known to affect the assembly of ecological communities by altering species' spatial distribution patterns, but little is known about how climate change may affect community assembly by changing species' temporal co-occurrence patterns, which is highly likely given the widely observed phenological shifts associated with climate change. Here, we analyzed a 29-year phenological data set comprising community-level information on the timing and span of temporal occurrence in 11 seasonally occurring animal taxon groups from 329 local meteorological observatories across China. We show that widespread shifts in phenology have resulted in community-wide changes in the temporal overlap between taxa that are dominated by extensions, and that these changes are largely due to taxa's altered span of temporal occurrence rather than the degree of synchrony in phenological shifts. Importantly, our findings also suggest that climate change may have led to less phenological mismatch than generally presumed, and that the context under which to discuss the ecological consequences of phenological shifts should be expanded beyond asynchronous shifts.

Keywords: China, climate change, community assembly, interspecific temporal overlap, phenological shift, temporal occurrence window

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Introduction

Of the strong, wide-ranging ecological and evolutionary impacts of climate change (Parmesan, 2006; Rosenzweig *et al.*, 2008), general consensus is that altered community assembly ensues from alterations in species' spatial distribution patterns (Williams & Jackson, 2007; Walther, 2010; Gornish & Tylianakis, 2013). Climate change affects species' spatial distribution either directly as species demographically track climatic niches (Böhning-Gaese & Lemoine, 2004; Parmesan, 2006), or indirectly as ecological interactions influence species' vital population rates (Miller-Rushing *et al.*,

2010; Encinas-Viso *et al.*, 2012). However, community assembly entails not only spatial, but also temporal, co-occurrence of species. For ecological communities that consist of many seasonally occurring species or their life stages, climate change could directly and, through species interactions, indirectly affect their assembly if it changes species' temporal overlap patterns (Forrest & Miller-Rushing, 2010; Nakazawa & Doi, 2012). Widely observed phenological shifts associated with climate change (Menzel *et al.*, 2006; Parmesan, 2006; Cleland *et al.*, 2007) and the interspecific variations in such shifts (Both *et al.*, 2009; Thackeray *et al.*, 2010) strongly suggest that species temporal overlap patterns can be highly susceptible to the impacts of climate change by way of shifts in species' temporal occurrence windows. Empirical evidence at the community level, however, remains sparse because available phenological records are predominantly focused on 'phenological firsts', that

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is, the timing when a phenological event initially occurs, and rarely provide information on the timing and span of the entirety of species' temporal occurrence windows (Roy & Sparks, 2000; Iler *et al.*, 2013; Caradonna *et al.*, 2014).

Both increases and decreases in interspecific temporal overlap can occur as a result of species' phenological shifts that alter the timing and span of their temporal occurrence windows, as illustrated by a conceptual model in Fig. 1a. Such changes can occur regardless of whether the shift directions of species' temporal occurrence windows are consistent or whether their spans remain constant (Fig. 1a). When the phenology of species' temporal occurrence shifts under climate change (Menzel *et al.*, 2006; Parmesan, 2006; Cleland *et al.*, 2007), changes in interspecific temporal overlap are probably widely expected. This is illustrated by a simple simulation exercise involving two hypothetical species (Appendix S1): When the temporal occurrence window of one or both species varies in position and span, there are regular incidences of sizeable increases and decreases in the span of interspecific temporal overlap (Fig. 1b). Empirical test of how interspecific temporal overlap changes as a result of climate-associated phenological shifts requires data on not only the beginning, but also the end, of species' temporal occurrence windows, and preferably at the community level.

We present a multitaxa phenological and weather data set collected simultaneously from across China to shed light on how climate change may be altering community assembly by shifting species' phenology of temporal occurrence. Both data sets were collected under the Chinese National Meteorological Observation Network (hereafter 'NMON') over 29 years (1981–2009). In the form of time series, the phenological data set recorded the annual first and last sighting dates and thus the spans of temporal occurrence windows of 11 seasonally occurring animal taxa and in turn provided information on the temporal overlap span between 27 pairs of taxa. We first analyzed how the temporal occurrence phenology of each taxon changed over time and in response to climate change. We then tested how the span of intertaxon temporal overlap changed over time, and examined the mechanism of the observed changes where they were detected. We accounted for spatial autocorrelation in analyses that combined data from across China, and applied four sets of data quality criteria in selecting time series for analysis to ensure the robustness of analysis results.

Materials and methods

Phenological data were collected following a nationally standardized protocol at local meteorological observatories

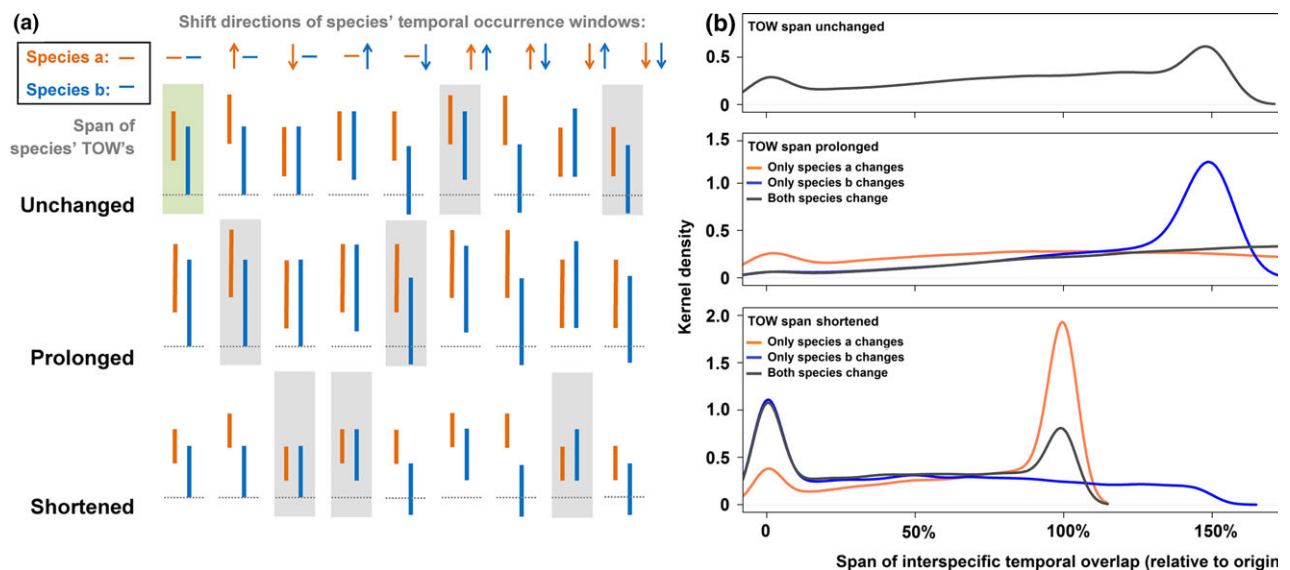


Fig. 1 Conceptual illustration of changes in interspecific temporal overlap resulting from shifts in the temporal occurrence windows (TOWs) between two hypothetical species. (a) Changes in interspecific temporal overlap can result from species shifting the position or span of their TOWs. In the current illustration, the extent of shift in the position or span of TOW is fixed at one time unit; (non)changes of TOW span apply to both species. Green box represents species' initial TOW patterns; gray boxes highlight scenarios where species maintain unchanged overlap. (b) Kernel density curves of different spans of interspecific temporal overlap under different scenarios of TOW shift. Original TOW patterns and top to bottom panels correspond to those in (a). For the two lower panels, orange and blue curves, respectively, represent scenarios where the orange-coded and blue-coded species in (a) were allowed prolonged/shortened TOWs, while gray curve represents scenarios where both species were allowed prolonged/shortened TOWs.

under NMON that is directed by the China Meteorological Administration (Ge *et al.*, 2014). This protocol was based on the protocol used in collecting agrometeorological observation annual records (protocol No. QX/T 21-2004) and incorporated additional guidelines specifically on phenological data collection (China Meteorological Administration 1993; Appendix S2). Phenological data from all meteorological observatories were submitted annually to the National Meteorological Information Center (<http://www.nmic.gov.cn/en/>) of China Meteorological Administration in the form of hardcopy data sheets and kept on file as such. In 2012–2013, with permission from NMON, we digitalized the entire collection of animal phenological records between 1981 and 2009, including all original information on the hardcopy data sheets. In all, we obtained 2133 raw time series on the first and last sighting of 50 animal taxa collected from 360 meteorological observatories between 1981 and 2009 (Table S1 in Appendix S2). We also obtained weather data from the same meteorological observatories where phenological data were collected, including records on the daily maximum, minimum, and mean temperature, and daily precipitation. In all, we obtained weather data for 349 sites within China.

We followed three steps in preparing phenological time series for analysis. First, because raw phenological records were not all accurately identified to the species level (e.g., 'frog' and 'toad'; Appendix S2), we collapsed the records into 11 'operational taxa' (hereafter 'taxa' unless noted otherwise) that represented the finest unmistakable taxon assignment (Table S1 in Appendix S2). As it turned out, no site had more than one original species/taxa under a certain operational taxon. Second, for quality control of the raw phenological records, we removed all first sighting dates falling on January 1 and all last sighting dates falling on December 31 because these dates may be the artifact of original data being missing and subsequently filled in, and removed, for each time series, date records that were ≥ 60 days away from $\geq 80\%$ of the other date records as outliers. We converted the remaining date records into day of the year, with January 1 as day one. Finally, we retained time series that consisted of ≥ 5 time steps and spanned ≥ 8 years to ensure adequate time series length (hereafter '5–8 criterion'). Despite these stringent data quality requirements, we recognize that the NMON phenological data set may suffer from some inherent data quality deficiencies related to the imperfect detection of phenological events, and the inconsistencies in the method and content of data collection introduced by the data set's large geographical and temporal coverage. However, we have no reason to expect them to cause anything more than noise in the data and therefore expect no systematic bias in our findings. We thus obtained a trimmed phenological data set that comprised 1942 time series from 329 meteorological observatories (hereafter 'sites') on the annual first and last sighting dates and the spans of temporal occurrence windows of 11 seasonally occurring animal taxa (Fig. 2a), and 497 time series from 161 sites on the temporal overlap span of 27 taxon pairs (Fig. 2b); the data set thus involved four types of phenological events. All taxa occurred during the Northern Hemisphere breeding season except for wintering goose (Table S2 in Appendix S2), which is expected

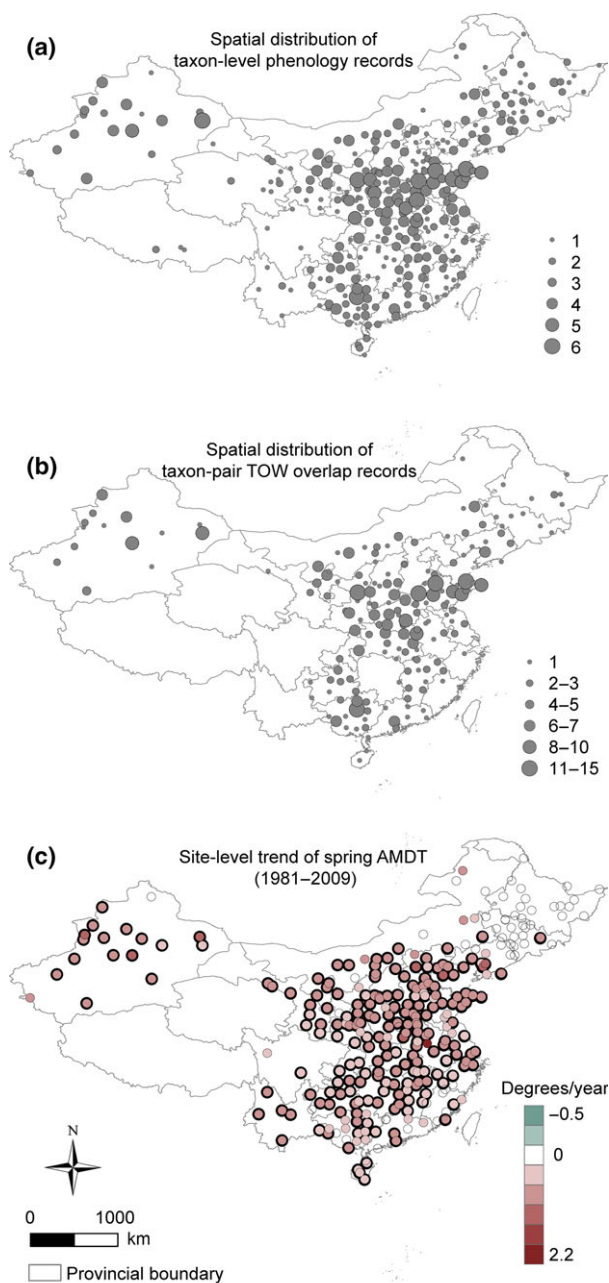


Fig. 2 Location of meteorological observatories (sites) that provided phenological data, with their trend of average minimum daily temperature (AMDT) in spring between 1981 and 2009. (a) Location of sites that provided data on the phenology of taxa's temporal occurrence. (b) Location of sites that provided data on the temporal overlap between taxon pairs. For (a) and (b), size of dots representing sites is proportional to the number of taxa/taxon pairs for which data were available at each site. (c) Site-level trend of spring (February–April) AMDT between 1981 and 2009. Color of dots representing sites is coded by degrees per year change in spring AMDT at each site ($P \leq 0.05$: color coded and bolded; $0.05 < P \leq 0.1$: color coded). Uncolored dots are sites where AMDT change was not significant.

to exhibit opposite patterns of phenological shift in relation to climate change compared to the breeding-season taxa. We have archived the data set on the online database Dryad (Hua *et al.* 2015; access number 68184).

We used the average minimum daily temperature as the measure of climate conditions. For analysis of the relationship between phenological shift and average minimum daily temperature, because phenological dates varied widely across taxa and sites, we calculated the average minimum daily temperature of 3-month windows specific to each taxon-site combination to provide relevant climate context for the phenological event in question. To achieve this, we identified the median date of the time series for each phenological event for each taxon-site combination. The 3-month window centering on the median date was thus taken as the window for the phenological event in question, for which the average minimum daily temperature was calculated. The span of temporal occurrence windows was considered in association with the average minimum daily temperature for the first sighting because of high correlations between the average minimum daily temperatures for the first and last sightings (e.g. $r_{\text{Pearson}} = 0.96$, $P < 0.0001$ between nationwide average minimum daily temperatures for February–April and September–November).

We conducted analyses of phenological time series for each taxon/taxon pair and its associated phenological event on two levels: separately for individual time series using linear regressions, and combining all time series in a linear mixed model framework that accounted for spatial autocorrelation; we conducted all analyses on variables that were centered to mean = 0 and scaled to SD = 1 to facilitate model convergence. For each time series, we first conducted simple linear regression; only when the relationship between residuals and fitted values indicated no violation of the linearity assumption did we accept the regression (Appendix S3). For regressions that violated the linearity assumption, we added a quadratic term of the predictor variable and again tested the relationship between residuals and fitted values (Appendix S3); time series that still violated the linearity assumption were discarded. All conclusions of phenological shift and its relationship with average minimum daily temperature were based on monotonic relationships indicated by simple linear regressions.

For each taxon/taxon pair and its associated phenological event, we used linear mixed models (LMMs) to model the temporal trend of phenological events and its relationship with average minimum daily temperature. Both the intercept and the time slope were allowed to vary across sites to reflect repeated measures of phenological events within each site (i.e., random intercept and slope LMM; Appendix S3). We assessed spatial autocorrelation across sites for time series of each taxon–phenology combination and each taxon pair that had ≥ 10 time series by examining Moran's I spatial correlograms (Cliff & Ord, 1981) of the level-2 (random slope and intercept) residuals, using a spatial lag interval of 200 km. We did not assess spatial autocorrelation for taxon–phenology combinations or taxon pairs with < 10 time series because of their limited sample size. Because sites closer together are likely to be more similar than sites farther apart, we adopted the smallest spatial lag distance at which Moran's I were statis-

tically insignificant (permutational $P > 0.05$; 999 permutations) as the distance at which sites were considered spatially independent. Cutoff distances for each taxon–phenology combination and each taxon pair that had spatial autocorrelation issues are provided in Figs S1 and S2 and Table S3 in Appendix S3.

For taxon–phenology combinations and taxon pairs whose time series had no spatial autocorrelation issues (i.e., cutoff distance was zero; these included four taxa for first sighting, seven taxa for last sighting, seven taxa for span of temporal occurrence window and 21 taxon pairs), we accepted the parameter estimates derived from random slope and intercept LMMs fitted to the full data set. Taxon–phenology combinations and taxon pairs whose random slope and intercept did not converge were instead analyzed with random intercept LMMs. For taxon–phenology combinations and taxon pairs whose time series were spatially autocorrelated up to their respective cutoff distances (seven taxa for first sighting, four taxa for last sighting, four taxa for span of temporal occurrence window and six taxon pairs), we conducted subsampling of the time series based on random draws to generate subsets of data consisting of the maximum number of time series from sites that were spaced apart by at least the cutoff distances (Appendix S3). We generated 1000 subsampled data sets for each taxon–phenology combination to which LMMs were fitted. We further calculated the mean and 95% percentile confidence interval of the 1000 time-slope parameter estimates derived from the 1000 subsampled data sets for each taxon–phenology analysis.

To examine the mechanism of the observed changes in inter-taxonomic temporal overlap, we classified individual time series that showed temporal overlap change between 1981 and 2009 into six categories in terms of the shift patterns of temporal occurrence windows of constituent taxa: (1) temporal occurrence windows advanced or (2) delayed in both taxa, (3) advanced or (4) delayed in only one taxon, (5) advanced in one while delayed in the other taxon and (6) no shift. We additionally compared the direction of temporal overlap change with that of the span change of temporal occurrence windows of constituent taxa. To ensure the robustness of our results against trimming using the 5–8 criterion, we additionally produced and analyzed three data sets applying progressively stricter trimming criteria that, respectively, yielded ~ 90 , 75, and 50% of the data amount of the 5–8 criterion. These alternative criteria respectively had ≥ 6 , 11 and 10 time steps and spanned ≥ 10 , 11 and 14 years (Table S2 in Appendix S2). Because results were generally consistent across trimming criteria (Tables S8–S10 in Appendix S4), below we only present results based on the full data set yielded under the 5–8 criterion. All analyses were conducted in R.3.0.2 (R Core Team 2013); we used 'spdep' package (version 0.5-88) to calculate Moran's I and 'nlme' package (version 3.1-120) for linear mixed-effects modeling. Scripts for all analyses are archived in the online script database github (accessible at: <https://github.com/yangliubnu/PhenologyChina>).

Results

Animal taxa exhibited widespread trends of phenological shift between 1981 and 2009 that fit into the

signatures of climate change (Roy & Sparks, 2000; Menzel *et al.*, 2006; Parmesan, 2006; Cleland *et al.*, 2007; Iler *et al.*, 2013; CaraDonna *et al.*, 2014), that is, advanced first sighting in spring, delayed last sighting in autumn and/or prolonged temporal occurrence windows, as reflected by individual (Fig. S3a and Table S4) and overall patterns of time series (Fig. 3a and b). Four taxa that failed to show overall patterns of shifts had extremely small numbers of time series after subsampling (Table S3), thus were likely associated with very low statistical power; indeed, analysis for these taxa that used the full data set (thus likely suffered from spatial autocorrelation problems) showed significant patterns of phenological shift consistent with climate change signatures for three of them (insets in Fig. S4a). Consistent with the global trend (Dudley *et al.*, 1997), China underwent an overwhelming trend of warming between 1981 and 2009 (Fig. 2c): Average minimum daily temperature for spring (February–April) and autumn (September–November) across the country increased at a rate of 0.616 and 0.442 °C per decade ($P < 0.0001$), respectively. Analysis of individual time series shows that consistent with the expected impacts of climate change (Roy & Sparks, 2000; Menzel *et al.*, 2006; Parmesan, 2006; Cleland *et al.*, 2007; Iler *et al.*, 2013; CaraDonna *et al.*, 2014), higher average minimum daily temperatures were predominantly associated with advanced first sighting in spring, delayed last sighting in autumn and prolonged temporal occur-

rence windows of animal taxa (Fig. S1b; Table S4). Overall analysis of time series, however, largely failed to detect such a pattern across taxa (Fig. 3c). For four taxa, this lack of an overall relationship between phenology and average minimum daily temperature across the country is at least partially the result of very low statistical power associated with extremely small sample sizes after subsampling (Table S3): analysis that used the full data set (thus disregarding the spatial autocorrelation problems) showed generally significant relationships between phenology and average minimum daily temperature consistent with the expected impacts of climate change (insets in Fig. S4b). Assuming sighting to reasonably represent animals' temporal occurrence windows, the NMON phenological data set thus suggests that the temporal occurrence phenology of our study taxa is widely shifting under the warming trend of climate change across China, generally toward advanced initial occurrence, delayed disappearance and prolonged temporal occurrence windows.

We found that taxon-level phenological shifts resulted in community-wide changes in the patterns of intertaxonomic temporal overlap across China and that such changes were dominated by increases rather than decreases. Of all time series, coming from almost all taxon pairs, 31.0% exhibited changes in the span of temporal overlap ($P \leq 0.1$; Table S5); these time series were divided between 21.2% that exhibited prolonged temporal overlap and 9.8% that exhibited the opposite,

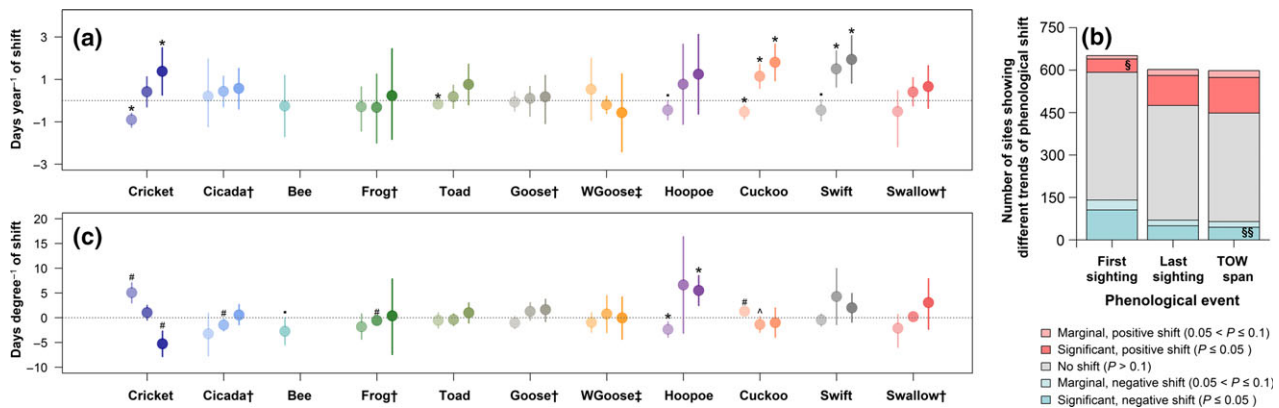


Fig. 3 Response of animal phenology to climate change across China between 1981 and 2009. (a) Taxon-level phenological shift as measured by days shifted per year. The three points (left to right; different color shades) for each taxon, respectively, represent first sighting, last sighting, and span of temporal occurrence windows (TOWs); error bars indicate 95% confidence interval. (b) Number of time series records showing different directions of shift ($P \leq 0.05$ and $0.05 < P \leq 0.1$, respectively). § indicates two time series were for wintering goose; §§ indicates one time series was for wintering goose. (c) Association between phenological shift and climate change as measured by days shifted per degree increase in average minimum daily temperature; error bars indicate 95% confidence interval. For (a) and (c), significant patterns consistent with expected impacts of climate change are indicated with * ($P \leq 0.05$) and • ($0.05 < P \leq 0.1$); significant opposite patterns are indicated with # ($P \leq 0.05$) and ^ ($0.05 < P \leq 0.1$). † indicates taxa for which subsampling yielded extremely small sub-data sets (Table S3) and thus were likely associated with very low statistical powers; ‡ – ‘WGoose’ refers to wintering goose.

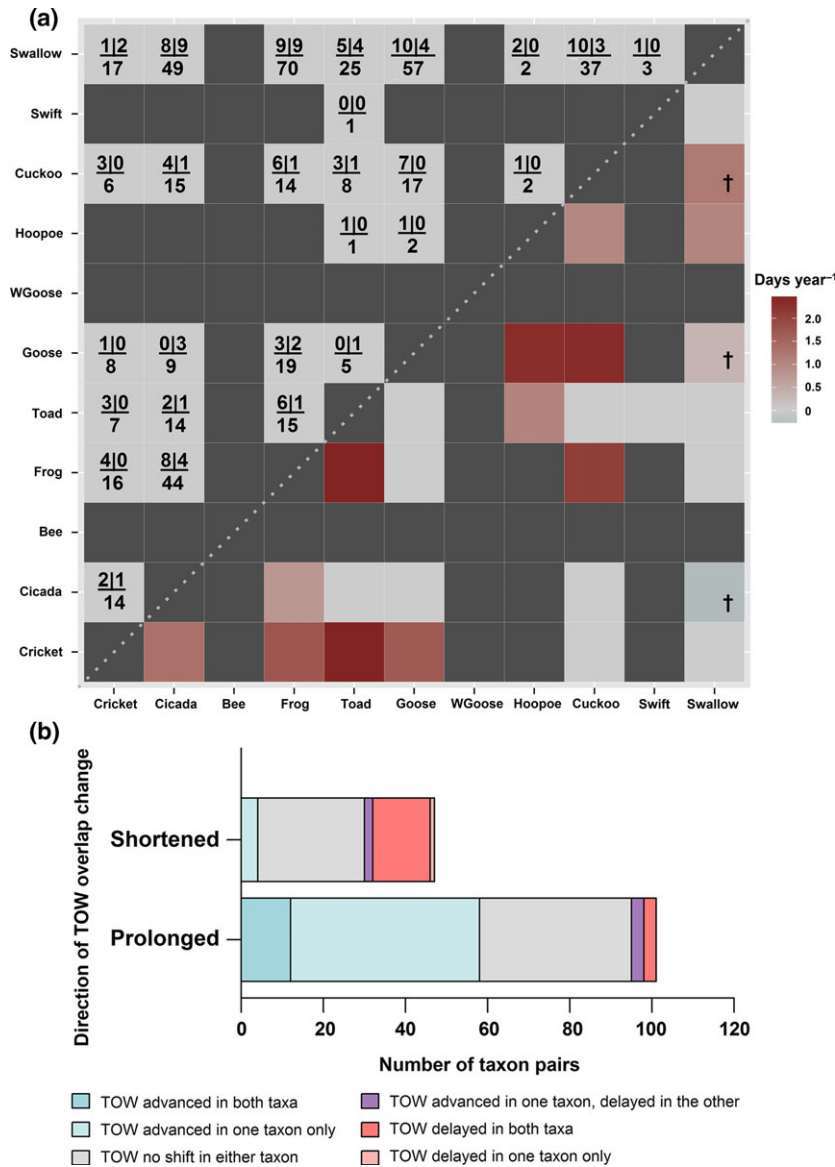


Fig. 4 Changes in the span of temporal overlap between taxon pairs between 1981 and 2009 and how they relate to taxa's shifts in temporal occurrence windows (TOWs). (a) Upper triangle shows site-level change of temporal overlap span for each taxon pair. Numbers above horizontal bars refer to the numbers of time series showing prolonged (left) and shortened (right) temporal overlap between 1981 and 2009 ($P \leq 0.1$); numbers below horizontal bars indicate the number of time series available for analysis. Lower triangle shows the overall change of temporal overlap span for each taxon pair. Cells are coded by the direction and degree of temporal overlap change ($P \leq 0.1$; all cells except for three marked with † have $P \leq 0.05$); dark gray cells represent taxon pairs for which data were not available. 'WGoose' refers to wintering goose. (b) Classification of time series that exhibited prolonged and shortened temporal overlap changes into six categories based on the TOW shift patterns of constituent taxa.

with opposite directions of change existing within most taxon pairs (Fig. 4a, upper triangle; Table S5). Linear mixed models showed that overall across the country, 14 and one of 27 pairs, respectively, exhibited prolonged and shortened temporal overlap between 1981 and 2009 ($P \leq 0.1$; all but three pairs had $P \leq 0.05$; Fig. 4a, lower triangle). Of the 148 time series that showed temporal overlap change, 51.4% involved taxon pairs that showed concerted directions of shift in tem-

poral occurrence windows (including pairs where both taxa showed no shift), 45.3% were between taxon pairs where only one taxon showed shift, and only 3.3% involved taxon pairs that showed opposite directions of shifts (Fig. 4b; Table S6). Thus, even given concerted shifts in temporal occurrence windows between constituent taxa, changes in the span of taxa's temporal overlap could still widely ensue following these window shifts. For 81.8% of time series, the direction of

intertaxonomic overlap change corresponded to that of the change in the span of temporal occurrence windows of at least one constituent taxon (Table S7); the vast majority of the observed intertaxonomic overlap changes were thus at least in part due to taxa's altered span of temporal occurrence windows.

Discussion

Our results show that climate change is associated with community-wide changes in intertaxonomic temporal overlap (Fig. 4a) through phenological shifts that alter the timing and/or span of the temporal occurrence windows of one or both constituent taxa (Fig. 4b). This finding does not represent temporal co-occurrence at the species level and/or species interactions, but ecological interactions such as competition and predation are implied by certain taxon pairs that exhibited changed temporal overlap (e.g., frog-toad, and cuckoo-cricket). In addition, the prevalence of observed temporal overlap changes suggests that temporal overlap change could be widespread among species within ecological communities (Todd *et al.*, 2011; Burkle *et al.*, 2013; Iler *et al.*, 2013; CaraDonna *et al.*, 2014). Recent understanding of the phenological responses to climate change at the levels of individual species (Menzel *et al.*, 2006), interacting species pairs (Visser *et al.*, 1998; Both *et al.*, 2006), ecological networks (Both *et al.*, 2009; Burkle *et al.*, 2013) and communities (Edwards & Richardson, 2004; Ovaskainen *et al.*, 2013) provides strong reasons to expect that climate change may extensively influence species temporal overlap patterns. Given that the temporal dimension of species co-occurrence is a fundamental component of species interactions and community assembly and functioning, our finding highlights the largely overlooked and potentially consequential temporal pathway through which climate change can influence community assembly (CaraDonna *et al.*, 2014) and in turn exert secondary ecological impacts (Nakazawa & Doi, 2012).

While our decision to collapse species/taxa in the original data set into organizational taxa was necessary under data quality constraints and did not mix different species/taxa into the same time series, it may have considerably increased the among-site variability of phenological signals within taxa and/or taxon pair and overall rendered more conservative findings (Figs 3 and 4) than would have been detected at the species level. For reasons pertaining to the distribution range of species and uneven data availability on a given species/taxon among sites, the same taxon and/or taxon pair were almost certain to involve varying identities of species or combinations of species across sites given the

wide geographical extent of China (e.g. Ge *et al.*, 2014). It is highly likely that the phenology of different species could respond to different climatic or environmental cues (e.g. temperature vs. photoperiod vs. precipitation; Forrest & Miller-Rushing, 2010; Pau *et al.*, 2011) and exhibit varying directions and/or levels of sensitivity to climate change (e.g., Parmesan, 2006; Ovaskainen *et al.*, 2013). For patterns of phenological shifts, their relationships with climate, and intertaxonomic temporal overlap, the 'shifting identity' of taxa and/or taxon pairs among sites is thus almost certain to increase among-site variability (Fig. S3), and dilute the overall across-country signals and underlie at least some of the non-significant findings in Figs 3 and 4a.

Our study suggests that current scope of discussion about the ecological consequences of phenological shifts under climate change ought to be expanded. For one thing, echoing previous findings (Todd *et al.*, 2011; Iler *et al.*, 2013), we found that intertaxonomic temporal overlap was predominantly prolonged rather than shortened, at least in part resulting from the predominantly prolonged temporal occurrence windows of the taxa involved. If prolonged temporal occurrence windows of species or their life stages in communities is common under climate change as generally understood (Roy & Sparks, 2000; Dunne *et al.*, 2003), the dependence of interspecific temporal overlap on the length of species' temporal occurrence windows should provide a safeguard against interspecific phenological mismatch unless there are dramatic interspecific asynchronies in species' phenological shifts. Climate change thus may have led to less phenological mismatch than generally presumed (Hegland *et al.*, 2009; Bartomeus *et al.*, 2011; Ovaskainen *et al.*, 2013). This conclusion, however, may not apply to the more nuanced, functional level of phenological mismatch such as the mismatch of peak activity timing (Visser *et al.*, 1998; CaraDonna *et al.*, 2014).

Second, of the observed changes in intertaxonomic temporal overlap, we found that $\geq 50\%$ ensued despite concerted phenological shifts of constituent taxa. These findings, together with the hypothetical scenarios illustrated in Fig. 1a, suggest that changed intertaxonomic temporal overlap and its associated ecological consequences (Encinas-Viso *et al.*, 2012) could ensue even under concerted phenological shifts. The ecological significance of phenological shifts under climate change has traditionally been tied almost exclusively to asynchronous shifts and the resultant loss of interspecific temporal overlap (Memmott *et al.*, 2007; Hegland *et al.*, 2009; Rafferty *et al.*, 2014). Our findings suggest that the context under which to discuss the ecological consequences of phenological shifts should be expanded beyond asynchronous shifts.

Phenological shifts are among the most sensitive and best documented ecological signatures of climate change (Parmesan, 2006; Rosenzweig *et al.*, 2008). However, how such shifts translate into ecological and evolutionary consequences across levels of biological organization largely remains an open question (Encinas-Viso *et al.*, 2012; Burkle *et al.*, 2013). At the center of such translation are ecological interactions, based crucially on species' spatial and temporal co-occurrence. Based on our findings, we therefore suggest that phenological research in the context of climate change must pay more attention to understanding how species' temporal overlap patterns and in turn, interactions, are affected by climate change at the community level.

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Availability of supporting data and analysis scripts

The data set and analysis scripts supporting the results of this article have been, respectively, deposited at Dryad repository (unique persistent identifiers and hyperlink to data set in <http://dx.doi.org/10.5061/dryad.68184>) and github (accessible at: <https://github.com/yangliubnu/PhenologyChina>).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Simulation of interspecific temporal overlap change as a result of phenological shifts.

Appendix S2. Description of data collection protocol and summary of original and trimmed phenological data set.

Table S1. List of taxa and their respective number of phenological records in the original data set transcribed from the National Meteorological Information Center of China.

Table S2. List of operational taxa/taxon pairs and their respective number of phenological time series records used in analysis under four different sets of trimming criteria.

Appendix S3. Supplementary methods.

Table S3. Cut-off distance for phenological events of different taxa/taxon pairs above which time series were considered not to be spatially autocorrelated, with corresponding size of subsampled data sets.

Figure S1. Correlograms of time series for phenological trend over time for each taxon-/taxon pair-phenological event combination that were identified to have spatial autocorrelation issues (i.e. cut-off distance >0).

Figure S2. Correlograms of time series for the relationship between phenological events and average minimum daily temperature for each taxon-/taxon pair-phenological event combination that were identified to have spatial autocorrelation issues (i.e. cut-off distance >0).

Appendix S4. Supplementary results.

Table S4. Number of time series for each taxon that exhibited advanced (–) and delayed (+) phenological shift between 1981 and 2009.

Table S5. Number of time series that showed decrease (–) and increase (+) in the span of temporal overlap between taxon pairs between 1981 and 2009.

Table S6. Classification of time series that showed change in inter-taxonomic temporal overlap according to the shift patterns of temporal occurrence windows of constituent taxa.

Table S7. Comparison of the direction of temporal overlap change between taxon pairs with the directions of change in the span of temporal occurrence windows of constituent taxa.

Table S8. Advanced (–) and delayed (+) trends or negative (–) and positive (+) relationships between phenology and average minimum daily temperature suggested by individual linear regressions based on different sub-data sets under progressively stricter trimming criteria.

Table S9. Overall patterns of taxon-level phenological response from linear mixed models based on different sub-data sets under progressively stricter trimming criteria.

Table S10. Overall patterns of temporal overlap change between taxon pairs from linear mixed models based on different sub-data sets under progressively stricter trimming criteria.

Figure S3. Trend of phenological shift by taxon at each site as measured by number of days shifted per year.

Figure S4. Lack of statistically significant patterns of phenological shift over time (a) and relationship between phenology and average minimum daily temperature (b) for four taxa that had extremely small sample sizes after subsampling (i.e. those marked with †) was likely due to low statistical powers.