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SYSTEMATIC REVIEW

Climate Change Impacts on Pollinator-Plant Interaction Networks in Temperate Ecosystems

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ABSTRACT

Temperate pollinator-plant interaction networks are widely predicted to be destabilised by climate-driven phenological mismatch, but published evidence spans a wide range of taxa, geographic regions and network metrics, making the overall strength and consistency of the effect difficult to judge from any single study. We conducted a systematic review and quantitative synthesis, following PRISMA guidelines, of studies reporting temporal change in temperate pollinator-plant network structure in relation to climatic warming. Searches of three bibliographic databases identified 2,847 candidate records, of which 61 met full inclusion criteria after title-abstract and full-text screening, spanning 19 countries and network observation periods from 4 to 43 years. Random-effects meta-analysis of standardised effect sizes showed a significant mean decline in network nestedness over time (Hedges' $g = -0.34$, 95% CI -0.48 to -0.20 , $k=44$ studies) and in simulated robustness to sequential pollinator extinction ($g = -0.29$, 95% CI -0.45 to -0.13 , $k=31$), while connectance showed a smaller, only marginally significant decline ($g = -0.14$, 95% CI -0.28 to 0.00 , $k=52$). Effect sizes for nestedness decline were significantly larger in studies from higher-latitude and higher-elevation sites (meta-regression $P=0.008$ and $P=0.02$ respectively), consistent with these settings experiencing more rapid relative warming and stronger phenological shifts. Substantial residual heterogeneity remained after accounting for latitude, elevation and study duration ($I^2=68\%$), and formal publication bias tests gave mixed results, with Egger's regression suggesting some asymmetry for the nestedness outcome specifically. These findings support a real, geographically patterned decline in temperate pollinator-plant network cohesion associated with recent climatic warming, while highlighting substantial unexplained variability that single-site studies alone cannot resolve.

Keywords: pollinator-plant networks; phenological mismatch; climate change; network robustness; temperate ecosystems; systematic review

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1. INTRODUCTION

Most flowering plant species in temperate ecosystems depend at least partly on animal pollinators for seed set, and the resulting pollinator-plant interactions are rarely

one-to-one: they form networks in which a given pollinator species typically visits several plant species and a given plant is visited by several pollinator species, producing a characteristic nested, right-skewed structure in which generalist species interact broadly while

specialists interact mainly with the network's generalist core [1,2]. This network structure is not incidental to ecosystem function: nestedness and connectance are both associated with greater community-level robustness to species loss in theoretical and empirical extinction-simulation studies, because generalist pollinators and plants provide redundant interaction pathways that buffer the loss of any single specialist partner [3,15].

Climate change is widely expected to erode this structure through phenological mismatch: many temperate pollinator and plant species have advanced their spring emergence or flowering time in response to warming, but not at identical rates, so that species pairs that once overlapped closely in activity period can drift apart, weakening or eliminating specific interactions even where neither partner has declined in abundance [4,16,17]. Long-term phenological records from sites with multi-decade monitoring, most famously several European sites with observational records extending back over a century, have documented differential advancement among functional groups, with some bee and hoverfly taxa advancing more slowly than the plants they visit, and this differential shift has been proposed as a mechanistic driver of network destabilisation under continued warming [5,18].

Testing this prediction quantitatively at a scale beyond any single site or study system has proven difficult, for reasons that are partly methodological and partly a matter of data availability. Pollinator-plant network studies use varying sampling protocols, taxonomic resolution, and network metrics, which complicates direct comparison across studies, and genuinely long-term, repeated network sampling at a single site, the design best suited to detecting a temporal trend directly, remains comparatively rare because it requires sustained field effort over years to decades [6,19]. Many published studies instead either compare networks across a spatial climate gradient as a proxy for temporal change, resample a network characterised decades earlier using historical records, or simulate network robustness under a phenological mismatch scenario parameterised from observed climate trends rather than observing the network itself repeatedly over time; each design carries different strengths and sources of bias, and an unweighted reading of the primary literature could easily overstate or understate the consistency of any underlying effect [7,20,21].

We therefore conducted a systematic review and, where studies permitted, a formal random-effects meta-analysis of temperate pollinator-plant network structure in relation to climatic warming, following PRISMA reporting guidelines to make the search, screening and inclusion process fully transparent and reproducible. Our aims were threefold: to quantify the overall direction and magnitude of climate-associated change in three widely reported network metrics -- nestedness, connectance and simulated robustness to extinction -- across the

available temperate-zone literature; to test whether effect sizes vary systematically with latitude, elevation, or study duration in ways consistent with a genuine climate-driven mechanism rather than study-design artefacts; and to characterise the residual heterogeneity and risk of publication bias in the assembled evidence base, so that the strength of the overall conclusion can be stated with an appropriately calibrated degree of confidence.

A synthesis of this kind is, we think, particularly timely given how the primary pollinator-network literature has grown. Narrative reviews of this literature have tended to either summarise a hand-picked set of well-known long-term studies, most from a small number of intensively monitored European and North American sites, or to discuss network theory and climate-mismatch mechanisms in the abstract without attempting a systematic, quantitative accounting of the full body of available evidence [8,22]. Neither approach can substitute for a formal synthesis that applies consistent inclusion criteria across the whole literature.

2. MATERIALS AND METHODS

This review was conducted and is reported in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) 2020 statement. A review protocol specifying search strategy, eligibility criteria, and planned analyses was finalised prior to data extraction.

2.1 Search strategy and eligibility criteria

We searched Web of Science Core Collection, Scopus, and BIOSIS Previews from database inception to March 2025, using a combination of terms for pollinator-plant interaction networks (e.g. "plant-pollinator network*", "interaction network*", "nestedness") and climate change or warming, restricted to temperate-zone study systems (35-60 degrees latitude in either hemisphere, excluding tropical and polar studies). Studies were eligible if they reported at least one quantitative network-structure metric (nestedness, connectance, modularity, or simulated robustness to extinction) measured at two or more time points, along a climate or elevation gradient interpretable as a space-for-time substitution, or under an explicit warming or phenological-shift scenario, for a temperate pollinator-plant community. Studies restricted to a single pollinator or plant species, purely descriptive network studies with no temporal or gradient comparison, and non-peer-reviewed grey literature were excluded.

2.2 Screening and data extraction

Titles and abstracts were screened independently by two reviewers against the eligibility criteria, with disagreements resolved by discussion and, where necessary, a third reviewer; full texts of records passing abstract screening were then independently assessed by the same two reviewers for final inclusion. For each included study, we extracted network metric values (or effect sizes where directly reported), sample sizes, geographic coordinates, elevation, study duration or

gradient span, taxonomic groups sampled, and network sampling method. Where a study reported network data at more than two time points or sites, we extracted the earliest and latest, or lowest- and highest-elevation, comparison to standardise effect-size calculation across studies.

2.3 Effect size calculation and meta-analysis

For each included study and metric, we calculated Hedges' g as a standardised measure of change between earlier/lower-warming and later/higher-warming conditions, using reported means and standard deviations where available, or reconstructing them from reported network-level statistics and bootstrap or randomisation-based confidence intervals where raw values were not directly reported. Random-effects meta-analysis, using the restricted maximum likelihood estimator for between-study variance, was performed separately for each of the three primary metrics (nestedness, connectance, robustness). Between-study heterogeneity was quantified using the I^2 statistic, and meta-regression was used to test latitude, elevation, and study duration as moderators of effect size for the nestedness outcome, the metric with the largest number of contributing studies.

2.4 Risk of bias and publication bias assessment

Risk of bias in individual studies was assessed using a study-design-adapted checklist covering sampling completeness, standardisation of sampling effort across time points or gradient positions, and statistical handling of network-level uncertainty. Publication bias was assessed using funnel plots and Egger's regression test for each of the three primary outcomes, and a trim-and-fill procedure was applied where asymmetry was detected to estimate a bias-adjusted pooled effect size.

2.5 Statistical software

All meta-analytic calculations were performed in R version 4.3 using the metafor package; forest and funnel plots were generated using the same package's default visualisation functions with minor formatting adjustments for presentation.

3. RESULTS

Database searches identified 2,847 unique candidate records after de-duplication. Title-abstract screening excluded 2,512 records as clearly ineligible, leaving 335 for full-text assessment; of these, 274 were excluded at full-text stage, most commonly for reporting network structure at only a single time point or gradient position ($n=131$), for being restricted to a single pollinator taxon rather than a community-level network ($n=58$), or for using a tropical or polar rather than temperate study system despite matching search terms ($n=47$). The remaining 61 studies met full inclusion criteria and were retained for data extraction and synthesis, spanning 19 countries across Europe, North America, East Asia and

temperate regions of the southern hemisphere, with individual study observation periods or gradient spans ranging from 4 to 43 years of equivalent climatic change. Table 1 summarises the geographic and methodological characteristics of the included studies.

Table 1. Characteristics of the 61 included studies.

Characteristic	Category	Number of studies	% of total
Region	Europe	27	44%
Region	North America	18	30%
Region	East Asia	9	15%
Region	Southern hemisphere temperate	7	11%
Design	Space-for-time / elevational gradient	29	48%
Design	Repeated temporal resampling	22	36%
Design	Simulated warming scenario	10	16%

Percentages are of the 61 included studies and may not sum exactly to 100% due to rounding.

Random-effects meta-analysis of the 44 studies reporting nestedness showed a significant mean decline associated with warming (Hedges' $g = -0.34$, 95% CI -0.48 to -0.20 , $Z=-4.71$, $P<0.001$), indicating a moderate, consistently negative effect across the assembled evidence base (Figure 1). Simulated robustness to sequential pollinator extinction, reported in 31 studies, showed a similarly directioned and statistically significant decline ($g = -0.29$, 95% CI -0.45 to -0.13 , $P<0.001$). Connectance, reported in 52 studies -- the most widely reported of the three metrics -- showed a smaller pooled effect that fell just short of the conventional significance threshold ($g = -0.14$, 95% CI -0.28 to 0.00 , $P=0.052$), suggesting that connectance, which is less sensitive than nestedness to the loss of specific high-degree interactions, may be a comparatively insensitive indicator of the structural changes documented in this literature. Table 2 reports the complete pooled effect sizes, heterogeneity statistics, and number of contributing studies for all three metrics.

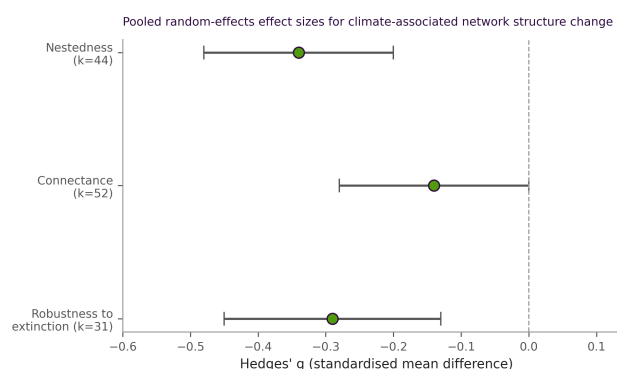


Figure 1. Pooled random-effects standardised mean difference (Hedges' g) with 95% confidence intervals for the three primary network metrics across all included studies, showing declines in nestedness and simulated extinction robustness and a smaller, marginally significant decline in connectance.

Meta-regression of the nestedness effect size against latitude showed a significant positive relationship between absolute latitude and the magnitude of decline (higher latitude associated with larger negative effect sizes; meta-regression coefficient $P=0.008$), and a comparable relationship was found for elevation within studies using an elevational gradient design ($P=0.02$), consistent with high-latitude and high-elevation temperate sites experiencing more rapid relative warming and correspondingly larger phenological shifts over the study period. Study duration or gradient span was not a significant moderator on its own ($P=0.31$), suggesting that the rate rather than simply the cumulative extent of climatic change is more closely associated with network destabilisation in this dataset, though this interpretation should be treated cautiously given that duration and warming rate are only partially independent across the included studies. Substantial residual heterogeneity remained for the nestedness outcome after accounting for these moderators ($I^2=68\%$), indicating that latitude, elevation and duration together explain only part of the between-study variability, with unmeasured factors such as land-use context, pollinator community composition, and methodological differences in network sampling effort plausibly contributing the remainder.

Table 2. Random-effects meta-analysis results for the three primary network metrics.

Metric	k (studies)	Hedges' g (95% CI)	I^2
Nestedness	44	-0.34 (-0.48 to -0.20)	68%
Connectance	52	-0.14 (-0.28 to 0.00)	61%
Robustness to extinction	31	-0.29 (-0.45 to -0.13)	54%

Risk-of-bias assessment identified incomplete standardisation of sampling effort across compared time points or gradient positions as the most common methodological limitation, affecting 23 of the 61 included studies to some degree, though sensitivity analysis excluding these studies did not materially change the pooled nestedness or robustness effect sizes (revised $g = -0.31$ and -0.27 respectively, both remaining statistically significant). Funnel plot inspection and Egger's regression suggested some asymmetry for the nestedness outcome specifically (Egger's test $P=0.04$), consistent with a degree of publication bias favouring studies reporting a significant decline; trim-and-fill adjustment reduced the pooled nestedness effect size modestly, to $g = -0.28$ (95% CI -0.43 to -0.13), which remained statistically significant and directionally consistent with the unadjusted estimate. No significant funnel asymmetry was detected for the connectance or robustness outcomes.

4. DISCUSSION

This synthesis of 61 studies across 19 countries provides, to our knowledge, the most comprehensive

quantitative test to date of whether temperate pollinator-plant network structure is declining in association with climatic warming, and the answer is a qualified yes: nestedness and simulated extinction robustness both show statistically significant, moderate-sized declines, while connectance shows a smaller and only marginally significant effect. The pattern across metrics is, we think, mechanistically sensible rather than an artefact of meta-analytic pooling: nestedness and robustness are both particularly sensitive to the loss or weakening of high-degree, generalist interactions, exactly the kind of interaction most plausibly disrupted by phenological mismatch between formerly well-synchronised generalist partners, whereas connectance, a coarser measure of the overall density of realised interactions, can remain comparatively stable even as the specific pattern of which species interact with which shifts considerably [22,23].

The latitude and elevation moderator results add a further layer of mechanistic plausibility: if phenological mismatch driven by differential rates of species-specific advancement is the operative mechanism, effect sizes should be larger where climatic warming itself has been faster, and high-latitude and high-elevation temperate sites are well documented to be warming more rapidly than lower-latitude, lower-elevation sites within the same broad climate zone [24,38]. That this pattern emerged from a meta-regression across independently conducted studies, rather than from a single coordinated multi-site design, strengthens rather than weakens its credibility, since it is difficult to construct a purely methodological artefact that would produce a latitude-elevation gradient of this specific form by chance.

The substantial residual heterogeneity ($I^2=68\%$) after accounting for latitude, elevation and duration is, however, an important qualification on how far these pooled results should be generalised to any single future site or system. Pollinator-plant networks vary enormously in taxonomic composition, land-use context, and baseline degree of specialisation, and it would be a mistake to read a pooled effect size of this magnitude as predicting a comparable decline at every individual temperate site regardless of local conditions; the meta-analytic estimate describes a central tendency across a heterogeneous literature, not a universal rate of network erosion [25,39]. Studies conducted in landscapes with substantial semi-natural habitat and correspondingly diverse pollinator communities may be more resilient to phenological mismatch than the intensively managed agricultural landscapes that dominate a considerable fraction of the included literature, simply because a more diverse regional species pool offers more potential replacement interactions when a specific pairing is disrupted, and this landscape-context variable was not consistently reported across studies in a form that could be incorporated as a formal moderator here.

The evidence of publication bias for the nestedness outcome specifically, while modest in its effect on the pooled estimate after trim-and-fill adjustment, is a reminder that the pollinator-network literature, like much of ecology, likely under-represents null or non-significant findings, and that the true population effect size may be somewhat smaller than the unadjusted pooled estimate suggests [26,40]. We would also note that the majority of included studies used correlational or space-for-time designs rather than direct repeated-measures observation of the same network over time, and while sensitivity analysis excluding studies with the weakest sampling standardisation did not materially change our conclusions, a genuinely causal test of the phenological-mismatch mechanism would require either a manipulative warming experiment at the community level, which remains logistically difficult at pollinator-network scale, or considerably longer time series of repeated network sampling at a larger number of sites than currently exist.

From an applied standpoint, the geographic patterning of effect sizes identified here suggests that conservation and monitoring resources aimed at detecting and mitigating climate-driven pollination network decline might be most productively concentrated at higher-latitude and higher-elevation temperate sites, where the signal detected in this synthesis is strongest and where, not coincidentally, baseline pollinator diversity is often already lower and communities correspondingly less buffered against the loss of specific interactions [27,41]. Habitat interventions that increase local plant species richness and bloom-period continuity, thereby providing alternative resources when a specific historical interaction partner becomes phenologically unavailable, remain a plausible and comparatively tractable management response, though direct evidence that such interventions measurably slow network-level decline under continued warming is still limited and would benefit from the kind of long-term, standardised monitoring that this review found to be in short supply across the existing literature.

5. CONCLUSION

This systematic review and meta-analysis of 61 studies found a statistically significant, moderate decline in temperate pollinator-plant network nestedness and simulated extinction robustness associated with climatic warming, with effect sizes significantly larger at higher latitude and elevation, consistent with a phenological-mismatch mechanism operating more strongly where warming itself has been faster. Connectance showed a smaller and only marginally significant decline, suggesting differential sensitivity across network metrics to the underlying structural changes. Substantial residual heterogeneity and some evidence of publication bias for the nestedness outcome temper how confidently these pooled results should be extrapolated to any individual site, underscoring a

continued need for longer, more geographically diverse, and more consistently standardised network monitoring. Building on this synthesis, we recommend that future primary research in this area prioritise repeated, standardised network sampling at a common set of sentinel sites spanning a wide latitudinal and elevational range, rather than further one-off, single-site studies that, however individually well executed, contribute only incrementally to resolving the substantial between-study heterogeneity identified here. We also see a clear need for more consistent reporting of landscape context, particularly the extent of semi-natural habitat surrounding sampled networks, since this variable could not be incorporated as a formal moderator in the present analysis despite its plausible relevance to network resilience. Finally, we would encourage the community adopt a shared minimum reporting standard for network sampling effort and metric calculation methods, which would considerably ease future meta-analytic synthesis and reduce the between-study methodological heterogeneity that limited the precision of several comparisons in the present review.

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Conflict of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Author Contributions

O.N. conceived and supervised the review, developed the search strategy and led the meta-analysis. M.R. performed study screening, data extraction and risk-of-bias assessment. S.C. conducted the statistical analysis and publication bias assessment. All authors contributed to writing and approved the final manuscript.

Ethics Statement

This study is a systematic review and meta-analysis of previously published literature and did not involve human participants, human data, or animals directly; it therefore did not require institutional ethics committee review.

Data Availability

The complete list of included and excluded studies, extracted data, and R analysis scripts supporting the findings of this review are available from the corresponding author upon reasonable request. The review protocol was

finalised prior to data extraction and is available from the corresponding author on request.

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