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Emergent functions in the chemodiversity landscape

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Abstract:

Nature produces countless metabolites that regulate organismal performance and the functioning of ecosystems. Specialised metabolites are particularly diverse and mediate ecological interactions across all geographic scales and levels of biological organisation. While chemodiversity, i.e., the richness, relative abundance and disparity of specialised metabolites within a blend of metabolites, has received substantial interest at the level of pairwise interactions (e.g. between plants and interaction partners), much less is known about how metabolites produced by multiple individuals across the tree of life merge into higher-level blends at population, community and ecosystem scales. We synthesise evidence for emergent functions that arise from such higher-level chemodiversity. We examine how blends change in composition as they move through air, water, and soil, and vary in time and space, thereby creating a dynamic 'chemodiversity landscape'. We further discuss the applied potential of these chemodiversity landscapes and the threats that could compromise them. We outline key questions that will help guide research on how higher-level chemodiversity contributes to ecological processes and functioning across scales.

Introduction

Chemical information is omnipresent on Earth. Volatile and non-volatile metabolites operate at various geographical scales across all levels of biological organisation, from within individual cells to entire ecosystems[1–4]. For instance, in the air, scavengers detect volatile compounds released from animal carcasses over large distances[5,6] and herbivore-induced plant volatiles attract natural enemies, thereby mediating predator-prey interactions[7]. In aquatic environments, chemical cues facilitate mate finding and habitat selection in a wide range of organisms, including lobsters[8], coral larvae[9], and fishes[10]. Belowground, plant volatiles guide soil-dwelling consumers to suitable foraging sites[11,12] and flavonoid exudates enable legumes to attract nitrogen-fixing bacteria[13]. From microbes to mammals and across air, water and soil, chemical information structures the interactions that sustain life, maintain vital ecological functions, and ecosystem health[14–16].

Chemical ecology traditionally sought to understand the chemical mediation of interactions by assigning specific ecological functions to individual metabolites[17,18]. However, recent work increasingly considers entire chemical blends as functional units of ecological information, recognising that mixtures of structurally different metabolites can produce interactive effects not predictable from individual metabolites[19–21]. Building on this paradigm shift, a growing body of work explores the ecological relevance of **chemodiversity**: the richness, relative abundance, and disparity of the metabolites forming such blends wherever they may co-occur[22,23].

Our current understanding of chemodiversity largely stems from studies at the level of interactions among individuals[18,20,23]. Recent research at population level, however, suggests that ecological processes are not only influenced by the chemical blends of individuals, but also by the collective chemodiversity that emerges from multiple neighbouring individuals[20,24–26]. For example, inter-individual variation in foliar secondary metabolites among neighbouring wild cabbage plants promotes plant growth and herbivore diversity while simultaneously reducing herbivore damage[27]. Such findings suggest that chemodiversity, arising from the combined chemical profiles of multiple producers across space and time, also generates mixtures that functionally contribute to broader ecological patterns and processes.

In nature, different biological sources produce volatile and non-volatile metabolites that mix to form spatiotemporally dynamic blends, which can be affected by both the abiotic and biotic environment[28,29]. This chemical mosaic likely influences manifold ecological interactions at community and landscape scales, thus representing a **chemodiversity landscape**, i.e., the spatiotemporally structured distribution of chemical compounds and mixtures within a landscape, shaped by biological production, abiotic transformation, and physical transport. Beyond the mere spatial arrangement of chemotypes, chemical landscapes represent emergent ecological properties whose functional consequences depend on organism-specific perception and processing of chemical information. As such, the same chemical environment may constitute different functional landscapes for different organisms, linking chemical complexity to ecological interactions, evolution, and ecosystem functioning across scales.

Even though the tools to accurately describe such blends are available, the patterns and ecological consequences of chemodiversity at larger scales remain poorly understood[30]. For instance, how do pollinating insects navigate a chemically diverse landscape, and which are the chemical cues that guide their decision-making as they search for nectar sources? A deeper understanding of how metabolites produced by multiple sources blend together and affect ecological processes is urgently needed, particularly at spatial and temporal scales relevant to ecosystem functioning and resilience in the face of accelerating global change. Despite a clear consensus on the increase in ecological complexity with increasing level of biological organisation, the research interest for chemodiversity has largely focused on the individual interaction level (Fig. 1). Consequently, important hypotheses regarding the contribution of individual organisms to higher-level chemodiversity and the resulting potential for emergent functions remain largely untested. Scientists must adopt a broader perspective that links the origins, dynamics, perception, and consequences of chemical diversity across levels of biological organisation and spatiotemporal scales.

We provide a conceptual overview of how chemodiversity scales across biological levels and spatial dimensions — from individuals to communities and landscapes — and evaluate its role in shaping the ecological processes that underpin ecosystem functioning. Section 1 describes how different actors and the environments they occur in interact to form chemodiverse landscapes. Section 2 conceptualises trajectories that metabolites may follow once released into the environment, and how these trajectories influence their fate and ecological function. Section 3 considers how spatiotemporal patterns of chemodiversity emerge on broader geographical scales by synthesising current knowledge and extending insights from the individual level to the levels beyond, i.e., population, community and ecosystem. We outline implications of such a chemodiversity landscape for biodiversity and ecosystem functioning, including the risks posed by the natural and anthropogenic degradation of chemical landscapes related to biodiversity loss. To align this conceptual synthesis with research priorities, Section 4 complements it with a survey among selected attendees of a two-day workshop on chemical ecology, who rated questions to identify key areas that require attention in order to advance research on landscape-level chemodiversity.

1. The actors in the chemodiversity landscape - from producers to responders

At the core of any chemical communication system are three fundamental components: a **producer** that synthesises the chemical metabolites; a **carrier** that transports and modifies these metabolites; and a **responder** that perceives and directly reacts to specific information, or in some cases may be directly affected by the emitted metabolites[31] (Fig. 2). In this section, we provide a conceptual outline of this system to improve our understanding of how chemodiverse mixtures arise through the combined metabolites of multiple producers, and how these mixtures are modified by environmental factors as well as through space and time.

A large diversity of metabolites is synthesised by a wide range of producers across the tree of life[32,33]. Many of these metabolites enable basic life functions, often referred to as primary metabolites. Secondary, or **specialised metabolites**, on the other hand, often mediate interactions with the abiotic and biotic environment. These metabolites are of ecological importance due to their roles in regulating ecological interactions. Once produced, metabolites may either be **stored or released** in volatile or non-volatile form. Storage occurs within specific cellular structures or compartments, such as vacuoles, or in specialised structures, like glandular cells, that enable producers to retain metabolites until they are needed, protect them from degradation or self-toxification, and control their release in response to environmental cues[34,35]. For instance, bufadienolide toxins are stored as constitutive defence compounds in parotid glands of toads, where they serve to deter predators[36]. Alternatively, producers may actively or passively release metabolites into the environment. Producers, in addition, may also move through the landscape, as is the case for animals. Released metabolites can act as information, such as trail pheromones used in ant recruitment[37], volatile compounds emitted by plants to attract natural enemies of herbivores[38–40], signals involved in plant–plant interactions[41–43], or substances that modify the (a)biotic properties of soil[44]. The release of metabolites contributes to a chemodiverse environment, while the stability of the metabolite, and the location and context of release strongly influence its ecological function[45]. Both stored and released metabolites contribute to the chemodiversity landscape.

A seminal principle of chemical ecology is that metabolites are *often* produced and released by organisms with a biological function[46,47]. For example, many plants produce feeding deterrents to deter antagonists[48,49], but in contrast, plant-emitted metabolites can also attract (often beneficial) organisms[50,51]. Many producers interact with multiple antagonists and mutualists at the same time, and hence some specialised metabolites are specific, have multiple functions, but also responses may be taxon-specific[52–54]. Many organisms eavesdrop on chemical information, having evolved or learned to associate certain metabolites (or blends) to locate producers (e.g., as resources[55,56]). In addition, many metabolites are produced for protective functions, including abiotic stress resistance[57], which could also be recognised by other organisms as they end up in the environment. Evidently, many metabolites mediate interactions well beyond any potential ‘biological purpose,’ raising the question how characteristics of chemical blends shift in time and space, and whether such shifts matter for biological interactions, and at what scale.

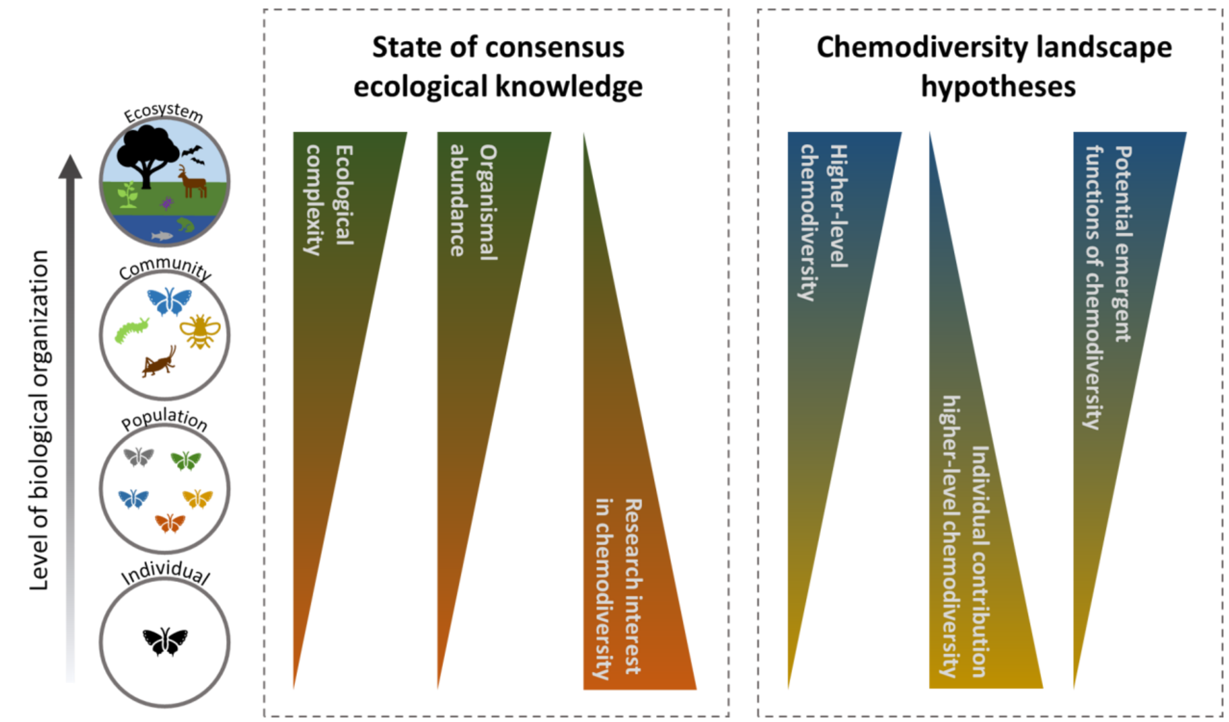

Figure 1

2. Spatiotemporal dynamics of chemodiversity – from single molecules to mixtures

A major challenge is to understand the influence of the environment on the chemical blend. In this section, we discuss how (a)biotic factors shape chemodiversity at different time and space levels (before the emission of the blend, during its transport and after reaching the responder) and why it matters at the ecosystem scale (Fig. 2). Prior to emission, (a)biotic conditions influence the chemical landscape by affecting the development, activity, and phenology of producers. Seasonal and diurnal changes in plant, microbial, and insect communities alter the production and availability of metabolites for storage and emission [58–60]. A significant fraction of the chemical blend can only be observed under herbivory and during photosynthetic periods[61]. Abiotic factors also directly affect production and emission rates, as well as compound properties (e.g., volatility) of volatile and non-volatile metabolites above- and belowground [62–65]. Once released into the environment, the fate of metabolites depends on the medium through which they travel: the **carrier**. Chemical information in the landscape is distributed through three primary carrier types: gaseous (i.e., air), liquid (i.e., water) and solid phases (i.e., substrates, including soil, where transport is mediated by air and liquids but also depends on solid particles). Intrinsic properties of each carrier influence the movement, transformation, and persistence of compounds, ultimately shaping the timing, location and extent to which a chemodiverse blend is perceived by responders[66,67].

To bridge the distance between producer and responder, air often serves as the carrier[64,68–70]. For instance, flying insects can reliably orient toward odour sources by following gradients of a chemical blend within odour plumes, using characteristic anemotactic upwind and crosswind flight behaviours[71,72]. These blends are then transformed over time and space according to the composition and physical properties of the carrier and to the rate of biosynthesis, volatility and persistence of each compound[68,73,74] (Fig. 2). Considerable progress has been made in quantifying intrinsic chemical properties such as volatility, reactivity and compound stability, which define the atmospheric lifetime and transport potential[73,75,76]. These properties are modulated by ambient environmental conditions, notably temperature and ultraviolet radiation, which can accelerate degradation processes such as photolysis and bond rupture in photosensitive molecules[77]. In the atmosphere, oxidants including ozone, hydroxyl ($OH^{-\cdot}$) and nitrate ($NO_3^{\cdot}$) radicals also degrade and transform chemical blends[78–81]. These oxidation processes can lead to the formation of secondary organic aerosols (SOA), which represent an additional chemical phase and may themselves be perceived and exploited as informational cues by responders[82]. Such changes in blends can have a consequent impact on signal quality and perception by the responders. For instance, the ability of herbivory-induced volatiles to reveal herbivory, a system used to attract natural enemies, depends on canopy conditions and is strongly dependent on the reaction rate of the compounds[45].

The liquid environment acts as a major carrier for non-volatile and semi-volatile compounds in nature via diffusion and advection, which in turn depend on temperature, the polarity of the compound and concentration differences between producer and carrier[89]. The transport of metabolites in soil is also partly ensured via air and liquid carriers, but also depends on solid particles. Hence, additional parameters such as substrate texture and moisture, pH, porosity, and percentage of organic matter are important to consider for the transport of non-volatile compounds, as well as the diffusion rate of volatile compounds[90–92]. In fact, these parameters influence the chemical gradient between emitters and responders. For example, the diffusion of the volatile sesquiterpene (*E*)-β-caryophyllene from corn roots into the soil, used by entomopathogenic nematodes to locate herbivore-damaged roots, is dependent on soil composition and humidity[11,91]. Improve measurements and predictions of the fraction of chemodiversity available at variable distances from the producer is key to understand how chemodiversity scales from individual to communities and landscapes (Fig. 2).

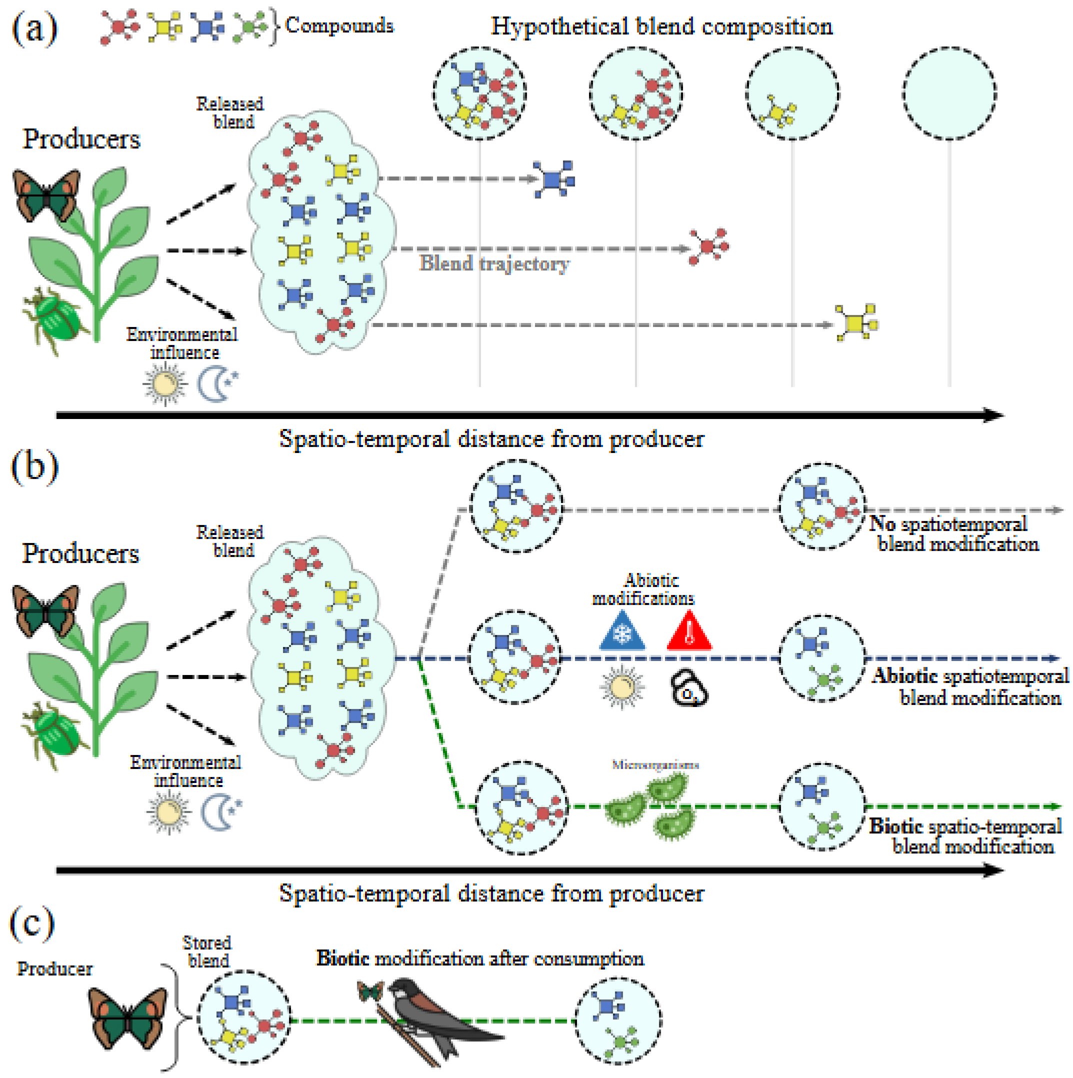

Figure 2

Influence of chemical blend modifications by other organisms

Many organisms can alter the chemical blend after release into the environment (Fig. 2b). Microorganisms have colonised most of the carrier environments and can, for example, metabolise plant exudates such as benzoxazinoids into antimicrobial compounds [93–95], degrade biogenic volatile organic compounds[96], or create new alkaloids to deter feeding insects[97,98]. Natural processes such as decay are also influenced by microorganisms that will shape volatile emissions, which in turn influence carcass foraging and choice by scavengers[99,100]. Mycorrhizal networks can even act as a new carrier by transporting (up to larger distances than diffusion) and shaping chemical signals between plants[101–103]. Chemical information can be modified, transported, and used for additional purposes beyond the producer's target interaction via **non-consumptive** and **consumptive processes** (Fig. 2b and 2c). For instance, lemurs fur-rub millipedes for their benzoquinone secretions, a defensive mechanism of the millipedes, over different parts of the body for social communication or self-medication[104]. Similar non-consumptive processes were observed in coatis and titi monkeys for disabling arthropods' defence or scent-marking, thus transforming *and* transporting the chemical blend[105,106]. Male orchid bees collect floral scents as part of their mating behaviour[107]. Such processes expand the spatiotemporal distribution of metabolites. Further transformation of the blend also occurs within the responder and depends on the rate of mass transfer and catabolic activity within the responders and on its internal microbiota or parasites[108,109]. Such transformations by or within the responder contribute to shaping the chemical blend at the ecosystem level. For instance, oral and gut microbiota influence taste perception and food processing[110]. Influenced by their microbiome, aphids can modify the honeydew chemical blend that mediates relationships with ants and natural enemies[111,112]. Further investigations of the selection and transformation of the chemical blends within (a)biotic carriers are crucial to improve our understanding of their consequences for producer-responder interactions and to fully appreciate the role of chemodiversity in ecosystem processes.

3. Scaling up chemodiversity: toward emergent functions at broader scales

When considering chemodiversity at broader spatiotemporal scales (i.e., when moving from the level of individual organisms to populations, communities, and ecosystems), the chemical environment becomes increasingly complex and dynamic. The ecological effects of chemical mixtures are determined by potential transformation through various processes (see Section 2), as well as the spatial and temporal overlap in emissions from multiple, co-occurring chemical sources (Fig. 3). This raises an important question: how does chemodiversity shape ecological functions when it emerges from the collective chemistry of entire systems rather than from individuals?

Although recent progress has been made, chemodiversity research predominantly focuses on the context of individual-level pairwise interactions, with limited exploration of the ecological effects of community-level mixtures or chemically complex landscapes[20,26,113]. Closing this gap requires a re-framing of fundamental ecological questions from the traditional "What function does this chemical compound or class serve?" to "Under which environmental conditions do the compound or mixture change its functional relevance?" This shift moves us toward the recognition of a chemical mixture as a complex adaptive system that gains some of its functionality through **emergent properties**: novel outcomes arising from the integration of multiple system components that cannot be predicted from those components in isolation[114]. In fact, the functionality of a chemical blend as an emergent property is at the core of chemodiversity theory: many central hypotheses, such as the synergy hypothesis or the multiple-signal hypothesis, explicitly build on the idea that the integration of multiple compounds may produce effects greater than the sum of their parts[20,21,115–117]. Consequently, the chemodiversity of blends has been shown to constitute a functional trait in its own right, rather than being an additive reflection of compound-specific functions[118,119]. However, if chemodiversity gives rise to emergent properties at broader spatial scales, a key challenge for chemical ecology is to understand when, where, and under which conditions these properties matter[113].

Though limited in number, plot- and community-scale studies represent a promising first step to understanding how chemodiversity functions across ecological scales. Experimental research has shown that manipulating intraspecific chemodiversity among neighbouring plants shapes insect community composition and alters plant reproductive success[24,25,27,69,120]. Complementary, observational work in natural systems shows that floral scent and colour traits in chemodiverse Mediterranean plant communities converge to match pollinator sensory preferences[121]. Experimental evidence further indicates that such convergences are not limited to flowering individuals: non-flowering plants also emit volatiles from their vegetative tissue that attract generalist pollinators[122], suggesting that plants in phenological stages previously considered functionally irrelevant nonetheless contribute to community-level pollinator attraction. These findings demonstrate that entire communities can form a common 'chemosensory landscape'[122], in which overlapping olfactory cues function as collective attractants whose effects cannot be predicted from individuals alone. Such intermediate-scale studies provide critical insights into how chemical mixtures may acquire novel functions, and offer an empirical foundation for investigating how chemodiversity might scale up to shape ecological dynamics across entire landscapes (see section 4).

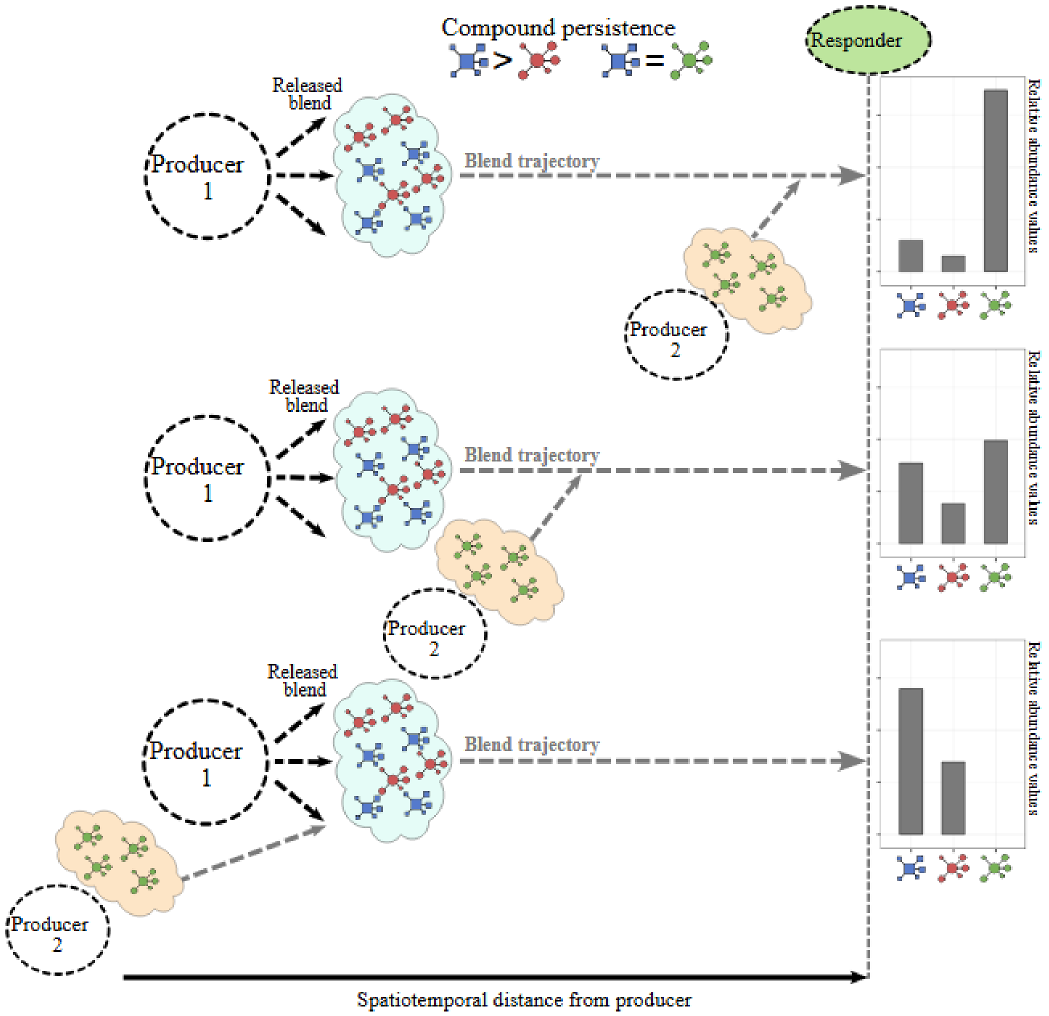

Figure 3

Potential of harnessing chemodiversity landscapes

Beyond their ecological importance, emergent functions of chemodiversity offer promising opportunities for practical applications, particularly in sustainable agriculture and ecological restoration. For instance, intentionally enriching chemical landscapes could promote beneficial ecosystem services such as pollination and pest suppression. In fact, concrete examples where humans actively manage phytochemical diversity to their advantage are already available. Push-pull agricultural systems provide a well-known case, where specific plant species are intercropped to emit repellent or attractive volatile blends, thereby pushing pests away from crops and pulling them toward trap plants[123,124]. In pasture systems, the emerging concept of 'healthscapes' explores how increasing the chemodiversity of forage plants can improve animal health by exposing grazers to a broader spectrum of bioactive compounds[125,126]. However, to fully harness the potential of chemodiversity, we must deepen our understanding of how chemodiversity translates into ecological functions across spatial and temporal scales. This includes identifying which chemical blends drive desired outcomes, how they interact with environmental context, and how they can be maintained or restored in managed ecosystems[127]. Gaining such mechanistic insights could ultimately enable the rational design of chemical landscapes as a sustainable tool for ecosystem management.

Loss and change of chemical functionality

The Earth is experiencing unprecedented rates of global change[128]. Biodiversity loss, land-use change, environmental pollution, and other anthropogenic pressures threaten the integrity of ecological processes that depend on complex chemical interactions[129]. Alterations in soil chemistry, air composition, or water quality can interfere with signal transmission and perception in ways that so far only remain poorly understood[130]. In aquatic systems, pollution with microplastic particles has been shown to adsorb chemical cues, thereby disrupting the ability of *Daphnia longicephala* to perceive vital chemical information on nearby predators[131]. Similarly, the extensive use of pesticides in agriculture interferes with legume-rhizobium chemical signalling and leads to reduced nitrogen fixation, thus impacting plant growth[132]. Elevated ozone levels have been shown to degrade the floral scent profiles of *Nicotiana suaveolens*, resulting in fewer pollinator visits[133]. Yet, the opposite trend, an increase in metabolites that enriches chemical blends on the landscape scale, is not inherently beneficial. Climate change is projected to make the world more heavily scented[134], while invasive species produce more unique chemical profiles than their native counterparts[135,136]. However, increasingly complex chemical backgrounds can also impair the ability of pollinators to identify biologically relevant signals[137]. These disruptions, whether caused by the loss or overabundance of chemical signals, are highly context-dependent and may unfold gradually, remaining undetected until their ecological consequences become difficult to reverse.

As natural communities simplify or change, the chemical interactions they once mediated may disappear as well, potentially disrupting long-standing ecological networks. Many organisms likely depend on the composition and predictability of the surrounding chemical environment, such as the community-level sensory landscapes described in pollination systems[121]. Surrounding chemicals are also essential for behaviour as illustrated by the relationships between the chemosensory complexity of the environment and brain volume in lizards[138]. A loss or gain of producers could alter these sensory environments, change the ecological meaning of chemical information and disrupt ecological networks. In complex, long-established communities where producers and responders have co-evolved over evolutionary timescales[139,140], the breakdown of such finely tuned interactions could compromise not only ecological functioning, but also the services ecosystems provide[141]. Similar losses occur in agri- and silvicultural systems, where the replacement of chemodiverse traditional cultivars with genetically uniform high-yielding varieties, coupled with a loss of weed and understory species diversity, reduces phytochemical richness[142]. This erosion of chemodiversity may weaken natural pest control and other ecological functions that depend on diverse chemical signalling[142,143]. Furthermore, the chemodiversity of one ecosystem compartment can directly shape ecological processes in another compartment through tight coupling between organismal groups at the landscape scale[144,145]. For instance, in freshwater systems, multifunctionality partly emerges from a tight chemical coupling between terrestrial and aquatic environments: Dissolved organic matter originating from the surrounding vegetation is transformed by microbes within the lakes, thereby fuelling the functioning of the aquatic ecosystem[146–148]. However, global change induced increases in terrestrial plant productivity are associated with shifts toward fast-growing plants that invest less in protective specialised compounds[149]. As a result, organic matter chemodiversity reduces aquatic ecosystem functioning and leads to higher CO_2 emission rates from lake ecosystems[150]. Yet, the critical role of such cross-system chemodiversity transfer in sustaining landscape-scale functioning remain so far only poorly understood[151,152].

These findings raise broader questions about the resilience of chemical landscapes. If chemodiversity underpins key ecosystem functions, can these functions recover once (chemo)diversity is lost or do ecosystems shift into new, chemically and functionally altered states? Conversely, will ecosystem functions be altered by the addition of metabolites, for instance via invasive species[136], or the introduction of synthetic chemicals, or can the potential effects be mitigated by the overall chemical blend? Although the concept of ecological resilience has been widely studied in other fields of ecology[153,154], the stability and recoverability of chemodiversity-mediated interactions remain poorly understood. In systems where ecological processes depend on the richness and structure of chemical mixtures, diminished chemodiversity could result in persistent functional loss, even if biodiversity or environmental conditions improve. However, the ecological consequences of a species loss may depend less on the species itself than on whether other producers maintain overlapping chemical functions, i.e., chemical redundancy. It is critical to understand when such shifts occur, whether they are reversible, and what thresholds govern transitions between functional states to reliably forecast ecological trajectories under global change and the design of strategies to sustain or restore the functional integrity of chemical landscapes.

4. Conclusion and future directions

Our broader ecological understanding of the consequences of chemodiversity remains incomplete but continues to develop[23,155]. To advance the field, research needs to clarify when and where chemical mixtures become functionally relevant, identify the abiotic and biotic factors that shape these dynamics, and develop approaches to manipulate and monitor chemodiversity across landscapes (see future directions proposed in Box 1). To reach these goals, future research must combine observational and experimental studies that allow chemodiversity to be manipulated in a systematic way on wider scales. Observational studies are essential for characterizing the natural variability of chemodiversity landscapes. Fine-scale measurements near emitting organisms as well as canopy- or atmosphere-level observations exist, but the mechanisms and spatio-temporal dimensions by which local chemodiversity integrates into larger-scale signals, as well as their ecological consequences remain largely unknown. In addition, researchers could experimentally vary the composition and richness of producer communities in a near-natural way to manipulate their forecasted cumulative chemodiversity, adjust abiotic parameters such as temperature or humidity, or modify the properties of the carrier medium through which volatiles are transported. Such experiments would help identify the ecological thresholds and tipping points at which new chemical functions emerge or vanish. Similarly, these studies could define critical thresholds for the improvement or loss of various ecosystem services and ultimately reveal whether chemical landscapes are flexible and resilient to global change or vulnerable to collapse.

While considerable research underpins our understanding of chemodiversity at smaller scales, the next significant challenge lies in scaling this knowledge up. In other words, the field should now move beyond asking what chemodiversity *is* towards asking how it *operates*, when it *matters*, and how its benefits can be *harnessed*. While the conceptual groundwork for understanding the importance of chemodiversity has been established, the next steps lie in translating these ideas into ecological insight across real-world systems (Box 1). Expanding research to encompass landscape-level chemodiversity will enable a deeper understanding of ecological dynamics, providing insights into how chemical communication shapes broader community interactions, ecosystem functions, and the benefits nature provides to people.

Box text:

Box 1: **A workshop survey to advance landscape-level chemodiversity research**

This perspective emerged from the workshop "Phenotypic Plasticity and Chemical Diversity" organized in November 2024 by the German research unit on the ecology and evolution of intraspecific chemodiversity in plants (FOR 3000), where experts working across all levels of biological organization and on a broad variety of taxa, discussed current challenges, conceptual gaps, and future directions in plant chemodiversity research. To support the development of a research agenda on landscape scale chemodiversity, we conducted a survey in which leading researchers in chemical ecology present at the workshop contributed and rated questions on the future of chemodiversity research.

Discussions during the workshop converged on the idea that chemodiversity at broader geographical scales represents a critical but underexplored dimension of ecological complexity that is present in nature, yet remains conceptually and methodologically challenging to tackle. To better identify near-term needs for advancing landscape-level chemodiversity research, participants were asked to submit their three most pressing questions after the meeting (Supplementary Information 1). These questions were then evaluated by the attending researchers. Importantly, the survey reflects the views of a self-selected group of experts in the field and although representing expertise across all levels of biological organization and various taxa, the survey should be read as a guide to emerging priorities rather than a field-wide consensus.

Emerging Priorities from the workshop survey

The survey yielded 54 questions that grouped into eight thematic categories, reflecting a broad spectrum of perspectives on chemodiversity from ecology and evolution to methodological perspectives (Fig. Box 1a; see Supplementary Information 2). Although all categories represent pressing research areas, respondents prioritized questions of ecological understanding and application to strengthening our understanding of *eco-evolutionary dynamics*, *chemical communication*, and *ecosystem functioning*, while questions rooted in *theory* and *measurement technology* received comparatively lower average ratings (Fig. Box 1). Our survey highlights a growing consensus that chemodiversity research is approaching a turning point: from conceptual and individual-based exploration towards larger-scale empirical testing and ecological integration to understand how chemodiversity operates under real-world conditions. To move forward, this transition calls for pairing existing knowledge and established methodologies with a renewed effort to expand experimental and observational work. In particular, there is a need to develop research designs that disentangle the drivers, dynamics, and ecological consequences of chemodiversity. This includes identifying spatial, temporal, and environmentally driven concentration thresholds at which chemical mixtures acquire or lose their ecological functions. The need to explore multitrophic interactions and the link between chemodiversity landscape and ecosystem services is also pinpointed.

Box 1 continued

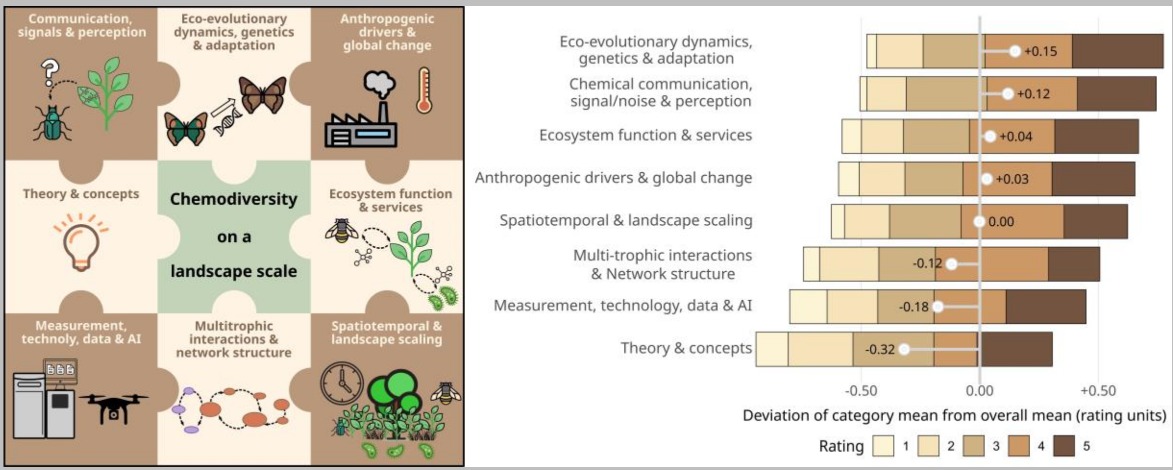

Figure Box 1

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Figures

Figure 1

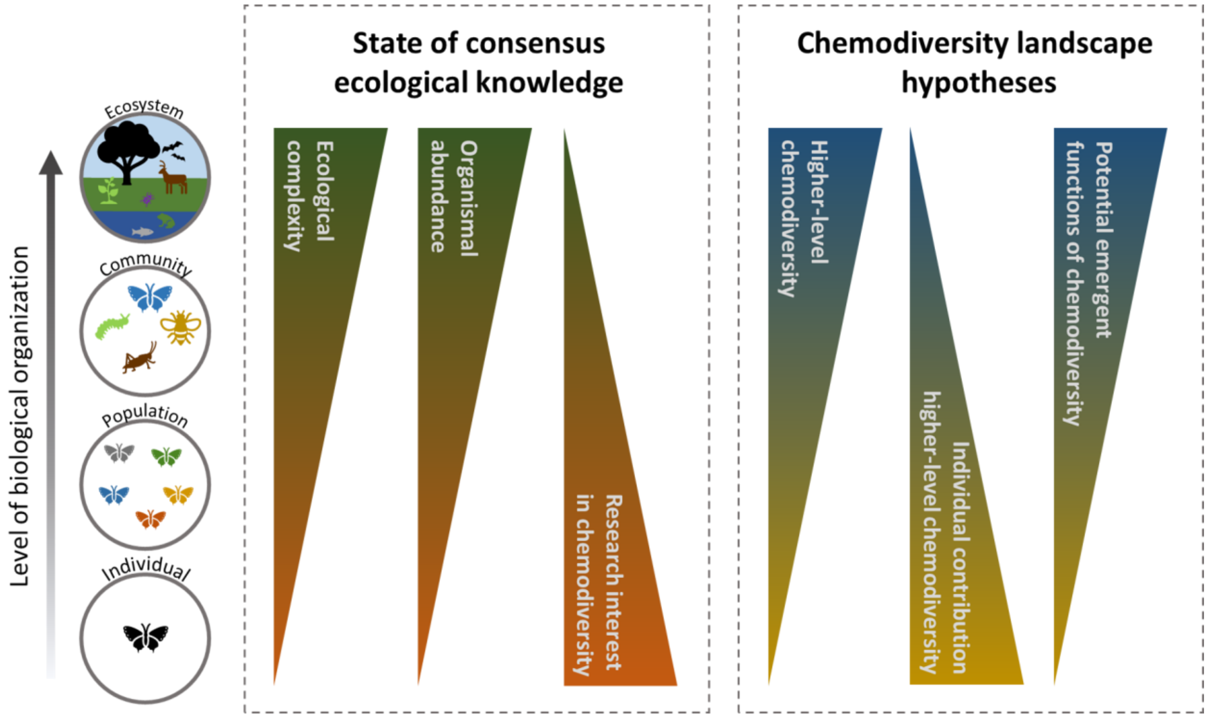
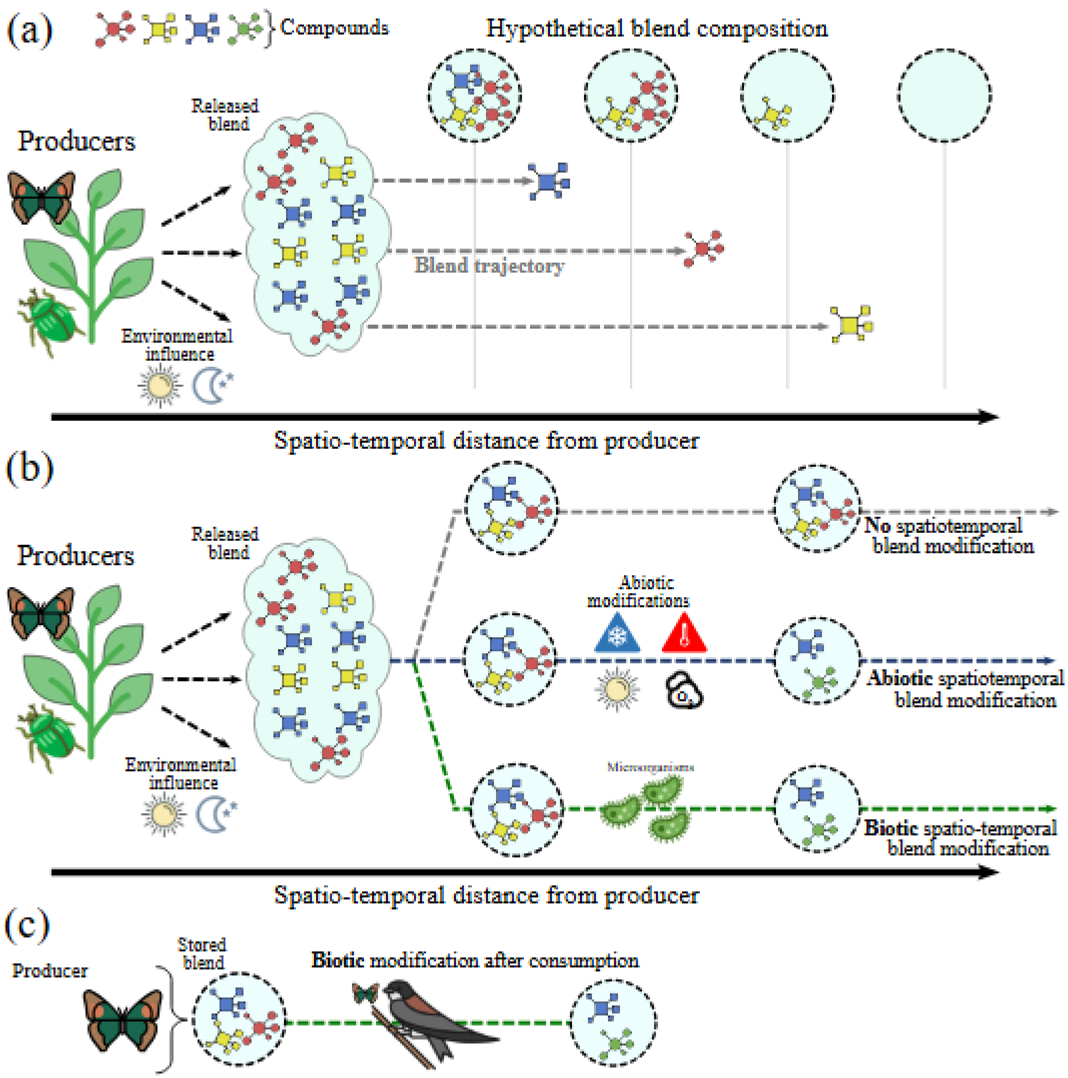


Figure 2



(a)
Compounds
Hypothetical blend composition
Producers
Released blend
Blend trajectory
Environmental influence
Spatio-temporal distance from producer
(b)
Producers
Released blend
Environmental influence
No spatiotemporal blend modification
Abiotic modifications
Abiotic spatiotemporal blend modification
Microorganisms
Biotic spatio-temporal blend modification
Spatio-temporal distance from producer
(c)
Producer
Stored blend
Biotic modification after consumption

Figure 3

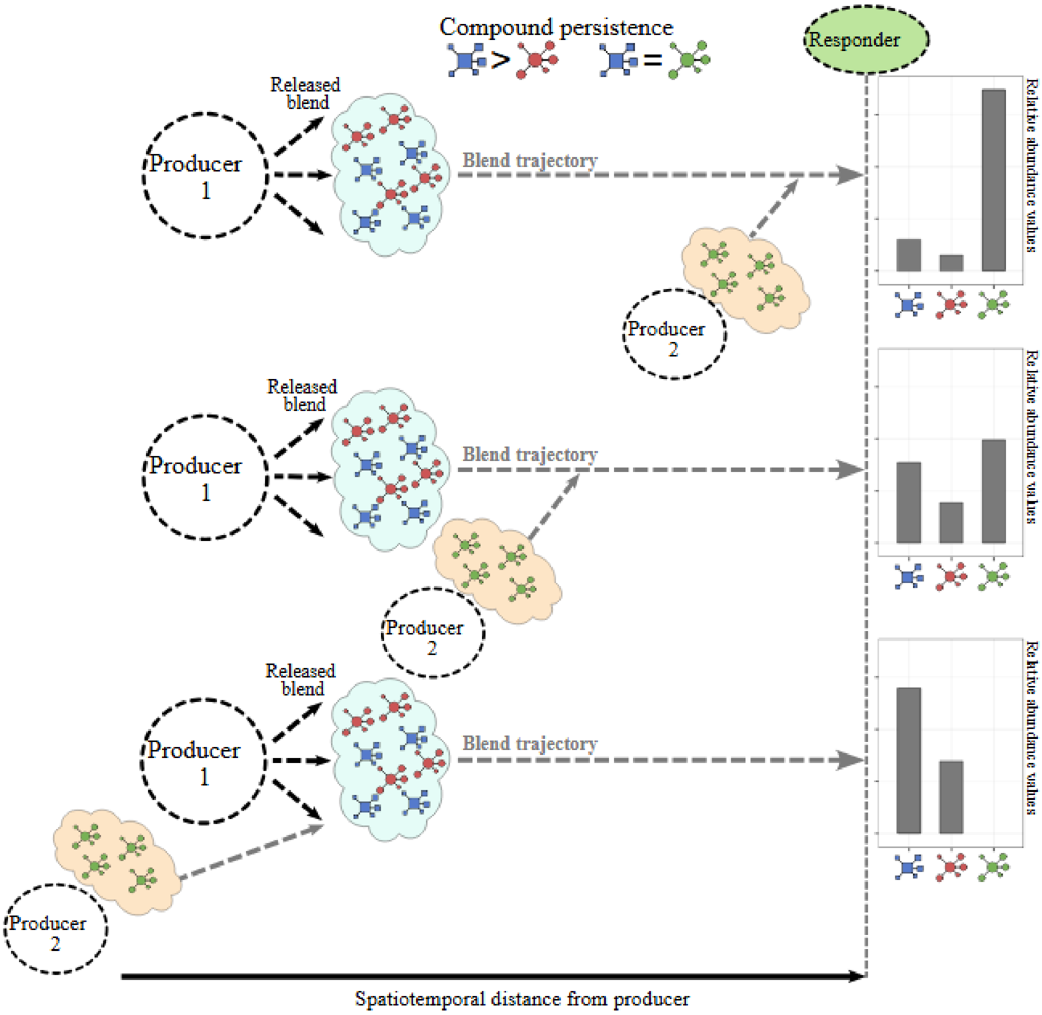

Compound persistence
Responder
Released blend
Producer 1
Blend trajectory
Producer 2
Relative abundance values
Released blend
Producer 1
Blend trajectory
Producer 2
Relative abundance values
Released blend
Producer 1
Blend trajectory
Producer 2
Relative abundance values
Spatiotemporal distance from producer

Figure Box 1

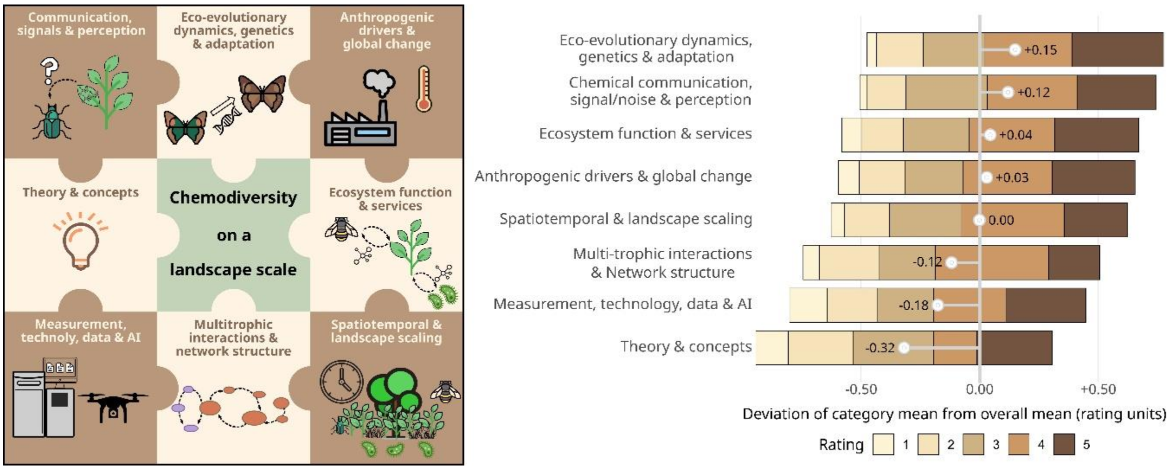

Communication, signals & perception
Eco-evolutionary dynamics, genetics & adaptation
Anthropogenic drivers & global change
Theory & concepts
Chemodiversity
on a
landscape scale
Ecosystem function & services
Measurement, technoly, data & AI
Multitrophic interactions & network structure
Spatiotemporal & landscape scaling
Eco-evolutionary dynamics, genetics & adaptation
Chemical communication, signal/noise & perception
Ecosystem function & services
Anthropogenic drivers & global change
Spatiotemporal & landscape scaling
Multi-trophic interactions & Network structure
Measurement, technology, data & AI
Theory & concepts
+0.15
+0.12
+0.04
+0.03
0.00
-0.12
-0.18
-0.32
-0.50
0.00
+0.50
Deviation of category mean from overall mean (rating units)
Rating
1
2
3
4
5

Figure legends:

Figure 1: Conceptual figure depicting the state of ecological consensus and hypotheses on ecological and chemical complexity across levels of biological organisation. The left panel depicts the general consensus that ecological complexity and organismal abundance increase with increasing levels of biological organisation and how this is incongruent with the research interest that chemodiversity has received in the different subfields of ecology in recent years. The right box posits novel hypotheses regarding individual- and higher-level chemodiversity across levels of biological organisation and the associated potential for emergent functions of chemodiversity.

Figure 2: Conceptual model illustrating the transformation of the emitted chemical blend during its transport toward responders. The model distinguishes non-consumptive and consumptive processes. **a.** Spatio-temporal, non-consumptive shifts in blend composition due to intrinsic compound properties (e.g. volatility, diffusivity), which determine how far and how long individual metabolites persist. **b.** Modification of the blend by abiotic and biotic factors, encompassing both non-consumptive (e.g. oxidation, photolysis) and consumptive (e.g. microbial transformation) processes that alter individual metabolites. Processes in panels a and b typically occur simultaneously. **c**. Additional biotic alteration through trophic consumption (e.g. predators consuming emitters or tissues thereof).

Figure 3: Conceptual model illustrating how the chemical blend received by a responder varies with spatial and temporal distance from multiple emitters, due to differences in compound persistence. Producers emit distinct compounds (coloured shapes) that vary in environmental persistence, depending on volatility, degradation, carrier properties, modifications or other factors. As blends move through space and change over time, the concentrations of their constituent compounds shift. The responder therefore receives different blends depending on its position: in the top and bottom scenarios, the signal is dominated by compounds emitted by the nearest producer, whereas the middle scenario shows a more even blend when the responder is situated between producers. These spatial and temporal dynamics shape the composition and evenness of the chemical blend, suggesting that emergent properties may depend not only on what is emitted, but when and where signals are perceived in the landscape.

Figure Box 1: Research priorities for advancing chemodiversity research at the landscape scale. a) Overview of identified research priorities, grouped into eight thematic categories. Each category represents a critical dimension of landscape-scale chemodiversity, and together they form an interconnected research agenda, illustrated here as interlocking puzzle pieces. b) Results from a workshop survey in which 54 questions (here grouped by category) were rated for importance on a scale from 1 (low) to 5 (high). Lollipops and placement of the bar represent deviation from the category mean from overall mean.