Living on the edge: ecological and evolutionary dynamics along invasion fronts

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Abstract:

Invasion fronts are the edges of non-native species' ranges and represent dynamic, non-equilibrium boundaries where colonization, ecological interactions, and rapid evolutionary processes converge. Although biological invasions are increasingly well studied, mechanisms operating at these advancing margins remain conceptually fragmented despite their disproportionate influence on spread dynamics, exerted impact, and management. Here, we synthesize how invasion-front geometries arise from interactions among propagule pressure, landscape permeability, long-distance dispersal, and environmental heterogeneity, producing continuous, fragmented, stratified, or coalescing fronts that shift with invasion stage and scale. We integrate ecological and evolutionary evidence to show how gradients from core to front include declining density, increased trait divergence, spatial sorting, serial founder effects, expansion load, and behavioural and physiological differentiation. We synthesise parallels with climate-driven range expansions of "neonative" species while emphasizing the stronger disequilibrium and novel biotic contexts characteristic of non-native fronts. Finally, we map these dynamics onto impact trajectories, demonstrating how trait-mediated interactions, resource reallocation, and system-level reconfiguration emerge sequentially along the invasion gradient. By unifying ecological and evolutionary processes across appropriate spatial and temporal scales, we establish invasion fronts as powerful, but understudied natural laboratories and critical leverage points for predicting, monitoring, and managing biological invasions.

Keywords: *range expansion, spatial sorting, eco-evolutionary dynamics, invasive species*

I. Why Fronts?

Amid accelerating globalization and climate change, biological invasions are reshaping ecosystems worldwide. Biological invasions describe the human-mediated introduction, establishment, and spread of species beyond their native ranges, where they can cause diverse ecological, economic, and socio-cultural impacts (Roy et al., 2024; Haubrock et al., 2025a [*in press*]). Spread forms the critical gateway between establishment and impact, determining whether a non-native species' impact remains locally confined or becomes a driver of environmental change (Haubrock et al., 2025b [*in press*]). As such, the capacity for spread is integral to invasion science (Hui & Richardson, 2017) and underpins the characterization of a species' "invasiveness" (*sensu* Soto et al., 2024).

Each new area colonized increases the number of ecological contexts in which non-native species interact with novel communities and environmental conditions. Even non-native species with initially low impacts in one part of their range may express much greater impact potential under different local conditions (Urban et al., 2008; Haubrock et al., 2024). Considerable work has examined how native and naturalised species evolve and persist at their range limits, where environmental gradients impose strong selective pressures and adaptive limits (Angert et al., 2020; Pannell et al., 2019; Bufford & Hulme, 2023; Radomski 2025). These works often conform with classical models of geographic range limits that emphasize equilibrium processes that naturally constrain native distributions through interactions among abiotic tolerance, biotic interactions, dispersal limitation, and demographic or historical legacies (Fagan et al., 2013; Radomski, 2025; Verzuh et al., 2025). Yet, invasion fronts, defined as the boundaries of non-native species distributions where colonisation (i.e. successful establishment), spread, and adaptation intersect (Arim et al., 2006; Philips et al., 2006), differ in several key respects from many natural range margins, even though climate-driven shifts in native ranges can also generate strongly nonequilibrium edge. These fronts represent transient, dynamic phases of expansion due to human-mediated, rapidly eroding biogeographic boundaries characterized by demographic disequilibrium, novel biotic interactions, and feedbacks between dispersal, adaptation, species sorting, and impacts. Thus, whereas many classical treatments of native range limits emphasise processes that constrain spread at quasi-equilibrium boundaries, invasion fronts represent the opposite tendency: processes that actively release and accelerate spread at strongly nonequilibrium edges.

Understanding where and how non-native species spread occurs is essential from both applied and fundamental perspectives, as the advancing ongoing invasion front captures the processes that transform localized establishment into large-scale range expansion (Giometto et al., 2014). The invasion front is an inherently scale-dependent feature, appearing as a single wave at broad spatial resolution but oftentimes fragmenting into multiple local *foci* at finer scales. It marks the actively expanding area of this process and a dynamic boundary where colonization, adaptation, and ecological interactions collectively determine the pace and trajectory of a population's spread as well as associated ecological and evolutionary dynamics (Rubenson and Olden, 2017; Azzurro et al., 2022). The invasion front can take multiple spatial forms—from continuous waves of expansion to patchy, stratified, fragmented, or coalescing patterns—each of these typologies emerging from interactions among propagule pressure, source locations, habitat permeability, environmental filtering, and biotic interactions (Balestri et al., 2018; Everts et al., 2025a). Invasion fronts may shift in typology over time as invasions progress through successive stages. Early in an invasion, multiple localized *foci* often emerge from repeated introductions, later coalescing into broader fronts as populations expand and admix (Shigesada & Kawasaki, 2016). Due to endogenous and exogenous factors, and as density increases and environmental heterogeneity shapes persistence, fronts can become heterogeneous (i.e. patchy) or diffuse, appearing as continuous, fragmented, stratified, or coalescing structures and eventually forming abrupt boundaries where environmental or biogeographic barriers constrain further spread (**Figure 1**). An invasion front is therefore not merely a product of movement but a consequence of numerous feedback loops intertwined among reproduction, recruitment, habitat permeability and fragmentation (e.g. presence of roads, railroads, dams and canals), biotic interactions, and the ability to utilize novel resources. This spatial variability reflects scale-invariant dynamics that recur from local to continental scales (Liebhold et al., 2020), where short- and long-distance dispersal events, satellite colonies, and the bridgehead effect combine to shape complex geometries of spread (Mineur et al., 2010; Blackburn et al., 2011, 2015; Everts et al., 2025a).

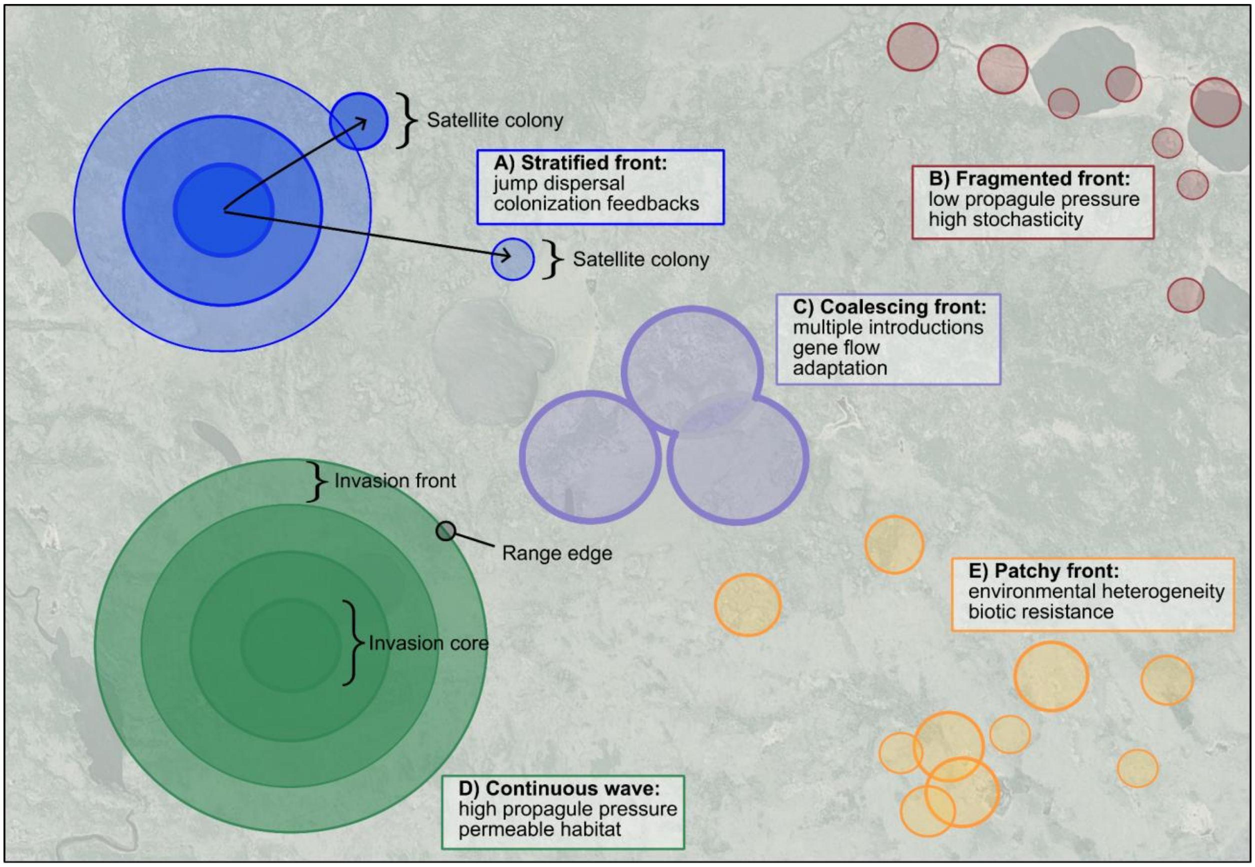

Figure 1. Conceptual illustration of typologies of invasion fronts showing how different, potentially overlapping spatial configurations reflect variability in structure and the underlying processes shaping invasion spread across landscapes**:** (**A**) Stratified front—local diffusion interspersed with long-distance jump dispersal that generates secondary *foci* and feedbacks sustaining expansion; (**B**) Fragmented front—low propagule pressure and strong demographic stochasticity that yield isolated, irregular colonies, that may or may not disappear in the future; (**C**) Coalescing front—spread occurs independently following multiple, geographically spaced-out introductions that may later merge through gene flow and adaptation, accelerating spread; (**D**) Continuous wave—a smooth, density-driven advance propelled by high propagule pressure and habitat permeability; (**E**) Patchy front—spread constrained by environmental heterogeneity and biotic interactions, forming discontinuous clusters of establishment.

By observing populations at the invasion front, researchers can witness mechanisms of colonization, adaptation, and biotic interactions that often become obscured once an invader is well-established (Dominguez Almela et al., 2022; Grayson & Johnson, 2018), inherently differing from natural range expansions in pace and underlying abiotic and biotic processes (Radomski, 2025). Indeed, these invasion fronts often undergo faster change and differ markedly from invasion cores (the high-density, demographically stable regions of a population established earlier in the invasion process). As a result, invasion fronts serve as both unique natural laboratories for testing ecological and evolutionary theories (Sexton et al., 2009) and also as strategic control points where management interventions can potentially alter invasion outcomes (Sharov et al., 2002; Tobin et al., 2011). Yet, despite their central role in determining invasive spread and management, invasion fronts remain an understudied focal point across ecology, evolution, and conservation. Few studies explicitly address invasion fronts, and no unified framework currently links their ecological, evolutionary, and management dimensions. This paper aims to highlight why studying invasion fronts matters conceptually and practically, and to outline the basis for an integrated framework that embraces the ability of invasion fronts to advance our understanding and managing biological invasions.

II. Ecological Insights at the Invasion Front

Invasion fronts are biologically active zones shaped by interacting ecological and evolutionary processes. Invasion-front dynamics can be represented as a progression from continuous waves of population expansion (Skellam, 1951; **Figure 2a**) through fragmented or stratified fronts driven by long-distance dispersal or additional primary or secondary introductions, followed by satellite formation (**Figure 2b**), to the coalescence of multiple introduction *foci* that generate complex spatial overlap and genetic mixing (**Figure 2c**). These spatial patterns, however, coincide with both ecological and evolutionary gradients (**Figure 2d**), where population density decreases but trait differentiation and dispersal capacity increase toward the expanding edge.

However, these spatial configurations are not static, but evolve concomitant with an invasion's progress through distinct temporal phases. Indeed, ecological mechanisms shaping the edge can differ between the introduction, early lag phase, acceleration phase of expansion, later stabilization phase, and potentially occurring boom-bust dynamics (Blackburn et al., 2011; Strayer et al., 2017). Limited propagule pressure and habitat permeability characteristic for initial invasion stages may result in small, fragmented, and isolated populations (Briski et al., 2012). Multiple isolated *foci* may arise through repeated introductions or long-distance dispersal events, forming discontinuous or "fragmented" fronts (possibly mistaken for satellite colonies; **Figure 2B**). Ecological interactions between these *foci* may be weak as establishment remains constrained by demographic instability and sometimes local environmental mismatches. As densities grow and introduced populations (or satellite colonies) begin to geographically connect, positive feedbacks between dispersal, reproduction, recruitment, and resource exploitation can emerge and promote front expansion momentum through spatial sorting and adaptive plasticity, ultimately leading to coalescing or stratified fronts **(Figure 2A–C**). Eventually, expansions will slow and perhaps even halt as populations stop growing in size due to environmental constraints, biotic interactions, or density dependence (Urban et al., 2008). Under some conditions, these slowdowns can become persistent, producing "pinned" invasion fronts where positive density-dependent growth and dispersal interact with environmental heterogeneity to halt further front advancements despite apparently suitable habitat beyond the front (Keitt et al., 2001; Morel-Journel et al., 2022), thus forming a biogeographic barrier. This range pinning, sometimes framed as a form of colonisation debt (Morel-Journel et al., 2023), implies that low-density edge populations can temporarily decouple habitat suitability from realised spread, with important consequences for forecasting and management. The invasion front can thus become diffuse or abrupt depending on habitat heterogeneity, and processes resembling those observed at native range edges (*cf.* Angert et al., 2020; Radomski, 2025). At this stage, ecological interactions may intensify and either result in (1) an increase in population density, transforming the former front into a newly established core, while the range edge continues to advance outward, or (2) face abiotic or biotic unsuitable conditions that effectively limit any additional spread.

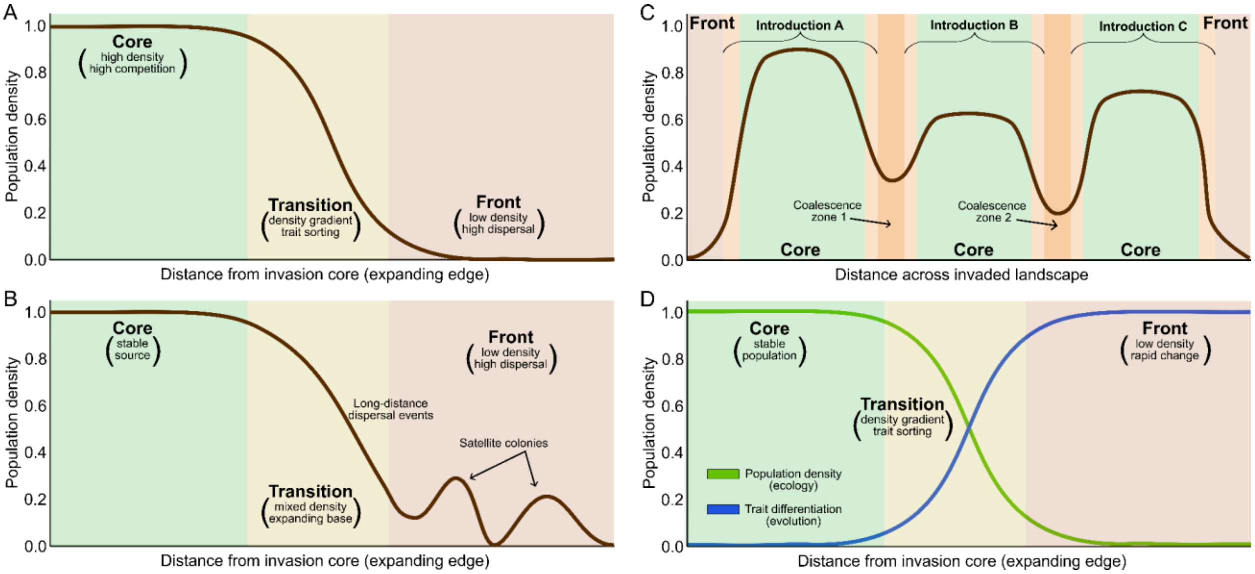

Figure 2. Conceptual representation of some commonly occurring invasion-front dynamics, shown as the relationship between population density and distance from invasion core, across spatial, ecological, and evolutionary contexts: (**A**) A continuous wavefront (a smooth gradient in population density from a high-density core through a transitional zone of trait sorting to a low-density, dispersal-dominated front). (**B**) A fragmented or stratified front (local discontinuities and secondary peaks produced by long-distance dispersal and satellite colonies that form ahead of the main front). (**C**) Multiple introductions and coalescing fronts (independent invasion *foci* expanding outward and merging in coalescence zones, thereby increasing spatial complexity and genetic mixing). (**D**) Integrated ecological and evolutionary gradients (population density declines while trait differentiation and evolutionary change increase toward the front, highlighting this zone as a hotspot for ecological dynamics and rapid evolution). Note: The occurrence and detectability of these invasion-front structures may vary with invasion phase (introduction, lag, expansion, or stabilization) and observation scale. Similar spatial configurations can emerge repeatedly at nested scales (i.e. fractal-like dynamics), reflecting the self-reinforcing nature of colonization and spread processes (*cf.* Blackburn et al., 2011).

These invasion stages, and thus invasion-front dynamics, can deviate from ideal isotropic diffusion and instead show anisotropic spread imposed by environmental heterogeneity, thus differ across ecological realms (Hastings et al., 2005). Freshwater systems often generate strongly directional expansion through dendritic network topology and hydrological flow (Laprieur et al., 2008; Osawa et al., 2013; Altermatt and Fronhofer, 2018). Marine environments offer broader connectivity but remain structured by persistent currents, retention zones, and mesoscale circulation that create patchy and directionally biased dispersal (Pringle et al., 2011; García-Gómez et al., 2021; Michie et al., 2024). Terrestrial landscapes, while less channelized, also impose anisotropy through habitat permeability, corridors, and barriers such as land use and elevation (Fraser et al., 2015; McRae et al., 2007). Thus, although constraints differ among realms, invasion fronts predominantly reflect anisotropic diffusion shaped by landscape structure, dispersal mode, species life history, and ecological plasticity (Hastings et al., 2005; Haubrock et al., 2024).

This inherent spatial and temporal complexity makes invasion fronts integral for understanding how spread translates into establishment and impact. At low densities near the expanding edge, demographic feedbacks such as Allee effects can influence the probability of persistence and the rate of further expansion (Keitt et al., 2001; Blackburn et al., 2016), while adaptive plasticity and flexible resource use promote continued advance (Luo et al., 2019). The invasion front of a non-native population thus functions as an ecological interface, often expressed as pulses, accelerations, and decelerations rather than smooth diffusion (Urban et al., 2008). At the same time, niche construction at the front of biological invasions may play a critical role in determining invasion dynamics and long-term ecosystem impacts. As populations expand into new habitats, individuals can actively modify local environmental conditions through processes such as soil alteration, nutrient cycling, physical engineering, resource depletion, facilitation of mutualists, among others (see Ferraro et al., 2025; O'Loughlin & Green, 2017). These modifications may enhance the invader's own fitness, creating positive feedbacks that accelerate range expansion. In addition, niche-constructing traits may interact with spatial selection at invasion fronts to favor phenotypes that both disperse effectively and engineer locally beneficial conditions, potentially leaving lasting evolutionary legacies.

III. Evolutionary Insights at the Invasion Front

Across ecosystems, individuals at the invasion front can differ from those in the transitional zone between core and front, as well as from individuals in the core (Kubisch et al., 2014). Range-expanding populations encounter and potentially adapt to novel selective environments, and the process of expansion itself can drive evolutionary change through mechanisms such as spatial sorting, genetic drift, and serial founder effects (Van Petergem et al., 2016). Consequently, range expansion often leads to evolved differences in reproductive life-history and dispersal traits between individuals in the range core and those at the expansion front (Peischl et al., 2013). Individual animals at the front often display enhanced body condition, size, boldness, or exploratory behaviour (Rebrina et al., 2015; Laparie et al., 2013; Myles-Gonzalez et al., 2015; Damas-Moreira et al., 2019; Alves et al., 2025) whereas plants at the front may show faster germination and greater capacity to self-fertilize (Tabassum & Leishman, 2018, 2019; Liu et al., 2021)—traits that can facilitate dispersal, resource acquisition, and competitive dominance. Ecologically, low-density invasion front populations often benefit from reduced intraspecific competition and abundant resources, enabling the emergence of density-dependent traits such as higher physiological condition and fecundity (Lopez et al., 2012; Rebrina et al., 2015). Yet trade-offs are common, with selection for dispersal often reducing reproductive investment, as in *Rhinella marina*, where morphological evolution increased invasion speed but lowered fecundity in individuals at the leading edge (Hudson et al., 2015, 2016). Similar *r*-selected strategies are documented in fishes and other taxa occupying invasion fronts, where rapid growth, early maturation, and high reproductive effort sustain population expansion (Bøhn & Admussen 2004; Gutowsky & Fox 2012; Tarkan et al., 2021), supported by male-biased dispersal and density-driven shifts in sex ratio (Marentette et al., 2011; Chuang & Peterson 2016). In contrast, individual animals in the core, where higher average population densities lead to increased intraspecific competition, may exhibit lower physiological condition and smaller body size, as well as a lower proportion of bold, exploratory, and aggressive individuals (Alves et al., 2025; but see Hudina et al., 2015). However, populations at the invasion front may encounter differing densities of enemies (predators, competitors, parasites, diseases) and mutualists, environmental conditions, and resource availability. These differences can translate into reduced fitness compared to those in the core when small population sizes at the edge allow genetic drift to override selection, enabling deleterious alleles to spread along the expansion front during repeated founder events (Edmonds et al., 2004; Slatkin & Excoffier, 2012). Furthermore, as a result, fecundity at the edge may decline relative to the core due to trade-offs among dispersal, reproduction, and competitive ability.

The recurrences of these patterns indicate that the processes of introduction and establishment are repeatedly recreated at invasion fronts (Blackburn et al., 2011), reinforcing invasion momentum through the transition of front populations into new invasion cores. Evolutionary processes at the invasion front arise from strong spatial and demographic structuring that creates distinctive and selective environments. Low population densities, high dispersal, and rapid population turnover can promote both spatial sorting and selection for traits that enhance range expansion, making invasion fronts both a high risk, high reward for the invasive species and a semi-natural experiment in evolution under disequilibrium. Stochasticity at low densities means that even small phenotypic advantages can disproportionately influence front dynamics, allowing traits that confer only marginal dispersal benefits to sweep rapidly along the expanding edge. However, while ecological and evolutionary mechanisms determine where a non-native species spreads, it remains unclear which processes determine *how fast* and *how consistently* through time a populations' spread occurs.

Parallel mechanisms occur in introduced non-native diseases and pathogens spreading among native and non-native hosts (Hulme et al., 2020), but also in native species undergoing range expansions under climate and land-use change. These "neonative species" (*sensu* Essl et al., 2019; i.e. range-expanding native taxa regardless of political borders) experience similar, albeit at a slower pace, evolutionary pressures (e.g. low density, strong selection for dispersal and rapid reproduction, and serial founder effects). This parallel indicates that invasion fronts and climate-driven range margins operate under convergent evolutionary dynamics. Transplant experiments and elevational range-limit studies revealed latent spread potential under shifting climatic regimes (Pannell et al., 2019; Bufford & Hulme 2023). Although both invasive and native range expansions are driven by and subject to similar evolutionary principles, invasion fronts differ fundamentally in their boundary conditions and evolutionary context. Non-native species expand into novel ecological and phylogenetic arenas, frequently encountering competitors, predators, and resources with which they share no coevolutionary history (Roy et al., 2011). Consequently, the behavioural and ecological cues guiding movement at invasion fronts may differ profoundly among sites and from those in the native range. Individuals must interpret unfamiliar environmental gradients and novel biotic interactions—often without any meaningful "memory" of local conditions—potentially shifting the relative importance of abiotic signals, resource distributions, predation risk, and intra-specific competition in determining spread dynamics. This absence of historical constraint, coupled with often repeated introductions and strong human mediation, can amplify selection for dispersal, plasticity, and rapid adaptation far beyond what is typical for native range shifts (Stewart et al., 2015). In addition, the constant influx of novel genotypes from repeated introductions can generate admixture and hybrid vigour at the invasion front, increasing evolutionary potential relative to native range expansions. As a result, invasion fronts provide an extreme yet highly informative model system for studying evolution in real time, where demographic disequilibrium and ecological novelty interact to accelerate evolutionary responses.

Spatial sorting—the non-random accumulation of dispersive individuals at the expanding edge—enhances the prevalence of traits that facilitate movement regardless of classical fitness trade-offs (Shine et al., 2011; Alford et al., 2009). Successive generations at the front may thus become increasingly composed of phenotypes optimized for colonization rather than local competition. This process could lead to rapid evolutionary change without the need for strong selection, as dispersive individuals mate assortatively and pass on traits that accelerate spread (Phillips et al., 2010; Huang et al., 2015; Courant et al., 2019). In turn, this spatial self-organization contributes to evolutionary acceleration, observed for instance in cane toads, where morphological and physiological adaptations—longer limbs, greater endurance—have increased invasion speed fourfold over eight decades (Hudson et al., 2016). Sexual dimorphism, characterised by female-biased dispersal, and morphological variation, particularly in female wing and head traits, in the invasive common myna (*Acridotheres tristis*) show strong correlations with distance from the range core (Berthouly-Salazar et al., 2012). This suggests that at invasion fronts, individuals frequently exhibit proactive behavioural syndromes—boldness, exploration, and low site fidelity—that enhance colonization (Holway & Suarez 1999; Chapple et al., 2012; Sih et al., 2012; Wong & Candolin 2015). However, the opposite has also been shown, with non-native round gobies (*Neogobius melanostomus*) and signal crayfish (*Pacifastacus leniusculus*) at the invasion front being equally or even less aggressive (Groen et al., 2012; Hudina et al., 2015; but see Gonçalves et al. (2025). Such "proactive" phenotypes are consistent with the pace-of-life syndrome, linking boldness and high activity to elevated metabolism, faster growth, and *r*-selected reproductive strategies (Biro & Stamps 2008; Réale et al., 2010; Raffard et al., 2022). Moreover, the underlying behavioural traits promote invasion momentum by coupling dispersal capacity with rapid resource exploitation, although highly dispersive individuals may exhibit reduced competitiveness or fecundity once densities increase, as observed in fish and crayfish invasions (Groen et al., 2012; Hudina et al., 2015; Tarkan et al., 2021). Together, these patterns highlight that invasion fronts often operate under distinct behavioural–evolutionary regimes compared to range cores, with trait combinations that maximize expansion but may incur performance costs as populations mature and densities rise.

Beyond behavioural and life-history traits, additional genetic processes can further shape evolutionary trajectories at the invasion front. Serial founder effects, genetic drift, and bottlenecks can reduce diversity and generate an accumulation of deleterious alleles that may constrain population performance (e.i. "expansion load"; Klopfstein et al., 2006; Excoffier et al., 2009; Peischl et al., 2013, Peischl & Excoffier, 2016). Conversely, gene flow from the core can restore genetic diversity and improve adaptive potential at the front, although excessive influx can dilute local adaptation and slow expansion (Berthouly-Salazar et al., 2013; Beer et al., 2024). Hybridization between related "lineages" at the front may also create novel genotypes with enhanced invasiveness, as seen in fungal and fish invasions (Diedericks et al., 2018; Hessenauer et al., 2020; Abreo et al., *under review*), illustrating how genetic and behavioural evolution can jointly determine the persistence and velocity of spread, sometimes outpacing abiotic constraints (Ochocki & Miller 2017; Szűcs et al., 2017). These interacting genetic processes together create an evolving mosaic of local adaptation, maladaptation, and admixture along the expanding range edge, producing spatially variable evolutionary outcomes that feed back into spread dynamics.

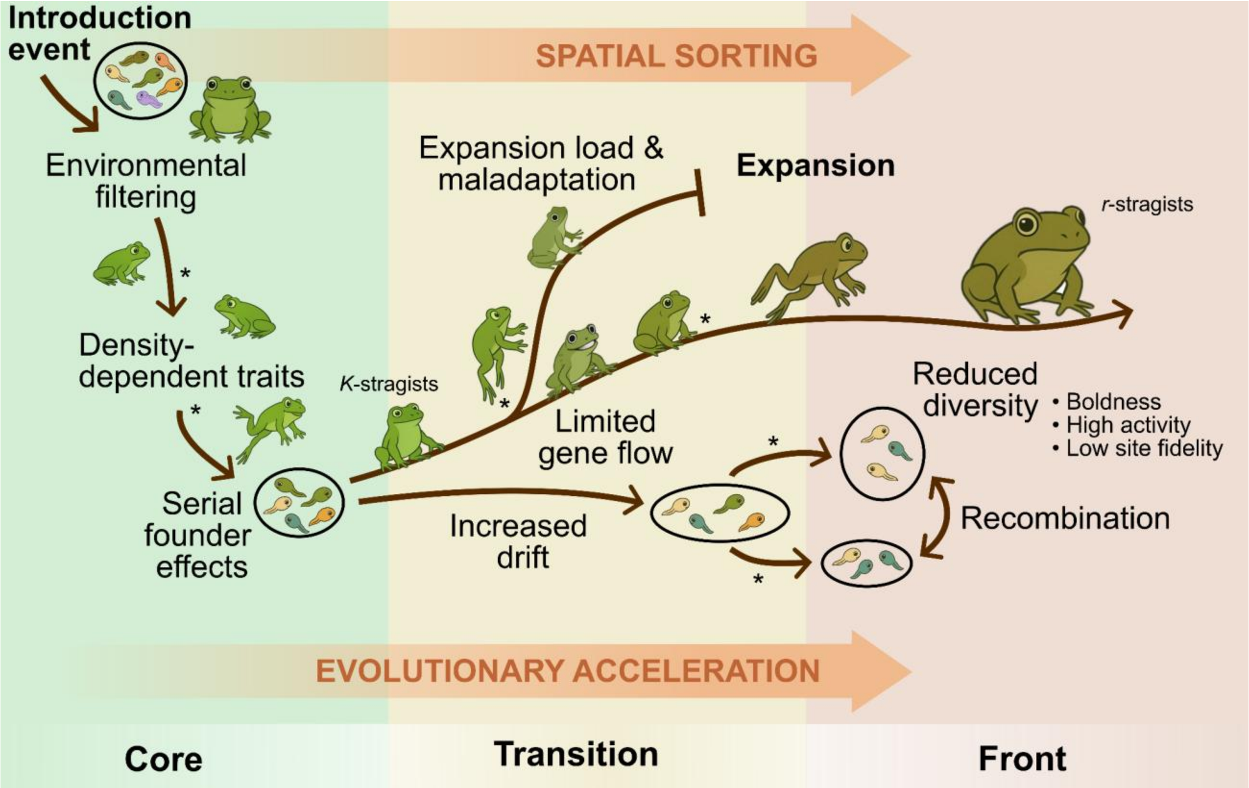

Figure 3. Conceptual synthesis illustrating how ecological, demographic, and genetic mechanisms interact from the invasion core to the expanding front. Following an introduction event, repeated founder effects and demographic bottlenecks (*) generate low-density populations dominated by specific traits. As expansion proceeds, spatial sorting and limited gene flow may promote assortative mating among dispersive phenotypes, increasing drift and accelerating evolutionary change. Toward the front, populations often exhibit reduced genetic diversity and expansion load, but gene flow from the core, hybridization, and recombination can restore variation and generate novel genotypes. Frog appearances (both morphological as colours) represent the spatial sorting progress, from light green (*K*-strategists) to dark green (*r*-strategists). Tadpole colours represent genetic diversity, with an increasing set of colours representing an increased diversity.

IV. Impact Dynamics at the Invasion Front

Understanding impact dynamics at the invasion-front requires viewing impacts as evolving properties of the invasion process rather than fixed outcomes. Indeed, although empirical quantification remains scarce, the mechanistic drivers of such stage-dependent impacts suggest predictable transitions from acute, transient disturbances to chronic, system-level ecosystem reconfiguration. Importantly, these transitions are not merely temporal but spatially structured and thus neither static nor uniform, arising from the shifting balance between invader traits, advancing populations (i.e. the invasion front's edge and followed zones) and ecosystem characteristics of the ecosystem they invade, including local community resistance and environmental feedbacks (Shine, 2010). Recognizing and measuring these transitions across invasion stages would thus provide a powerful framework for linking population dynamics with ecosystem impact trajectories, a relationship still largely unexplored in invasion ecology.

Each invasion represents a unique spatio-temporal trajectory shaped by local context, propagule pressure, and species-specific traits as invasions expand not only in space but also in functional depth (Haubrock et al., 2024). Consequently, impact magnitude and type vary not only among species but also among populations of the same species (e.g. in function of species density) and along the invasion gradient itself (Shine, 2010; Sousa et al., 2024). Early in the spread process, newly established front populations may trigger short-term disruptions such as altered resource flows, behavioural shifts in native species, or temporary dominance due to predator or competitor naïveté (Heavener et al., 2014; Anton et al., 2020; Stewart et al., 2021). As the invasion advances, "transitional" populations bridge conditions between the front and the core, where local adaptation, biotic interaction, and density regulation progressively modify community composition and ecosystem function. For instance, by exploiting novel resources and modifying nutrient fluxes, expanding populations may reshape local food webs and biogeochemical cycles, thereby influencing resource subsidies and ecosystem functioning both ahead of and behind the moving front (Alves et al., 2025; Lopes et al., 2025). Even, in some circumstances, organisms at the front exhibit higher concentrations of certain potentially toxic elements, which may be associated with a distinct diet and higher trophic position, more exploratory behaviour, and lower epibiotic associate load (Gonçalves et al., 2025). Such physiological and trophic shifts indicate that front individuals often occupy different ecological niches than core individuals, implying that impacts propagate not only through abundance but through trait-mediated pathways (Van Kleunen et al., 2010). Yet at the same time, density and biomass at the front remain lower than in the core, meaning that exerted total impact at the front may be assumed as lower (Parker et al., 1999). However, *per capita* impacts may ultimately be higher at the front because individuals face less intra-specific competition and many times are larger, more aggressive, bolder, and have a higher metabolism (Alves et al., 2025). Impacts may therefore shift from direct interactions at the front to indirect, system-level alterations as populations mature and stabilize, representing a temporal sequence in which both the invader's traits and the invaded system coevolve and co-adapt (Dostál, 2024), where, after the front passes, invaded systems may undergo additional changes through "relaxation" phases in which impacts may persist through legacy effects or subside as new equilibria emerge (Cuddington, 2011).

V. Management at the Invasion Front

Invasion fronts should be regarded as strategic management zones where intervention can meaningfully alter invasion trajectories. Indeed, management actions targeting biological invasions are most effective and economically efficient when implemented at or ahead of the advancing front. Specifically, targeting populations from an outward to inward direction (i.e. starting at the front and progressing towards the core) generally is most beneficial for preventing reinvasion following management (Epanchin-Niell & Wilen, 2012). Additionally, populations at the front sometimes exhibit distinct traits, such as greater exploratory tendency or aggressiveness (Hudina et al., 2015; Groen et al., 2012; Thorlacius et al., 2015), which for certain species could make trapping methods more effective at the front than in the core. Because populations at the front are typically small, spatially restricted, and demographically unstable, early intervention is more feasible than once populations become established (Sharov et al., 2002; Leung et al., 2002; Liebhold & Bascompte, 2003). Accurately delineating and forecasting invasion fronts (on a macro-ecological scale commonly done with Species Distribution Models; Srivastava et al., 2019) often faces inherent flaws due to non-equilibrium dynamics of the invasion front, which calls for dynamic species distribution model that can take into consideration both the non-equilibrium nature (Hui, 2023) and the transitions of selection forces along the core-front gradient. For such endeavours to be more accurate requires emergent monitoring tools with improved sensitivity (Fricke & Olden, 2023), such as environmental DNA (Everts et al., 2023), real-time acoustic monitoring (Wood et al., 2024), or remote sensing (Gränzig et al., 2023), also increasingly by citizen science and local ecological knowledge (Gervazoni et al., 2023). Complementary to these approaches is landscape genetics, which analyses the relationship between genetic connectivity and landscape features, and can reveal barriers to gene flow within populations that appear to be continuously distributed. In doing so, it can reveal 'internal invasion fronts' with important implications for management (Sherpa et al., 2020; Everts et al., 2025a). Although managing long-established core populations may produce localized benefits—such as reducing local impacts (Green & Grosholz, 2020) or limiting the production of propagules capable of reaching invasion fronts via long-distance dispersal events (Everts et al., 2025a)—such interventions typically only slow, rather than prevent, overall spread (Pepin et al., 2019). Moreover, suppressing core populations can generate unintended ripple effects that facilitate the emergence of new satellite populations, ultimately giving rise to multiple secondary fronts (Shigesada & Kawasaki, 1997; Liebhold & Bascompte, 2003). Thus, management strategies that focus disproportionately on established cores risk overlooking the dynamic processes that sustain spread at the front, where intervention leverage is highest. Shifting management towards the invasion front is therefore invaluable for effectively containing and reducing the distribution of biological invasions.

The spatial form of a front largely determines how predictable and manageable an invasion is. Continuous or "pushed" wavefronts are comparatively easy to forecast and control, whereas fragmented or stratified fronts—composed of multiple asynchronously established foci each with unique front characteristics shaped by local environmental conditions—pose a larger management challenge as they continuously reseed new outbreaks (Zhao et al., 2019). In fragmented or stratified fronts, management has multiple important lines for intervention. First, management should focus on preventing the establishment of new foci by blocking additional human-mediated introductions or long-distance dispersal events, as preventing a new population from getting a foothold is more cost-efficient than removing it once established (Leung et al., 2002; Keller et al., 2007). This requires a multifaceted and layered approach, consisting of policy interventions, decontamination strategies (e.g. Check, Clean, Dry), and a good understanding of a species' spread behaviour through a given landscape matrix. Second, the management of fragmented or stratified invasion fronts should prioritize preventing the coalescence of existing foci, as multiple small and spatially isolated populations are considerably easier to contain or eradicate than a single, large, continuous population due to the proportionally larger coverage of front relative to core areas (Bohling, 2016). Moreover, limiting coalescence reduces opportunities for genetic admixture, thereby constraining increases in genetic diversity and subsequent gains in fitness or adaptive potential that can promote invasion success (Qiao et al., 2019). Restricting access to or affecting habitat suitability of sites that hold high centrality within the network of suitable habitats, including anthropogenic habitats such as roads, railroads or canals, can substantially contribute to this objective, as limiting movement through these key nodes disproportionately reduces the likelihood of foci merging and thereby slows large-scale population consolidation (Tingley et al., 2012; Drake et al., 2017).

A practical approach could involve using physical barriers or poisoning to prevent access to critical stepping-stone sites or delay or stop the advance of the front (Jones et al., 2021). This strategy has been widely applied across ecosystems: fences in Australia have been used to contain rabbits, foxes, and cats (Dickman, 2011), electric barriers limit dispersal of invasive fishes in the USA (Collins et al., 2024), and other structures, such as dams and weirs, are also effective in restraining the movement of non-native species (Carvalho et al., 2025; Jones et al., 2021). Although these strategies are effective in containing certain invasive species, such barriers can have an impact on native communities by fragmenting their habitats (Bradby et al., 2014; Jones et al., 2021). Furthermore, while these barriers prevent certain species from proliferating, they have enabled other invasive species to spread (Brown et al., 2006). These management interventions should not be limited to source populations. From a practical standpoint, sink populations, those currently non-reproductive or limited by environmental constraints, are frequently disregarded because they do not contribute to immediate spread. However, environmental or anthropogenic changes can transform these sinks into viable sources, converting dormant populations into new invasion fronts. For example, introduced trees may not spread until their pollinators, seed dispersers, or ectomycorrhizal symbionts are introduced into the same area, enabling reproduction and subsequent expansion (Le Roux et al., 2017; Spear et al., 2021). Moreover, sites colonised near the range edge may initially function as sink habitats, but as the invasion front advances, they may transition into source sites, contingent on local habitat suitability (i.e. not being intrinsically limited by persistent abiotic constraints such as soil or water chemistry; Everts et al., 2023). Therefore, proactive management must incorporate the potential future activation of sink populations within adaptive surveillance frameworks. Anticipatory treatment of sinks can prevent the sudden emergence of new fronts, especially in systems prone to environmental regime shifts or human-induced landscape changes. While technically feasible, the application of these management measures in the field can be affected by different jurisdictions during a cross-boundary invasion (Everts et al., 2025b), conflicting management priorities among agencies (Simberloff et al., 2020), no access to privately owned sites (Vimercati et al., 2017), and low detectability and latency of early-phase populations (Bylemans et al., 2016).

VI. Conclusion / Future directions

Invasion fronts have been studied for decades through ecological theory and conceptual models, long before high-resolution movement data became available. Classic work on diffusion-like spread (Skellam 1951; Okubo & Levin, 2001), Allee-effect dynamics (Lewis & Kareiva, 1993; Kot et al., 1996), and patchy or stratified spread frameworks (Hengeveld 1989; Andow et al., 1990) laid the foundation for our understanding of how fronts form and propagate. Recent technological advances now complement this theory, with organism tracking at invasion fronts continuing to be propelled by the accumulation of increasingly detailed data. Although researchers are applying sophisticated modelling approaches to these expanding datasets (e.g., artificial intelligence and machine learning; Elith et al., 2008; Schlägel et al., 2019; Zeng et al., 2021), identifying the cues and mechanisms that drive invasion fronts remains challenging. Specifically, the increasing availability and resolution of molecular tools allow a better understanding of the gene-level drivers and consequences of range-expanding species (Kołodziejczyk et al., 2025). Modern tracking technologies now deliver not only high-resolution movement data but also information from accelerometers and physiological sensors, producing comprehensive, individual-level data streams for non-native species (Meira et al., 2024).These tools allow researchers to provide deeper insight into the factors that shape invasion-front dynamics, and—building on the integrative framework and front typologies synthesized here—when integrated with ecological context and landscape structure, enable a shift from pattern description to mechanistic prediction of when, where, and how invasion fronts emerge, accelerate, stall, or collapse. Together, this synthesis reframes invasion fronts from descriptive spatial patterns into dynamic eco-evolutionary systems.

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