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Ecology LETTER

Gymnosperm host expansion in the fall webworm challenges global quarantine frameworks

Kai Tang,[1,5] Mao Lin,[1,5] Dejun Hao,[3] Letian Xu,[4,*] and Shouke Zhang[1,2,*]

[1]State Key Laboratory for Development and Utilization of Forest Food Resources, Zhejiang A & F University, Hangzhou 311300, China

[2]Zhejiang Key Laboratory of Non-wood Forest Products Quality Regulation and Processing Utilization, Zhejiang A & F University, Hangzhou 311300, China

[3]College of Forestry, Co-Innovation Center for the Sustainable Forestry in Southern China, Nanjing Forestry University, Nanjing 210037, China

[4]State Key Laboratory of Biocatalysis and Enzyme Engineering, School of Life Sciences, Hubei University, Wuhan 430062, China

[5]These authors contributed equally

*Correspondence: letian0926@163.com (L.X.); socrazhang@zafu.edu.cn (S.Z.)

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Dear Editor,

Invasive herbivores are shattering phylogenetic barriers assumed to limit their host ranges. The colonization of cupressaceous conifers by the fall webworm in East China exposes a critical blind spot in global phytosanitary protocols and implies a "sleeping giant" of pre-adapted traits threatening forests beyond Asia.

The capacity of invasive species to exploit novel resources determines their ecological impact and management difficulty.[1,2] For over a century, the fall webworm (*Hyphantria cunea*), a super-generalist moth native to North America, has been characterized globally as a defoliator of broadleaf angiosperms.[3,4] With a documented host range exceeding 600 species, it is a quintessential polyphage.[5] However, pest risk analyses (PRAs) and quarantine protocols worldwide have largely operated under the assumption that gymnosperms—specifically conifers—represent a negligible resource pool. Here, we present evidence that *H. cunea* has successfully bridged the 300-million-year phylogenetic distance between angiosperms and gymnosperms to complete its full life cycle on *Taxodium distichum* and support adult emergence on the endangered relict gymnosperm *Metasequoia glyptostroboides* in East China. This shift directly imperils the wild populations of the endangered relict gymnosperm *M. glyptostroboides*, representing a significant setback for the genetic diversity conservation targets mandated by the Kunming-Montreal Global Biodiversity Framework (KM-GBF).[6]

ECOLOGICAL FITTING: RE-AWAKENING ANCIENT TRAITS

Historically, the exclusion of conifers from the primary host list of *H. cunea* appeared well-founded.[5] While sporadic feeding on bald cypress (*T. distichum*) has been recorded in its native range, these events were often viewed as "spillover" rather than sustainable colonization.[3] However, our multi-year surveillance in the Yangtze River Delta (2020–2023) indicates a shift from incidental feeding to sustained population establishment.[3] We documented *H. cunea* establishing larval web nests, feeding, and pupating on *T. distichum* and, most alarmingly, on the endangered relict gymnosperm (*M. glyptostroboides*), a "living fossil" native to China (Figure 1).[3]

This rapid colonization likely represents a case of ecological fitting rather than *de novo* evolution. The concept of ecological fitting posits that organisms can colonize novel environments by co-opting existing traits evolved in a different context.[4] *H. cunea* shares an evolutionary history with *Taxodium* in North American wetlands. We hypothesize that the metabolic machinery required to detoxify conifer defenses—such as specific cytochrome P450 monooxygenases or gut symbionts capable of degrading terpenoids—has been retained as a latent "sleeper trait" within the species' genome. In the invasive range, where nonnative pests can exert substantial impacts on forest biomass and ecosystem function,[7] ancestral pre-adaptations may be further amplified under phenological mismatch or intensified host competition. Beyond mere establishment, we observed a distinct behavioral shift in nest architecture on these novel hosts. While nests on broadleaf trees are typically voluminous and globose, those on *T. distichum* and *M. glyptostroboides* exhibited a more compact, elongated morphology, tightly appressed to the branchlets.[1,4] This architectural plasticity maximizes structural integrity and protective coverage despite the reduced surface area of individual needles, illustrating how behavioral tracking facilitates the exploitation of evolutionarily distant lineages.

Crucially, laboratory rearing assays confirm that this host shift involves a classic life-history trade-off (Figure 1). Larvae reared on *Taxodium* and *Metasequoia* required approximately 15.6% and 42.8% more time (Figure 1C), respectively, to reach the seventh instar than those on preferred angiosperms, yet pupal eclosion remained relatively high on *Taxodium* and still exceeded 50% on *Metasequoia* (Figure 1D_2). This phenotype is indicative of a bet-hedging strategy: sacrificing rapid growth for survival on a suboptimal but abundant resource. Notably, although survival to adulthood on *Metasequoia* remained high, the lack of laboratory oviposition (Figure 1$E_{1\text{-}2}$) suggests that it currently acts as a marginal host or larval sink. This strategy helps reconcile the discrepancy between our laboratory findings and field observations. This plasticity allows the invader to utilize gymnosperms as "potential hosts" or "bridge resources", facilitating persistence when preferred hosts are unavailable. In this context, the role of *Metasequoia* as a cryptic reservoir may be particularly important. The possibility of completing a full life cycle in the field, potentially via compensatory cross-host feeding, warrants further investigation.

A TRANS-CONTINENTAL THREAT: FROM ASIA TO EUROPE

The implications of this niche expansion extend far beyond East China. *H. cunea* is firmly established across Europe, having invaded over 20 countries since the 1940s.[4,5] European landscapes are punctuated by ornamental and native Cupressaceae, including the iconic Italian cypress (*Cupressus sempervirens*) and various *Juniperus* species. If the capacity to feed on Cupressaceae is an intrinsic trait of the *H. cunea* lineage (an outcome of ecological fitting) rather than a unique mutation in the Chinese population, then European conifer forests and urban green infrastructures sit on a similar precipice. Given the continued rise of emerging alien species from newly accessible source pools,[8] current monitoring in Europe, still largely informed by traditional host assumptions, would likely miss early infestation signals on these putative "non-host" trees. The convergence of this cryptic host potential with the widespread planting of susceptible ornamental conifers creates a vast, unmonitored highway for secondary spread across the Eurasian continent.[9]

IMPLICATIONS FOR THE GLOBAL BIODIVERSITY FRAMEWORK

The realization that *H. cunea* can sustain populations on Cupressaceae challenges the static nature of current biosecurity lists. The Kunming-Montreal Global Biodiversity Framework (KM-GBF), adopted in 2022, aims to reduce the rate of introduction and establishment of invasive alien species by at least 50% by 2030 (Target 6),[6] alongside preventing the introduction of priority species and strengthening pathway management. Achieving this target requires predictive tools that can anticipate host shifts before they result in ecological catastrophe.

Current risk models for *H. cunea* typically overlay the pest's climatic niche with the distribution of known broadleaf hosts (> 600 spp. broadleaf angiosperms).[5,6,10] By ignoring the potential for conifer utilization, these models systematically underestimate the area at risk. In China alone, where coniferous forests comprise approximately one-third of the total plantation area (exceeding 26 million hectares), the inclusion of Cupressaceae into the host matrix expands the threatened area by millions of hectares. Furthermore, globally distributed ornamental conifers, such as *Metasequoia* planted

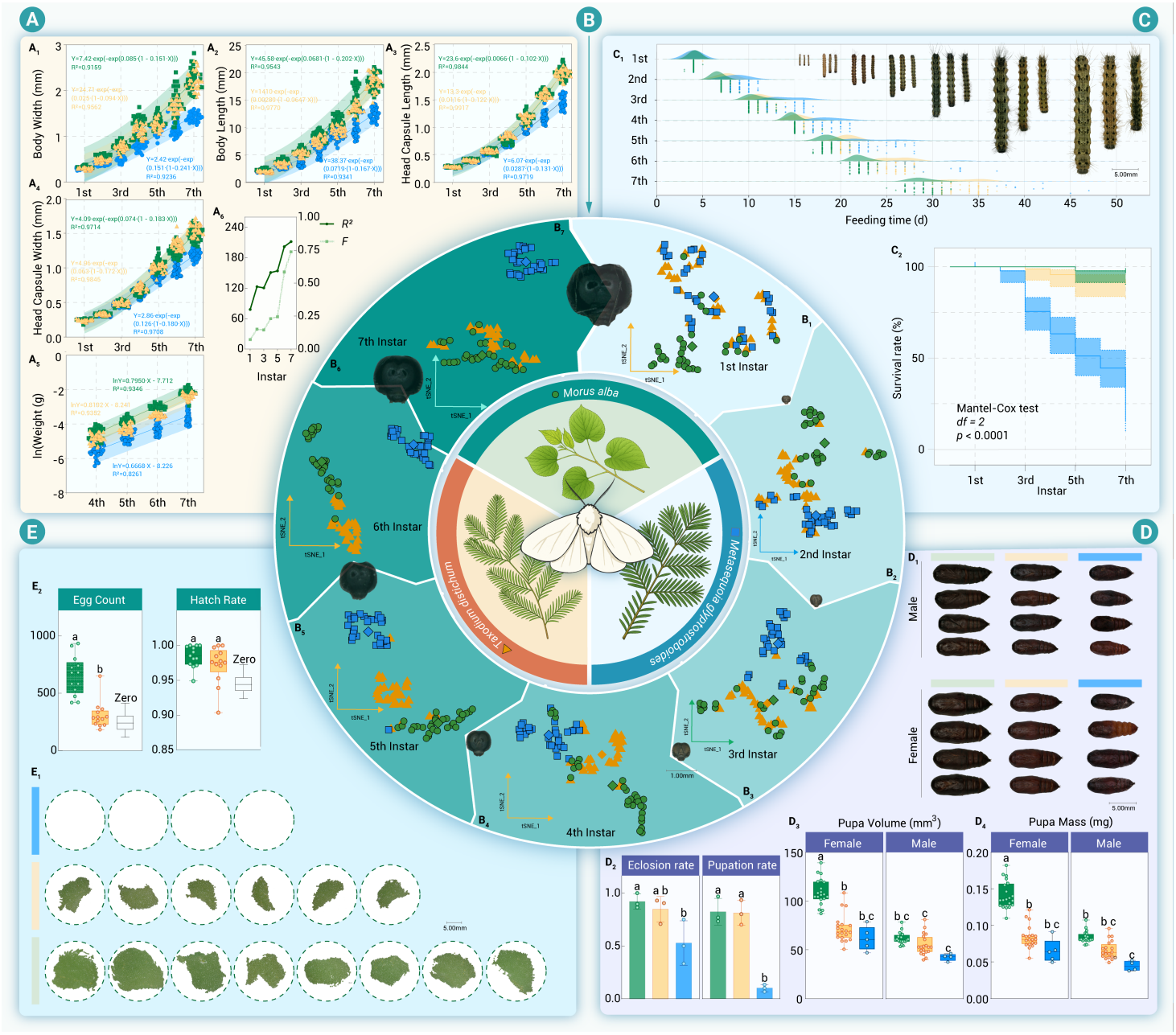

Figure 1. Host plant quality shapes the developmental trajectory and fitness landscape of *Hyphantria cunea* (A_{1-5}) Ontogenetic growth curves for five morphometric traits across seven instars (L1–L7) on *Morus alba* (green), *Taxodium distichum* (orange), and *Metasequoia glyptostroboides* (blue). Lines represent Gompertz model fits ($R^2 > 0.75$, $P < 0.05$); shaded regions indicate 95% confidence intervals ($n = 30$). (A_6) Quantitative assessment of host-driven phenotypic divergence using PERMANOVA. The Pseudo-F statistic (separation strength, left y-axis) and R^2 (explained variance, right y-axis) increase with instar, indicating cumulative phenotypic plasticity. (B_{1-7}) t-SNE visualization of multidimensional morphometric space (5 traits in panel A) across development. Each point represents a single larva, illustrating systemic phenotypic restructuring initiated at L2. (C_1) Rain-cloud plots displaying the distribution of developmental duration for each instar (density estimation, box plot with median and IQR, and jittered raw data). Note the increased variance and right-skewed delay in conifer-fed larvae. (C_2) Kaplan-Meier survival curves for larvae from hatching to pupation (Log-rank (Mantel-Cox) test, $n = 90$). Shaded bands represent 95% confidence intervals. (D_1) Representative pupal morphology. (D_2) Comparative pupation and eclosion rates (One-way ANOVA, Tukey's HSD). Bars represent means ± SEM ($n = 3$, 30 larvae per replicate). (D_{3-4}) Pupal mass and volume metrics. Box plots show median, interquartile range (box), and full range (whiskers). $n = 15$ for *Morus*/*Taxodium*; $n = 4$-5 for *Metasequoia*. (E_1) Representative egg masses produced by adults from different larval host treatments; dashed circles indicate the absence of oviposition. (E_2) Reproductive output (fecundity and hatch rate, $n = 13$ pairs) (One-way ANOVA, Tukey's HSD). "Zero" indicates no oviposition observed. Different letters denote significant differences ($P < 0.05$).

in parks from Milan to Tokyo, not only serve as unrecognized reservoirs for the pest but also form a highly connected network of ornamental hosts. This connectivity amplifies invasion risks, as these trees may act as ecological "stepping stones" for secondary spread following the breach of host-utilization barriers, thereby compromising current containment paradigms focused solely on broadleaf trees.[10]

A CALL FOR DYNAMIC BIOSECURITY

To align with the ambitious goals of the KM-GBF, the international phytosanitary community must pivot from reactive host logging to proactive, trait-based risk assessment. We propose three urgent actions:

Redefine sentinel surveillance

National plant protection organizations (NPPOs) and regional bodies (e.g., EPPO) must officially incorporate Cupressaceae into *H. cunea* monitoring protocols. Sentinel plantings in high-risk entry points in Europe and North America should include these taxa to detect early signs of host shifting.[10]

Genomic and microbial vigilance

Monitoring should move beyond simple species identification to tracking

functional genomic changes. Sequencing invasion-front populations for selection signatures in detoxification genes, such as cytochrome P450 monooxygenases specialized in degrading gymnosperm-specific terpenoids, or shifts in gut microbiome composition could serve as an early warning system for metabolic adaptation to novel hosts. Such molecular insights provide the necessary basis for trait-based risk assessments, enabling biosecurity frameworks to anticipate metabolic adaptation to novel hosts before widespread establishment occurs.

Conservation shielding

The verified threat to *M. glyptostroboides* necessitates immediate conservation triage. Protecting these relict populations from *H. cunea* is no longer a localized forestry issue but a global conservation priority under Target 6 of the KM-GBF. Immediate proactive intervention is required to shield these evolutionary legacies from the synergistic effects of habitat fragmentation and invasive-driven defoliation. Integrated Pest Management (IPM) plans for protected areas containing relict gymnosperms must now account for *H. cunea*.

The colonization of conifers by the fall webworm is not merely a biological curiosity; it is a signal of the evolutionary agility of invasive species. By viewing invasion through the lens of ecological fitting, we recognize that "new" hosts may simply be "forgotten" ones.[10] If our quarantine policies remain tethered to historical host lists, we will remain perpetually one step behind the invaders we seek to control.

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AUTHOR CONTRIBUTIONS

Shouke Zhang, Letian Xu, Kai Tang, Mao Lin, and Dejun Hao conceptualized the study. Shouke Zhang and Dejun Hao provided project administration. Kai Tang and Mao Lin conducted the experiments. Shouke Zhang, Letian Xu, Kai Tang, and Mao Lin wrote the original draft. Letian Xu and Shouke Zhang revised the manuscript. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

All data are available in the main text.