1   **Beyond Observed Diversity: A Completeness-Based Invasion Theory**

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11 *Abstract*

12 Charles Elton proposed that species-rich communities resist invasion better, but support is

13 mainly from local studies, possibly because studies use observed richness alone, ignoring the

14 dark diversity. I propose Completeness-Based Invasion Theory, linking invasibility inversely

15 to community completeness, an index linking observed and dark diversity, enabling unified

16 insights across scales.

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Observed diversity and alien plant invasion

Biological invasions pose a profound threat to global biodiversity, impacting nearly all terrestrial and aquatic ecosystems. Invasion outcomes are determined by two fundamental factors: the invasiveness of non-native species and the invasibility of recipient ecosystems. A key existing framework for invasiblity of recipient ecosystem is the classic diversity-invasibility hypothesis (Elton 1958), poisting that high native species diversity confers greater resistance to invasion. This resistance can emerge both within and across trophic levels (Huang et al. 2025). While influential, empirical support for this negative diversity-invasibility relationship is largely confined to local, experimental scales (Fridley et al. 2007). At broader scales, a positive correlation is frequently observed, where greater native diversity coincides with higher non-native species richness (Fridley et al. 2007). This scale-dependency constitutes the core of the invasion paradox, often attributed to a shift in underlying mechanisms from local species interaction to regional environmental filtering or dispersal limitation (Fridley et al. 2007). However, these contrasting patterns remain unresolved, likely because current approaches rely solely on observed native diversity, thereby overlooking the community's potential niche space and actual assembly state. To transcend this limitation and advance a scale-independent understanding, I propose a Completeness-Based Invasion Theory. This framework shifts the focus from observed diversity to community completeness (Pärtel et al. 2013), the degree to which a community's realized diversity fills its potential niche space, informed by dark diversity (Pärtel et al. 2011, Pärtel et al. 2025). By integrating these dimensions, our theory offers a unified mechanistic basis to resolve the invasion paradox and predict ecosystem susceptibility.

Community completeness: a unified index for observed diversity and its potential

Relying solely on observed species richness to infer the invasibility of recipient ecosystems represents a fundamental limitation in invasion ecology. This conventional approach fails to

consider the available species pool, thereby undermining comparisons across ecosystems and scales. The concept of dark diversity, introduced by Pärtel et al. (2011) and defined as the pool of species that are absent locally yet present in the regional species pool and ecologically suitable for the site, helps to address this gap by accounting for the missing component of biodiversity. Building on this, community completeness (Pärtel et al. 2013) can be derived as the ratio of observed diversity to potential diversity, reflecting the degree to which a community saturates its available niche space. In essence, completeness integrates observed and dark diversity into a single, scalable metric. By normalizing biodiversity relative to its potential, it allows for consistent comparisons across scales and systems. While the promise of this integrative framework for invasion ecology is mentioned by Pärtel et al. (2013), its specific theoretical utility requires further clarification. I propose that it offers a novel mechanistic basis for reconciling the invasion paradox, the discrepancy diversity–invasibility relationships across scales, and for reframing our understanding of ecosystem invasibility through the lens of niche saturation, rather than biodiversity alone.

Rethinking biological invasion through the lens of community completeness

To formalize this perspective, I propose a Completeness-Based Invasion Theory, which posits that ecosystem invasibility is inversely related to community completeness. In other words, higher community completeness confers greater invasion resistance (i.e., lower invasibility). This proposition aligns with empirical patterns across spatial scales. At small scales, high observed diversity typically coincides with low dark diversity, implying high completeness (Fløjgaard et al. 2020), as limited niche space restricts the pool of absent but suitable species. Therefore, the well-documented negative relationship between local diversity and invasibility corresponds to the resistance afforded by high completeness. In contrast, at large scales, high observed diversity is often associated with greater dark diversity and lower completeness (Wan and Wang 2025), because larger areas encompass greater habitat heterogeneity and thus a larger

pool of regionally suitable but locally absent species. Consequently, the positive diversity–invasibility relationship observed at broad scales mirrors the increased susceptibility linked to lower completeness. By integrating dark diversity and community completeness, this framework provides a coherent, scale-independent explanation for the invasion paradox. The only one supporting evidence comes from (Akatov and Akatova 2010), who found that plant communities with higher completeness exhibit lower invasibility. Further empirical and experimental studies are now needed to test and refine this theoretical proposition across different ecosystems and invasion contexts.

Important for biological invasion management

Integrating community completeness and dark diversity into invasion management advances the field toward a predictive science. This framework assesses an ecosystem's vulnerability by quantifying its completeness gap (i.e. the disparity between realized and potential biodiversity). Low completeness signals both high dark diversity and substantial vacant niche space, indicating elevated invasion risk. I propose that successful invaders likely fill these vacancies, yet their phylogenetic and functional relationships to dark diversity species may vary with the dominant invasion mechanism. Under environmental filtering and pre-adaptation, invaders may closely resemble dark diversity species; under competitive release or novel niche occupation, they may be phylogenetically and functionally distinct (Cadotte et al. 2018). This perspective enables proactive identification of high-risk invaders as those capable of exploiting specific ecological gaps. In restoration ecology, this approach strategically prioritizes the reintroduction of functionally key species revealed by community completeness to enhance both horizontal (within-trophic-level) completeness and vertical (cross-trophic-level) completeness, thereby strengthening community resistance across these complementary dimensions. For prevention, it directs monitoring and early-detection efforts toward non-native species within the dark diversity pool (Paganeli et al. 2025). Consequently, management shifts

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97 from reactive measures to theory-guided, proactive strategies aimed at building ecosystems

98 with intrinsic invasion resistance.

99 *Concluding remarks and future perspectives*

100 The concept of community completeness reframes ecosystem invasibility around the principle

101 of niche saturation, moving beyond the limitations of observed biodiversity alone. By shifting

102 focus from observed biodiversity to this integrative index, we can develop a unified, scale-

103 independent understanding of invasion resistance. While grounded in theory and emerging

104 evidence, this framework requires rigorous observational validation. A promising approach lies

105 in globally coordinated research employing standardized estimates of dark diversity but focus

106 on invaded communities by non-native species. Conceptually, this framework aligns with

107 empty niche theory (MacArthur 1970), addressing the critical question of available niche space

108 for invaders. Community completeness operationalizes this inquiry directly, offering a

109 quantifiable measure of an ecosystem's niche saturation and, consequently, its susceptibility to

110 invasion.

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117 **Declaration of interests**

118 The author declares no conflicts of interest.

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120 **Author contributions**

121 YL conceived the idea, design the framework of the study, and wrote the manuscript.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the writing process, the author used DeepSeek (www.deepseek.com/) to improve the

clarity and language of the manuscript. The author reviewed and edited the content as needed,

and take full responsibility for the content of the publication.

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Figure

Figure 1 Conceptual illustration of Completeness-Based Invasion Theory. In general, dark diversity is inversely related to community completeness (A). At small spatial scales, observed diversity is negatively correlated with dark diversity (B), as a higher number of realized niches leaves fewer suitable species in the dark diversity pool. Thus, high observed diversity indicates high community completeness (C). Given that observed diversity is negatively related to ecosystem invasibility at small scale (D), the high completeness translates to low ecosystem invasibility (H), as most available niches are occupied. At large spatial scales, observed diversity and dark diversity are often positively correlated (E). This pattern arises because

204 greater environmental heterogeneity in large, diverse regions can simultaneously support a high

205 number of resident species and a large pool of potential but absent species (dark diversity).

206 Consequently, at large scales, high observed diversity does not necessarily indicate high

207 community completeness (F), and the relationship with invasibility could shift accordingly (G).

208 Therefore, while the core premise that higher completeness leads to lower invasibility still

209 holds at large scale (H), the drivers and manifestations of completeness differ fundamentally

210 across scales.

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