Meta-CHANS: Linking Metacommunity Ecology with Coupled Human and Nature Systems to Foster Conservation Management

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Abstract

Spatial processes shape both ecological dynamics and human decision-making. Here, we propose a unifying framework – Meta-CHANS – that integrates metacommunity ecology into the concept of Coupled Human And Natural Systems (CHANS). We highlight how recent theoretical and methodological advances, especially in species distribution modeling and process inference, allow the identification of dominant metacommunity dynamics and their consequences for biodiversity and ecosystem function. We discuss how coupling between human and natural systems across spatial scales might influence ecosystem processes and properties, and how this can inform a decision-making process using elements of structured decision-making. We demonstrate the applicability of our Meta-CHANS framework with three selected examples from river management, urban green space planning, and invasive species management. We illustrate how local- and landscape-level intervention alternatives might lead to different outcomes in terms of metacommunity processes, emerging metacommunity archetypes, and ecosystem properties, and highlight the potential of Meta-CHANS to bridge ecological theory and applied environmental decision-making.

Introduction

Since millennia, humans have been part of natural systems, but we have now reached a point where virtually no part of Earth is free of human influence. Over the past decades, conservation thinking has shifted from the concept of “nature for itself” through “nature despite people” and “nature for people” to the current view of “people and nature”, which emphasizes the reciprocal links between humans and natural systems (Mace 2014). This perspective is addressed explicitly in the concept of Coupled Human And Natural Systems (CHANS; Liu *et al.* 2007, 2021), which builds on the idea that both ecological and socio-economic systems are complex with coupling effects between them. The two systems share many characteristics, including nonlinear relationships, adaptive components, feedback loops, multiscale structures in space and time, and have multiple connections and interdependencies. This complexity is a challenge for developing conceptual frameworks that can efficiently address the links and feedback routes between the two systems.

A key feature of both socio-economic and ecological processes and dynamics is their strong spatial components. Local systems are influenced by the regional context, while ecological processes and management decisions at local scales can also have regional consequences. Meta-ecology (Schiesari *et al.* 2019) - a collective term encompassing metapopulation (Hanski 1998), metacommunity (Leibold *et al.* 2004) and meta-ecosystem ecology (Loreau *et al.* 2003) - explicitly accounts for spatial dynamics and landscape structure (Cid *et al.* 2022; Little *et al.* 2022; Schiesari *et al.* 2019). We propose that integrating meta-ecology (Schiesari *et al.* 2019)

105 with the CHANS concept (Liu *et al.* 2007, 2021) therefore provides a useful framework for a
106 better understanding of the joint human and ecological spatial components, which can support
107 more realistic and effective conservation management decisions.
108
109 For this integration into the CHANS concept, we here focus on metacommunity ecology
110 because it has rapidly developed into a sufficiently mature field that encompasses all the major
111 factors underlying dynamics of ecological communities across spatial scales. Depending on the
112 context, this may also involve metapopulations (when single species are of interest or species
113 of interest do not interact with each other) and/or meta-ecosystems (when the flux of materials
114 and energy in a landscape are of interest). Metacommunity ecology incorporates key aspects of
115 metapopulation ecology, especially when evolutionary processes and landscape genetic
116 structure are included, such as in the evolving metacommunity framework (Urban *et al.* 2008).
117 In addition, it has important implications for meta-ecosystem dynamics through the structure,
118 diversity, and evenness of metacommunities.
119
120 Below, we first outline fundamental features of socio-economic dynamics in decision-making
121 and the CHANS concept in a simplified form, highlighting its key elements most relevant for
122 biodiversity conservation. We then describe the fundamentals and multi-scale dynamics of
123 metacommunity ecology and how these two perspectives can be integrated within a CHANS
124 framework, resulting in a new framework that we call Meta-CHANS. We illustrate the
125 applicability of this framework with three examples of applied environmental issues that have a
126 clearcut spatial component: river management, urban green space planning, and invasive

species management. Using these examples, we highlight how shifting the scale (from local to regional) in management alternatives can modify spatial processes, with consequences for ecosystem properties and nature's contributions to people (NCP).

Structured decision-making and the concept of Coupled Human And Natural Systems (CHANS)

At the practical level of environmental management, we draw upon the structured decision-making framework developed by Gregory *et al.* (2012), building on the work of Clemen & Reilly (1999). This framework integrates three key components: a) science-based approaches, b) consensus-based societal procedures, and c) technocratic tools, e.g. economic evaluation based on multi-criteria approaches, typically focused on utility. The structured decision-making framework emphasizes the balanced use of these three components using sequential steps (depicted in **Figure 1a**) with useful decision-making as its final goal. We argue that such an approach can be especially useful for practical decision-making when there is sufficient understanding of many of the specific issues involved, which is typically the case in issues occurring at local or smaller regional scales.

However, CHANS can also involve more general policy issues at larger spatial, socio-economic, and temporal scales (Díaz *et al.* 2018). Here, we incorporated elements from the ecosystem

147 services literature (Daily *et al.* 2009; Mandle *et al.* 2021; Xu & Peng 2022) and political theory
148 (Ostrom 2009; **Figure 1b**).

149

150 There is a parallel structure on the human side of CHANS and metacommunity dynamics, as
151 more immediate, context-dependent decisions take place at local scales and interact with
152 broader policy components at regional or international levels. Here, we aim to provide tools to
153 support pragmatic decision-making, especially at the local scale, e.g. managing a single lake or a
154 forest lot in a nature reserve corresponding to a local community in ecological terms. However,
155 just as local communities are shaped by regional processes, local human decisions are also
156 affected by broader policy and political context. This can also feed back to affect local decision-
157 making (albeit more slowly; **Figure 1c**). This interaction is mediated via a two-fold
158 understanding of NCP and nature-based solutions (Díaz *et al.* 2018; IPBES 2019; Pascual *et al.*
159 2017 – amended from "ecosystem services" in earlier literature). On one hand, the NCP
160 framework defines a general value system for ecosystems (**Figure 1b**), which affects the ways
161 societies develop institutions (both private and governmental) that in turn influence policies
162 affecting the regulation and legal context of decision-making. On the other hand, NCP have a
163 central role in structured decision-making as part of evaluating trade-offs (**Figure 1c**),
164 interacting with other human drivers, such as economic or socio-cultural factors, that affect the
165 utility (economic substitutability) of NCP in pragmatic decision-making (see e.g. Langhans *et al.*
166 2019).

167

What is metacommunity ecology, and how does it work?

Community dynamics that determine the composition of local biotic assemblages in a landscape involves four primary processes: selection, dispersal, drift (stochasticity), and speciation (novelty) (Thompson *et al.* 2020; Vellend 2010) (**Figure 2** and **Table S1, SI**). The first of these five processes is density-independent selection (usually involving selection in response to local abiotic conditions) in which species have intrinsic growth rates related to environmental factors that are thought to be unaffected by the biota (e.g. temperature, salinity, incoming light, etc.). The second process is density/frequency-dependent selection in which different species are favored depending on the presence/abundance of other species and feedback among their interactions. This can involve direct interactions among species or indirect ones (involving e.g. resource competition, predation, mutualism, etc.). The third process is dispersal or the movement of individuals among localities. If this is insufficient, some localities will not be occupied by all appropriate species, even though they might be favored there, because they cannot colonize or have not yet been able to do so. In contrast, if dispersal is in excess, some localities may be occupied by species that would otherwise be selected against, because they immigrate at sufficient rates to maintain sink populations due to dispersal from source populations where they are successful. The fourth primary process is stochasticity which accounts for a variety of effects that cannot be related to the processes above, including disturbances due to outside forces and drift that accounts for the stochastic nature of demographic events (e.g. births, deaths) or colonization events that can determine the order of arrival of different species. The fifth and final process is 'novelty'. (Vellend 2010) originally

conceived of this as primarily involving speciation, but it may make sense to include any process that changes the nature of the regional biota, such as long-distance colonization, perhaps due to human activities. To date, novelty has received much less attention in metacommunity ecology than the other four processes (but see Leibold *et al.* 2022a; Urban *et al.* 2008). However, given the accelerating pace of human-induced changes to ecosystems, it may become increasingly relevant (e.g. Heger *et al.* 2019). While we do not explicitly analyze novelty in the present framework, we include it as a placeholder among metacommunity processes to reflect its potential importance and to encourage future work on this emerging concept.

The interactions of these processes in a landscape can be extremely complex. However, work done to date in metacommunity ecology has characterized the possible outcomes into a set of 'archetypes' that can be seen as rough characterizations (**Box 2**, see Leibold *et al.* 2004; Leibold & Loeuille 2015). These range from outcomes that strongly relate species distributions to abiotic environmental factors (called 'species sorting') to outcomes that include high stochasticity (these include 'patch dynamics' and 'neutral theory' archetypes) to intermediate outcomes (that include 'mass-effects', 'harlequin patch dynamics', and 'priority effects').

As a first approximation, the basic processes described above can be studied using Joint Species Distribution Models (JSDMs, **Box 1**). Although there are several technically distinct implementations of such models (e.g. Ovaskainen *et al.* 2017; Pichler & Hartig 2021), they aim to partition the total variation in community composition among sites in a metacommunity into components that are due to measured environmental factors, spatial patterns that should

reflect dispersal, and patterns in co-distributions that are likely to be affected by species interactions (Leibold *et al.* 2022b; Ovaskainen *et al.* 2017, **Box 2**). While such methods have important limitations (e.g. Blanchet *et al.* 2020; Poggiato *et al.* 2021; Zurell *et al.* 2018), ongoing efforts are likely to produce important improvements in the future.

One key feature of JSDMs, that contrasts with previous approaches like variation partitioning of community data, is that they can be used to isolate how each species in a metacommunity affects the overall structure of the metacommunity (Leibold *et al.* 2022b; Ovaskainen *et al.* 2017). And they can also be used to assess how each locality in a landscape affects overall metacommunity structure (Leibold *et al.* 2022b). Consequently, it is easier to diagnose which species and which sites are most important in determining the overall structure of the metacommunity. At a rough level, the overall structure of the metacommunity can be characterized as primarily falling into a limited set of archetypes (**Figure 2**). Four of these, including species sorting, mass effects, patch dynamics and neutral theory, have long served as the conceptual foundation of metacommunity ecology (Holyoak *et al.* 2005; Leibold *et al.* 2004; Leibold & Chase 2018), whereas the others, harlequin patch dynamics and priority effects (**Box 2**) are less integrated and therefore might still be somewhat underrepresented. JSDMs (**Box 1**), via partitioning of co-occurrence, environmental and spatial components of species distribution patterns, allow us to link the distributions of individual species and sites to these archetypes and, as such, this can help target conservation and restoration efforts in a more precise manner than would have been possible before. Because these archetypes are associated with different metacommunity attributes, including biodiversity conservation, stability of metacommunity

234 structure (e.g. Gravel *et al.* 2011; Shoemaker & Melbourne 2016), and productivity, and may
235 have possible extensions to harvesting and use of natural resources, they provide important
236 insights into the metacommunity and how it may be altered by management and policy issues.
237
238 At a local scale, ecosystem-level attributes depend on how abiotic factors interact with
239 community composition to produce some aggregate property of a locality. In general, it is the
240 case that some major ecosystem attributes, including local ecosystem production and biomass
241 (Thompson & Gonzalez 2016), invasion resistance (Case 1990; Howeth 2017) as well as
242 regional-scale stability (Shoemaker & Melbourne 2016), are generally highest when species
243 composition tracks local abiotic environmental conditions as characterized by the species
244 sorting archetype. Other archetypes typically have lower levels of ecosystem function for most
245 of these attributes. For illustrative purposes, here we focus on species coexistence as a form of
246 stability where we can draw directly on Schoemaker and Melbourne (2016). To illustrate the
247 link between metacommunity archetypes and some key metacommunity attributes, we chose
248 mean local and regional diversity, mean local biomass (or abundance), and mean local stability
249 in terms of species coexistence (**Figure 2**).
250

251 Contextualizing metacommunity ecology with an integration of pragmatic
252 structured decision-making and socio-economic elements of CHANS

253

Here, we aim to link ecological dynamics, as approached through the lens of metacommunity ecology, to human activities, involving both narrowly defined practical management, and more general policymaking by integrating the metacommunity framework and the structured decision-making framework.

Our general approach is described in **Figure 3**. We integrate a general decision-making scheme used in conservation ecology (e.g. Backstrom *et al.* 2018; Gregory *et al.* 2012; **Figure 1a**) with a conceptual approach directed at policy-making (Daily *et al.* 2009; **Figure 1b**) and insert the concept of CHANS that describes relevant socio-economic dynamics (**Figure 1c** and the right side of **Figure 3**, which could be also imagined as a third dimension; gray) as well as relevant ecological dynamics (processes and ecosystem consequences in the green and blue fields of **Figure 3**). Integrating multiple spatial scales into the CHANS framework is essential to better understand the links and feedback routes between human and natural systems (Kramer *et al.* 2017). We argue that integrating metacommunity theory within the proposed framework is the most direct and effective approach to do this, given the scale-explicit nature of the metacommunity approach toward understanding ecological dynamics.

The left side and the central part of the figure combine structured decision-making (central part in brown ovals) at both local (left side, green background) and landscape (right side, blue background) levels. The final elements of structured decision-making (optimization and implementation) are shared to show that these aspects should integrate and optimize options jointly at both scales. In parallel with structured decision-making, we consider how

276 metacommunity ecology at the local scale (left side in green rectangles) and landscape scale
277 (right side in blue) link relevant processes and basic effects to emergent ecological properties at
278 both scales. Jointly, these effects can then be evaluated into their contributions to NCP to affect
279 the optimization step in the structured decision-making.
280
281 The right side of the figure (gray boxes and arrows, modified from Daily *et al.* (2009) identifies
282 the process that evaluates the consequent NCP of the system to affect socio-economic values
283 for humans. These then affect socio-political dynamics, perhaps by leading to the creation or
284 modification of appropriate (regulatory or policymaking) institutions that then implement
285 policy in the form of regulations or other legal or institutional tools. These are then
286 incorporated with other more socio-economic factors (e.g. financial, cultural, political). In
287 principle, this can then allow changes in the utility functions that can inform optimization by
288 technically based criteria, e.g. cost-benefit analyses.
289
290 **Figure 3** thus provides a structural synthesis of metacommunity ecology (emphasizing aspects
291 driven by ecological processes) and human ecology (emphasizing complex socio-economic and
292 cultural aspects) into a single synthetic framework. We especially wanted to separate these
293 various components into local-scale components (referring to management-scale) that are
294 often more transparent, and larger-scale components that are important because they
295 indirectly (and sometimes more slowly, but perhaps more permanently) feedback to alter this
296 decision-making process.
297

Application of the Meta-CHANS framework

The proposed framework incorporates basic ecological principles into the analysis and implementation of CHANS. We next illustrate how this framework could be used in conservation policies and management by providing three worked-out examples (**Figures 4-6**) that differ in terms of how both human and natural systems are coupled to each other, covering riverine management, urban green space planning, and invasive species management. Our goal is to illustrate how local and regional (landscape) narratives might arise as different management alternatives for the same decision context and general objectives. Usually, any decision-making includes several tradeoffs and a multitude of different approaches; for our examples, we will show the outcome of different scales of management decisions in four cases within each example and how they might alter metacommunity processes and basic effects. Some of these management alternatives are more inspired by human utility, while others primarily aim for restoration. It should also be noted that the results of the management choices presented here as part of the Meta-CHANS framework will also vary a lot among taxa with different life cycles, trophic position, body size, or dispersal abilities, and therefore, these cases should be only used as hypothetical, complementary examples to illustrate the manifold consequences of management choices for metacommunities and ecosystem attributes.

a) River management

Modern riverscapes typically consist of heavily regulated, fragmented sections alongside a few intact floodplain and riverbed remnants, embedded in complex decision contexts (Langhans *et al.* 2019). Due to their naturally high connectivity, dispersal is a key metacommunity process influencing species distributions and ecosystem properties in river ecosystems. Human activities such as dam constructions can strongly influence local habitat conditions, leading to strong abiotic selection and altering competitive interactions among species (He *et al.* 2024). Consequently, the initial state in **Figure 4** reflects multiple metacommunity archetypes: well-connected sections exhibit species sorting, while sections downstream of reservoirs and sets of isolated sites may experience mass effects or priority effects due to surplus or limited dispersal.

Local scale management (cases “a” and “b”) focuses on stabilizing water supply incorporating local flood risk reduction. Retaining water in reservoirs (“a”) reduces connectivity and changes the strength of abiotic selection (it often becomes stronger upstream, and weaker downstream). It increases stochastic effects and decreases stability in fragmented river sections. In contrast, dynamic flow regulation (“b”) balances water use with biodiversity needs, enhancing downstream dispersal of some taxa (e.g. plants and plankton) with controlled water release from local reservoirs. However, when flow regulation is abrupt or poorly timed, fluctuating conditions weaken species sorting while promoting mass effects that homogenize communities thereby decreasing gamma diversity. There has been increasing interest in using controlled water release to mimic natural flow regimes (i.e. environmental flow) to fulfill

ecological needs of species in downstream sections (Arthington *et al.* 2024). The functional elements of natural flow regimes brought back by environmental-flow implementation could facilitate the recovery of extirpated native species due to altered flow regimes downstream of dams, which could enhance gamma diversity when implemented effectively.

Cases “c” and “d” are both landscape-level management alternatives, with a similar aim (increasing connectivity), but with different approaches. Case “d” prioritizes ecological restoration by reconnecting floodplains, removing migratory barriers and ensuring minimum ecological flows to support multiple taxa. Case “c” also increases connectivity but primarily for human use. This might result in similar outcomes as “d”, as ships and migratory animals share some of the same physical barriers (e.g. dams). Hence in spite of differing objectives, both approaches may alter metacommunity processes in similar ways.

b) Optimizing urban green spaces

Metacommunity processes in urban landscapes can be similarly constrained as in fragmented riverine systems. Remnants of natural habitats are often isolated in the urban matrix, limiting dispersal. Our example here is a city dominated by built-up surfaces and in need of more urban green space. While this need can be primarily human-driven (e.g. for recreation, well-being, or microclimate regulation), there is an increasing focus on optimizing the design of green space for both people and biodiversity. Although this holistic approach integrates multiple objectives,

different management alternatives can still strongly influence the scale and the outcomes for metacommunities.

Focusing on local benefits often leads to prioritizing the size and complexity of individual green patches. This can still create functional habitats supporting multiple taxa and ecosystem services, e.g., unmanaged lawns and flower strips benefit pollinators, while tree-lined streets provide shading and mitigate urban heat island. While these features may incidentally improve connectivity within the urban matrix (reflected in slight increases in patch and harlequin patch dynamics in cases “a” and “b” in **Figure 5**), a more explicit landscape perspective would also consider the spatial positioning of new green spaces (“c”). This might favor multiple smaller patches in a stepping-stone design or the addition of green corridors, which can even add further ecosystem services provided by urban green spaces. Additionally, enhancing overall urban blue-green connectivity may influence decision-making by increasing not only habitat, but also landscape complexity, introducing underrepresented microhabitats, or incorporating habitat types like urban ponds to strengthen ecological connectivity (“d”).

In both local and landscape-scale approaches, dispersal rates may increase - either as an incidental outcome of independent decisions or through explicit management aimed at connectivity. Locally optimized designs, such as larger green spaces with improved microclimate, may reduce abiotic stressors, weakening species sorting relative to initial conditions (“a” and “b” in **Figure 5**). Larger habitats may also reduce stochasticity linked to

small population sizes, while increased habitat complexity can enhance resource availability, lessening density-dependent selection and priority effects ("b" in **Figure 5**).

Landscape-scale decisions may lead to shifts in metacommunity processes including stronger patch dynamics or harlequin patch dynamics due to the increased number of habitats in the landscape. Conversely, mass effects might decrease, as larger patches with reduced edge effects limit the mass arrival of species from non-target habitats and lower human pressure.

c) Managing invasive species

The metacommunity context also provides a useful framework for understanding the spread and impacts of invasive species. For monitoring, modeling, and mitigating the spread of invasive species in a landscape, an explicit spatial context is necessary. This does not mean that at the local level, targeted management of high-impact invaders already arrived and established would not be imperative. Nonetheless, management interventions in, for example, a nature conservation area, can be more successful in the early phase of establishment (**Figure 6**, case "a"), whereas they become more costly and resource-intensive later, often needing repeated interventions to manage the local population of these species in the long term (cf. Robertson *et al.* 2020; Sankaran *et al.* 2024). Overall, this might inhibit regional-scale decisions and result in managing only a few (high-impact) invaders in the area (case "b"). While these local actions might be successful at keeping things at bay, they are not sufficient to inhibit the spread of these species in a well-connected landscape, for which synchronized control would be

403 necessary (case “d” in **Figure 6**). The introduction of a given species to new habitats can be
404 strongly facilitated by human movement. Limiting the spread of these species by relevant laws
405 can help decrease dispersal rates, thereby slowing their spread in the landscape (case “c”).
406 Regarding these two optional landscape-level measures, one might draw parallels to the failure
407 to globally control the recent COVID pandemic due to the absence of such globally
408 synchronized control (“d”) and lockdown measures (“c”; see also Vilà *et al.* 2021 about
409 similarities between epidemics and invasions).
410
411 As seen in three of the four cases, managing dispersal rates can be critical in the management
412 of invasive species. At the same time, we can only expect long-term effects in cases “c” and “d”
413 (landscape-scale measures), where dispersal rates of the invasive species would drop
414 synchronously in the entire landscape as a result of a systematic intervention, inhibiting the
415 movement of invasive species also over time (lessening patch dynamics from the aspect of
416 these species). The quick local eradication of newly arrived species (case “a”) can also have a
417 similar effect (less realized dispersal and weaker patch dynamics), but it would only last as long
418 as the necessary management steps are repeatedly carried out.
419
420 By eradicating invasive species (regardless of the local or spatial context), we can also expect
421 the role of density-dependent selection to weaken, given that these species are usually quite
422 strong players in their new communities. Hence, removing them from local habitats, or
423 preventing them from colonizing to begin with, will lessen biotic selection and at the same time

enable stronger abiotic selection and species sorting dynamics, which are visible in all four cases to a certain extent.

Discussion and Conclusions

Metacommunity ecology offers an important structural foundation for integrating ecological processes with human activities, providing tools for understanding how biodiversity responds to anthropogenic stressors (McFadden *et al.* 2023; Simmons *et al.* 2021), or even conservation management (Chase *et al.* 2020; Patrick *et al.* 2021). Our goal is to provide a framework using Coupled Human And Natural Systems (CHANS; Liu *et al.* 2007, 2021) outlining how recent advances in metacommunity theory and methods can inform environmental decision-making linked to human activities across spatial scales.

First, the rapid methodological progress in metacommunity ecology allows the analysis of complex, species-rich communities. While earlier work in metacommunities was useful for smaller species sets, the rise of eDNA-based metabarcoding methods and the use of artificial intelligence (Fajgenblat *et al.* 2025; Ruppert *et al.* 2019; Waldock *et al.* 2024) can now help detect formerly unseen members of these communities, offering deeper resolutions of community patterns (Hartig *et al.* 2024). The remaining challenge is to improve the inference of processes from these patterns, which is also critical for understanding the consequences of human activities. There is an upsurge to increase the capability to analyze spatial community

445 data with powerful, pattern-finding statistical tools such as Joint Species Distribution Models
446 and related methods (Leibold *et al.* 2022b; Ovaskainen *et al.* 2017; Pichler & Hartig 2021) as
447 well as the more conventional analysis using multivariate analyses coupled with variation
448 partitioning approaches. Future work in simulation methods and alternative approaches is also
449 likely to continue to improve pattern-to-process inference (Chang *et al.* 2021; Guzman *et al.*
450 2022; Huang *et al.* 2024; Leibold *et al.* 2025; Thompson *et al.* 2020) and thus increase the value
451 of metacommunity ecology to management and policy.
452
453 Second, taking a metacommunity perspective can improve practical decision-making within the
454 structured decision-making framework described by (Gregory *et al.* 2012). This widely-used
455 framework combines the various decision-making tools used in the management of complex
456 ecosystems as part of CHANS, making it a powerful decision tool (Martin *et al.* 2009).
457 Metacommunity approaches can be utilized to describe initial conditions in nature and then
458 forecast the impact of management actions (**Figure 2c**). While the reliability of these
459 projections depends on how well the pattern-to-process inference works, the currently
460 available tools already provide useful insights that future work will improve further. By
461 exploring several management options and their impacts on landscape-level dynamics, this
462 framework can support more informed decision-making that builds on the metacommunity
463 perspective.
464
465 Third, we place our proposed framework within a broader socio-economic and policy context
466 that focuses on the enhancement of ecosystem services and NCP. We address this with a

simplified version of the general approach of Daily *et al.* (2009), suggesting that more complex frameworks would likely lead to similar conclusions (e.g. Díaz *et al.* 2018; Mace 2014; Mandle *et al.* 2021; Soga & Gaston 2020; Xu & Peng 2022). Within the Meta-CHANS framework, the most important element of this dynamic is the use of regulations or incentives that alter the utility functions that affect the optimization of management decisions, in interaction with other economic and ecological aspects. While the actual utility functions can be altered by a range of complex cultural or technocratic factors, mostly beyond the scope and scale of metacommunity ecology, ecological factors can still contribute to altering societal values, for example by changing public perceptions of the complexity and aesthetic values of nature. While in the current study, the NCP - ecosystem services occupy a key position, we kept it rather general, as a collective term. However, this could be further expanded within the Meta-CHANS framework in the future.

Applying the Meta-CHANS framework has several practical implications, such as the use of sophisticated monitoring and analytical methods. For example, while Joint Species Distribution Models can be powerful tools in the analysis of metacommunity data, their complexity can mean a methodological barrier or lead to misinterpretations. The development of standardized, user-friendly approaches and platforms would be a critical step forward to their wider application. Similarly, the use of scenario modeling using simulations or other approaches such as disordered systems models is technically challenging. This suggests that classic empirical metacommunity tools will likely remain in use for a while, given their relatively simple and easy-to-use toolkits. Their application for study cases, e.g. for comparing ecosystem states in a

489 before-after-control-impact setup making these cases highly comparable, could still yield useful
490 and reliable data for management.
491
492 One of the challenges in applying our proposed framework is the potential mismatch between
493 the scales of metacommunity processes and those involving decision making processes. Here,
494 we simplified reality by assuming two levels of spatial scale in both realms, and assuming that
495 they match. Our examples illustrate that this can offer important perspectives. Yet, in many
496 cases, what is called regional processes in metacommunities do not necessarily correspond to
497 the scales at which larger policy decisions are made, so that it is conceivable that both local and
498 regional processes of a given regional metacommunity relate to local structured decision
499 making, whereas policies influence country and continental scale processes instead. In our river
500 example, for instance, policies may affect how rivers are managed and protected across a very
501 large political entity (e.g. Europe), whereas both the management of a given river catchment as
502 well as the management of different habitats within such a catchment are part of (different)
503 decision making processes that are considered local in our example. This matching of spatial
504 scales and the more precise outcomes of spatial mismatches between policy making and
505 metacommunity processes deserve further study.
506
507 It is also important to recognize that nature does not always conform to theoretical
508 expectations. Ecological systems are notoriously (and grandiosely) idiosyncratic, and
509 unexpected outcomes frequently emerge from complex feedbacks and context-dependent
510 interactions. These dynamics are often shaped by the natural history of the organisms involved,

511 which are difficult to generalize and rarely captured in abstract frameworks. As a result,
512 predictions based on metacommunity theory will always involve some levels of uncertainty and
513 should be rather seen as robust approximations, identifying likely outcomes that capture key
514 patterns. Our proposed framework should thus be seen as a flexible guide that can support
515 adaptive management refined over time through ongoing monitoring.
516
517 Our proposed framework also highlights the need for interdisciplinary collaboration to improve
518 the integration of the ecological and human systems in Meta-CHANS. This coupling could be
519 improved with input from ecologists with advanced methodological skills, practitioners with
520 local knowledge and authority for decision-making, and policymakers with the capacity of
521 making changes to legislation. Most of the examples we provide here are feasible at lower
522 levels of governance, e.g. regional municipalities, cities, or national parks, where habitat
523 networks can be managed using the metacommunity concept. Here, ecologists and
524 conservation practitioners could directly collaborate, combining robust data, practical
525 experience, and knowledge on socio-economic limitations, leading to informed decision-
526 making. These mutual insights could be further improved by combining our framework with a
527 social-ecological network approach (e.g. Bodin & Tengö 2012; Kluger *et al.* 2020). The insights
528 can help bridge the gap between basic ecology and practical conservation by inspiring
529 ecological research towards real-world, solution-oriented approaches.
530
531 Strengthening our understanding of how nature and human dynamics are coupled remains a
532 major challenge. Here, we have focused on the multiscale dynamics shared by ecological and

social systems. These dynamics operate at both local and regional scales. Most of the processes occur at local scales where it is relatively straightforward to understand the dynamic feedback that is only indirectly affected by what happens elsewhere. And both have dynamics that occur at larger spatial scales. Some of these larger-scale effects simply reflect aggregated effects of local dynamics, but others reflect feedback routes that transfer the consequences of local dynamics across space through both metacommunities and human activities in non-additive ways. We argue that a metacommunity approach on the nature side can be effectively paired with structured decision-making and NCP frameworks on the human side. This can enhance our understanding of the dynamics of CHANS and improve the relevance of ecology in addressing human-driven ecosystem changes through the resulting Meta-CHANS framework.

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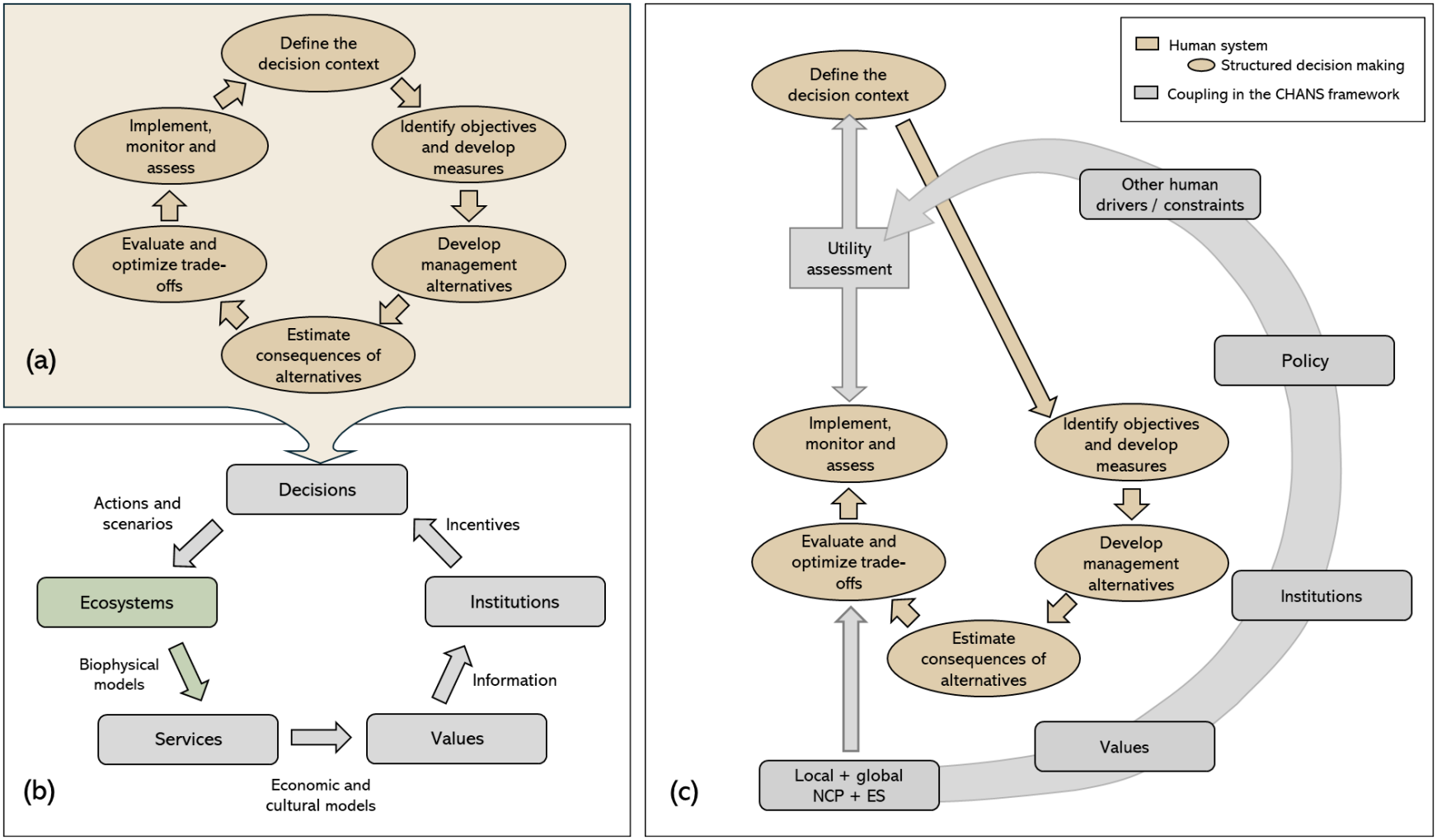
741 **Figures**



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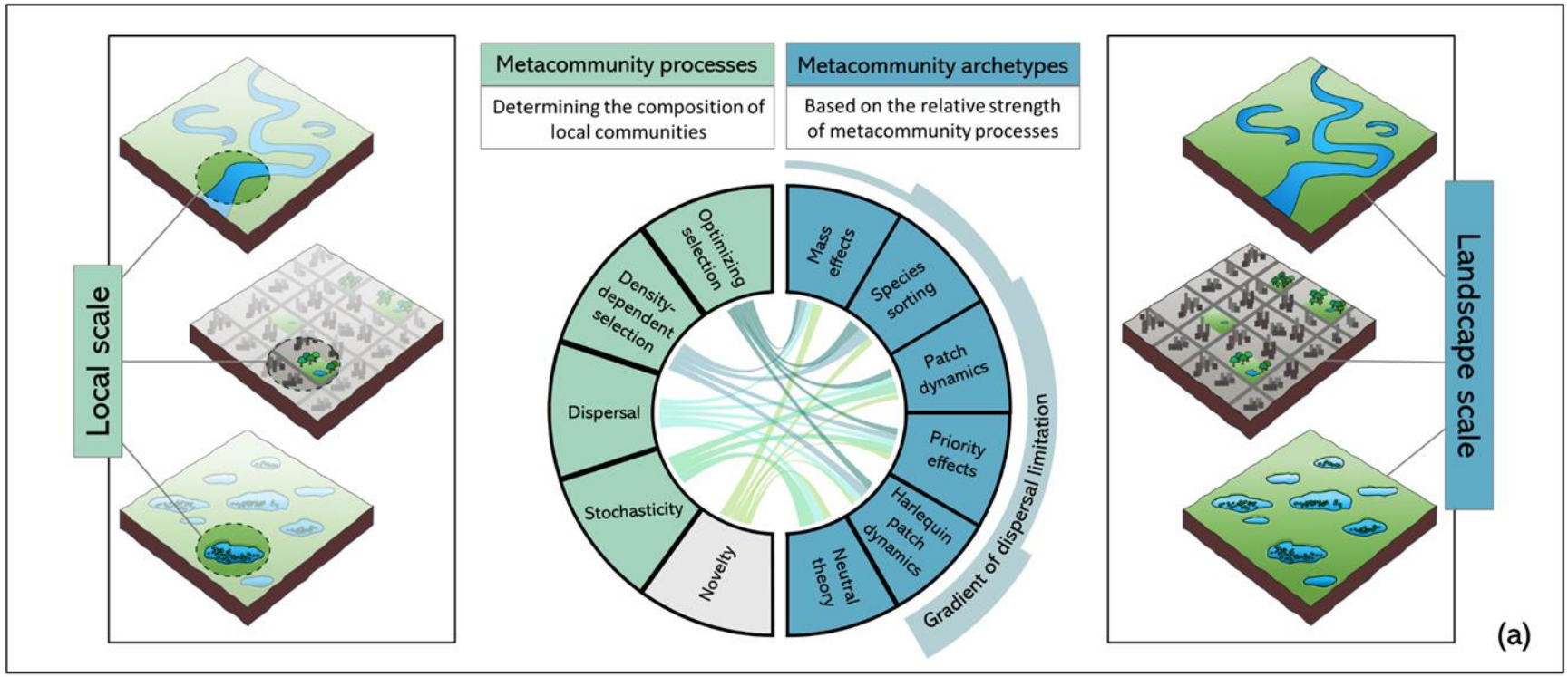
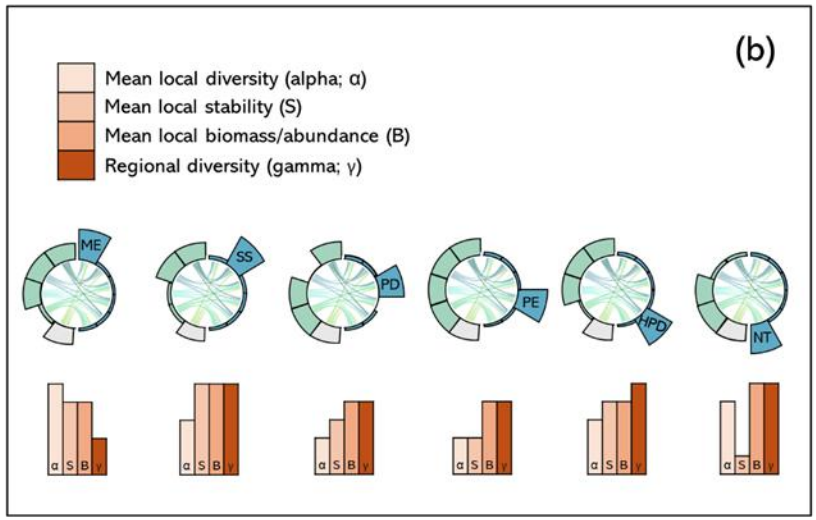
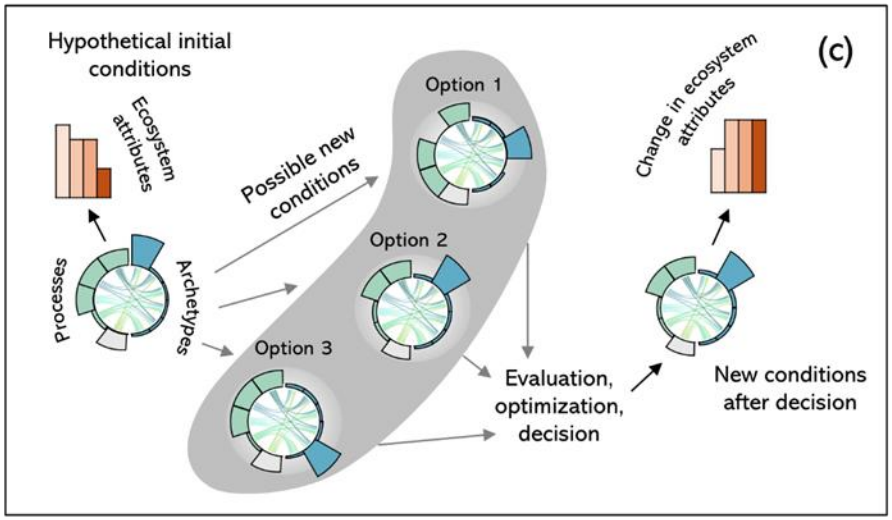
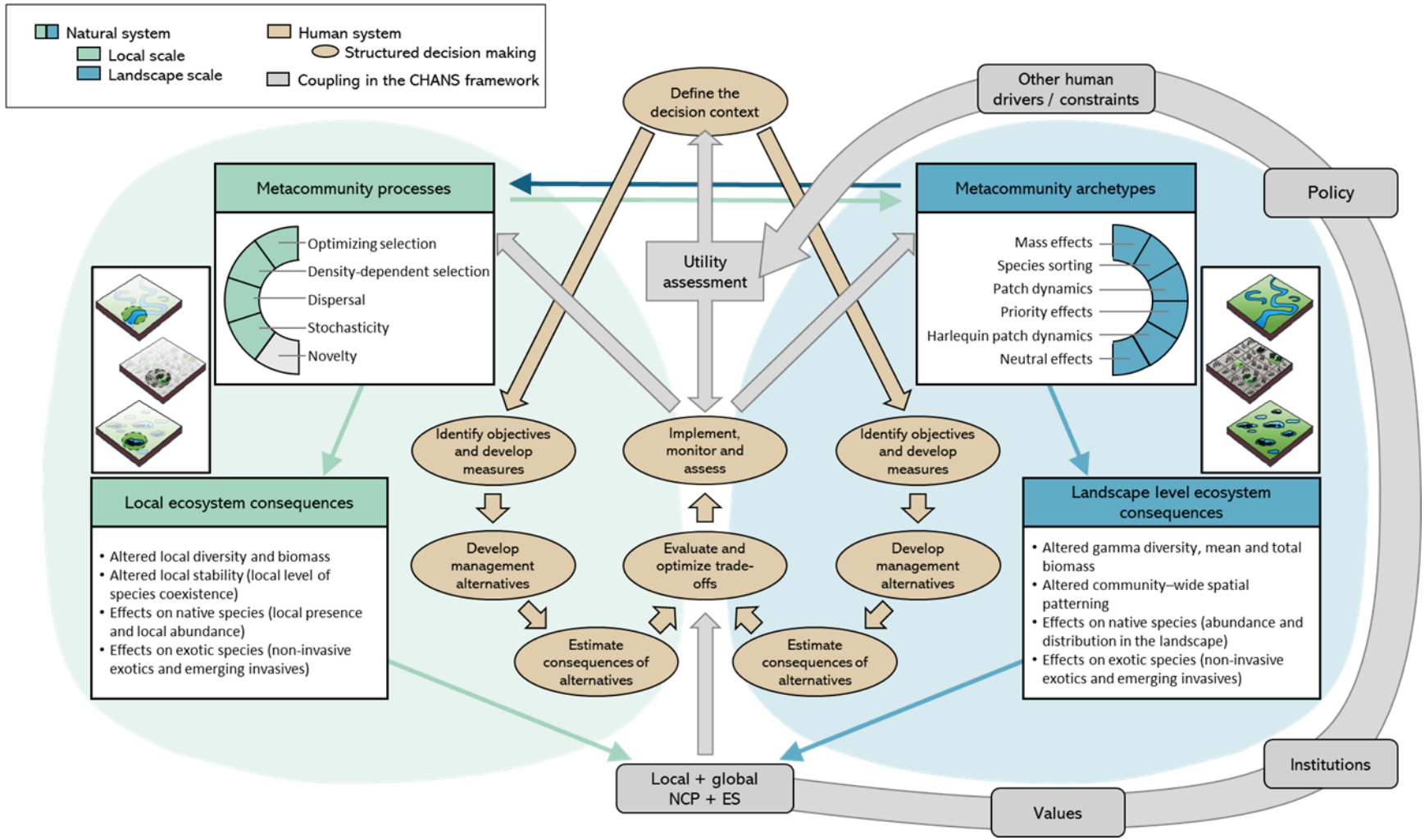

Local scale
Metacommunity processes
Determining the composition of local communities
Metacommunity archetypes
Based on the relative strength of metacommunity processes
Optimizing selection
Density-dependent selection
Dispersal
Stochasticity
Novelty
Mass effects
Species sorting
Patch dynamics
Priority effects
Harlequin patch dynamics
Neutral theory
Gradient of dispersal limitation
Landscape scale
(a)


(b)
Mean local diversity (alpha; α)
Mean local stability (S)
Mean local biomass/abundance (B)
Regional diversity (gamma; γ)
ME
SS
PD
PE
HPD
NT
α S B γ

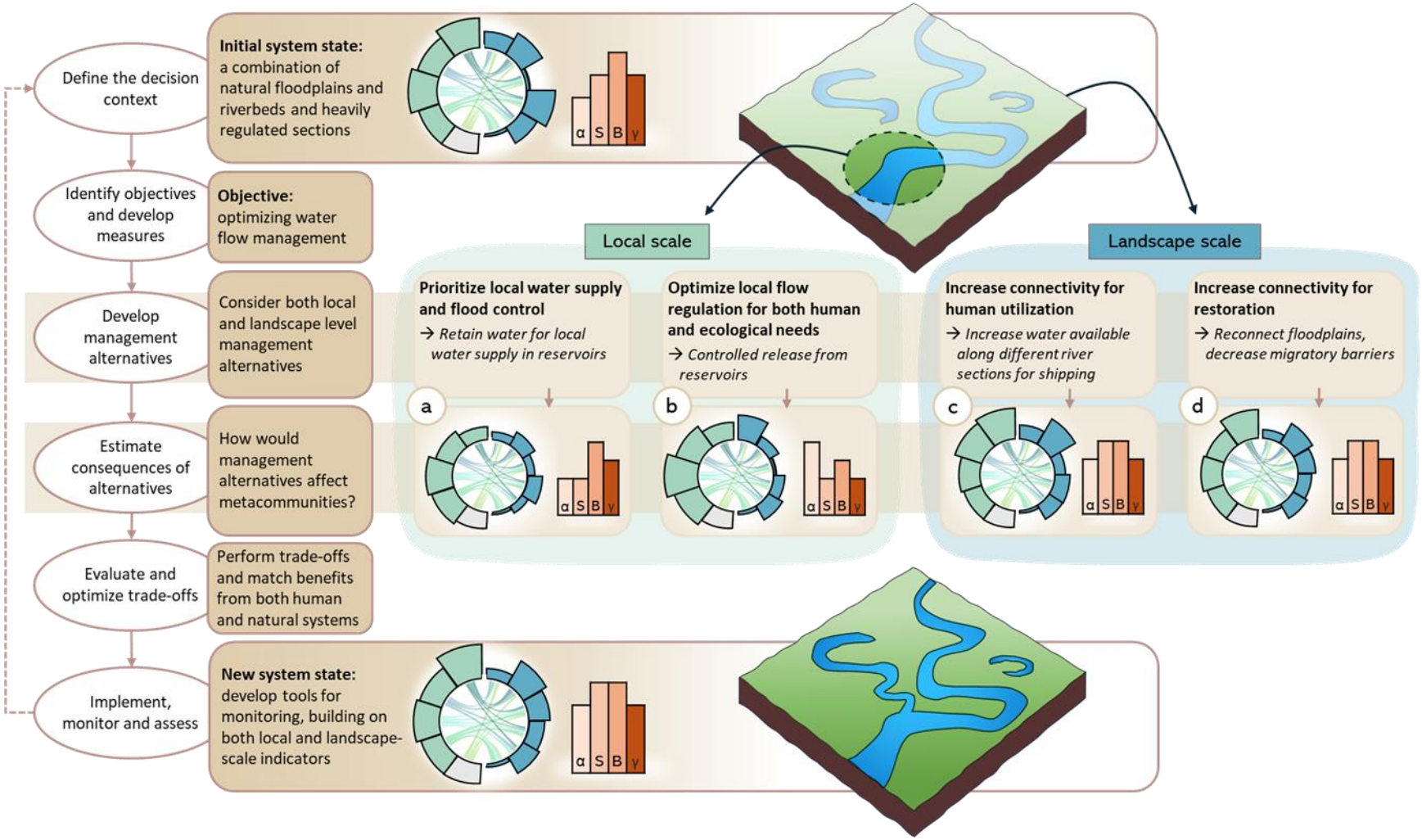

Hypothetical initial conditions
Ecosystem attributes
Processes
Archetypes
Possible new conditions
Option 1
Option 2
Option 3
Evaluation, optimization, decision
Change in ecosystem attributes
New conditions after decision
(c)

744

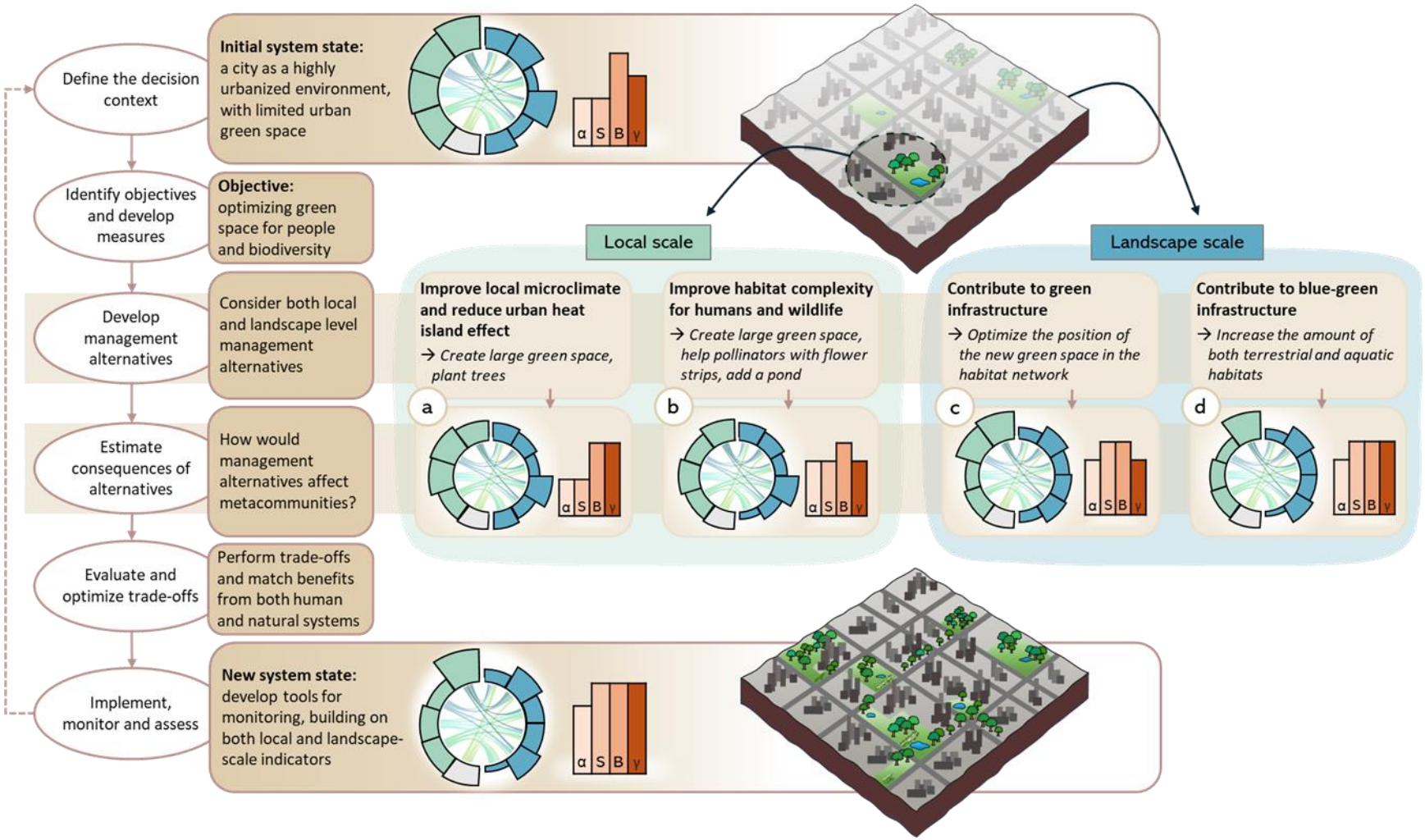

Natural system
Local scale
Landscape scale
Human system
Structured decision making
Coupling in the CHANS framework
Define the decision context
Other human drivers / constraints
Policy
Metacommunity processes
Optimizing selection
Density-dependent selection
Dispersal
Stochasticity
Novelty
Utility assessment
Metacommunity archetypes
Mass effects
Species sorting
Patch dynamics
Priority effects
Harlequin patch dynamics
Neutral effects
Identify objectives and develop measures
Implement, monitor and assess
Identify objectives and develop measures
Local ecosystem consequences
• Altered local diversity and biomass
• Altered local stability (local level of species coexistence)
• Effects on native species (local presence and local abundance)
• Effects on exotic species (non-invasive exotics and emerging invasives)
Develop management alternatives
Evaluate and optimize trade-offs
Develop management alternatives
Landscape level ecosystem consequences
• Altered gamma diversity, mean and total biomass
• Altered community–wide spatial patterning
• Effects on native species (abundance and distribution in the landscape)
• Effects on exotic species (non-invasive exotics and emerging invasives)
Estimate consequences of alternatives
Estimate consequences of alternatives
Institutions
Local + global NCP + ES
Values

745

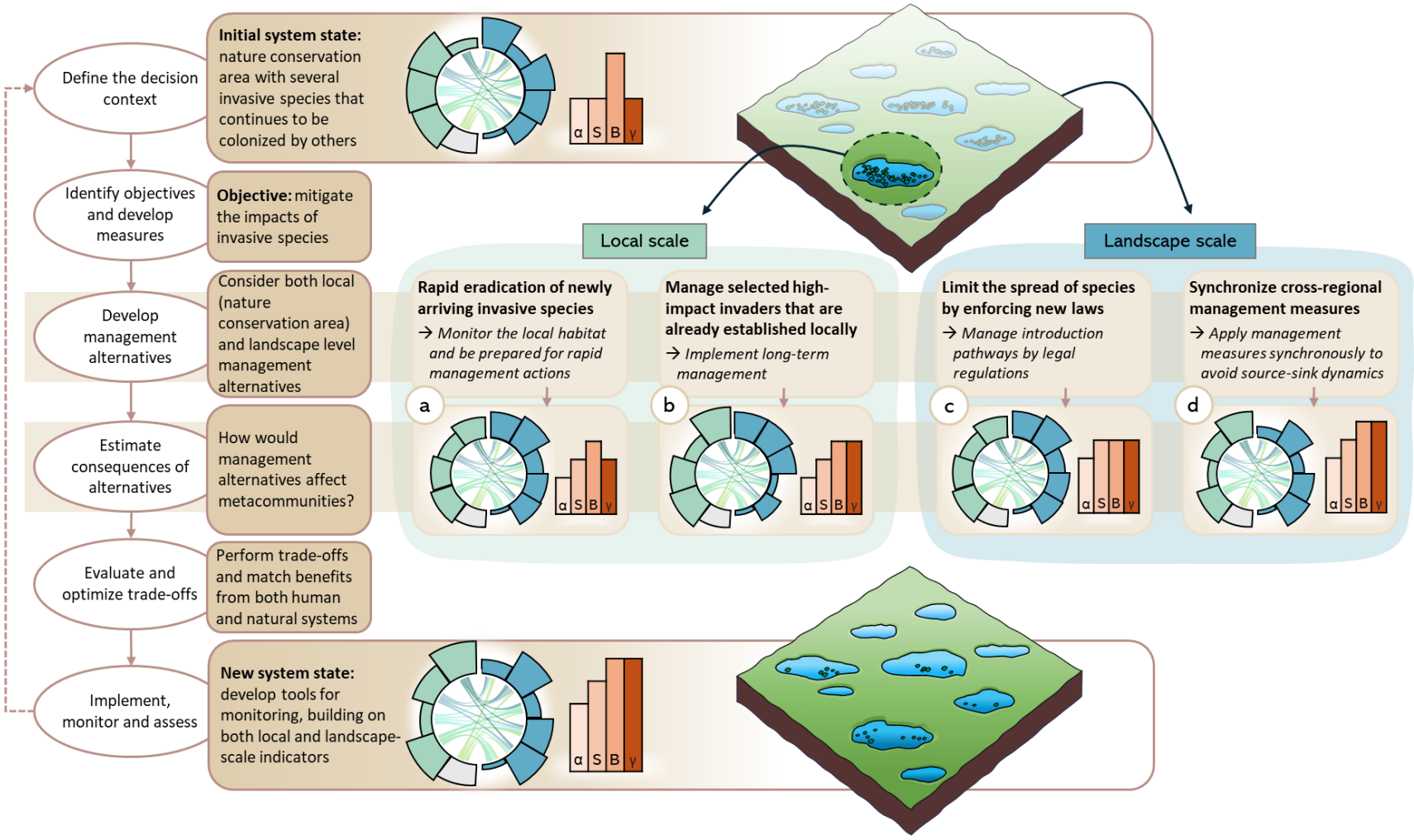
746


Define the decision context
Initial system state: a combination of natural floodplains and riverbeds and heavily regulated sections
α S B γ
Identify objectives and develop measures
Objective: optimizing water flow management
Develop management alternatives
Consider both local and landscape level management alternatives
Local scale
Landscape scale
Prioritize local water supply and flood control
→ Retain water for local water supply in reservoirs
Optimize local flow regulation for both human and ecological needs
→ Controlled release from reservoirs
Increase connectivity for human utilization
→ Increase water available along different river sections for shipping
Increase connectivity for restoration
→ Reconnect floodplains, decrease migratory barriers
a
b
c
d
Estimate consequences of alternatives
How would management alternatives affect metacommunities?
Evaluate and optimize trade-offs
Perform trade-offs and match benefits from both human and natural systems
Implement, monitor and assess
New system state: develop tools for monitoring, building on both local and landscape-scale indicators

747


Define the decision context
Initial system state: a city as a highly urbanized environment, with limited urban green space
Identify objectives and develop measures
Objective: optimizing green space for people and biodiversity
Develop management alternatives
Consider both local and landscape level management alternatives
Estimate consequences of alternatives
How would management alternatives affect metacommunities?
Evaluate and optimize trade-offs
Perform trade-offs and match benefits from both human and natural systems
Implement, monitor and assess
New system state: develop tools for monitoring, building on both local and landscape-scale indicators
α S B γ
Local scale
Landscape scale
Improve local microclimate and reduce urban heat island effect
→ Create large green space, plant trees
Improve habitat complexity for humans and wildlife
→ Create large green space, help pollinators with flower strips, add a pond
Contribute to green infrastructure
→ Optimize the position of the new green space in the habitat network
Contribute to blue-green infrastructure
→ Increase the amount of both terrestrial and aquatic habitats
a
b
c
d

748


Define the decision context
Identify objectives and develop measures
Develop management alternatives
Estimate consequences of alternatives
Evaluate and optimize trade-offs
Implement, monitor and assess
Initial system state: nature conservation area with several invasive species that continues to be colonized by others
Objective: mitigate the impacts of invasive species
Consider both local (nature conservation area) and landscape level management alternatives
How would management alternatives affect metacommunities?
Perform trade-offs and match benefits from both human and natural systems
New system state: develop tools for monitoring, building on both local and landscape-scale indicators
α S B γ
Local scale
Landscape scale
Rapid eradication of newly arriving invasive species
→ Monitor the local habitat and be prepared for rapid management actions
Manage selected high-impact invaders that are already established locally
→ Implement long-term management
Limit the spread of species by enforcing new laws
→ Manage introduction pathways by legal regulations
Synchronize cross-regional management measures
→ Apply management measures synchronously to avoid source-sink dynamics
a
b
c
d

749

Figure Legends

Figure 1: Two approaches for decision-making in CHANS and their integration. **a)** Sequential steps of structured decision-making, applicable to relatively small-scale issues that can be implemented in relatively short time (Gregory *et al.* 2012). **b)** Key elements in CHANS across multiple socio-political dimensions, with the aim of integrating ecosystem services (based on Daily *et al.* 2009). Here, elements from the human system are shown in gray, where ecosystems (green) and their services are integrated into the decision-making process. This loop typically operates at longer timeframes than the structured decision-making loop. **c)** Direct integration of structured decision-making into the human system side of CHANS, including nature's contributions to people (NCP) and ecosystem services (ES) at local and global scales.

Figure 2. (a) Processes shaping metacommunity patterns in a landscape shown as their bipartite network, where metacommunities that can be grouped under six existing archetypes (in blue, right half of the rosette figure) emerge from the different contributions of multiple processes (in green, left half). The archetypes might depend on several processes, illustrated by connections in the central part of the rosette diagram (details on this are also presented in **Table S1, SI**). Hence, changes in these processes will induce changes in the strength of the dominant metacommunity archetypes, resulting in community- and possibly ecosystem-level consequences. **(b)** Metacommunity archetypes are linked to emerging metacommunity attributes. We provide an example for species coexistence as a form of metacommunity stability, based on Shoemaker & Melbourne (2016), expressed as the mean local level of

771 coexistence across the landscape. Mean local and regional diversity in the case of the pure
772 archetypes of species sorting (SS), mass effects (ME), patch dynamics (PD), priority effects (PE),
773 Harlequin patch dynamics (HPD), and neutral theory (NT) are predicted according to Leibold *et*
774 *al.* (2004); Leibold & Chase (2018); Mouquet & Loreau (2003); Thompson *et al.* (2020). **(c)**
775 Management decisions are based on options with which multiple possible new conditions of
776 the natural system might be achieved. (The relative strength of processes and dominant
777 metacommunity archetypes in the rosettes, indicated by the height of each bar, are
778 hypothetical in the present figure and are only used to illustrate the multitude of changes these
779 decisions might induce.
780
781 **Figure 3:** A proposed conceptual framework for integrating metacommunity ecology and
782 decision-making within the CHANS framework. The connections between local (green
783 background, left) and regional-level ecological processes (blue background, right) are addressed
784 by metacommunity ecology in the natural system. The human system (CHANS framework, gray
785 boxes and arrow on the right; after Daily *et al.* 2009), **Figure 2b**) has an overarching effect on
786 utility, which, through a decision-making process (brown oval boxes in the middle; based on
787 Gregory *et al.* 2012), **Figure 2a**) is connected to the natural system via several specific
788 connections and feedback loops. Our choice of showing the human system on the right is
789 arbitrary (we used the same design as in **Figure 1c**), as it influences utility assessment, and by
790 that, decision-making in a way that has consequences for both the local and regional scale in
791 natural systems.
792

Figure 4*:* An example of a riverine system heavily impacted by human activities. The general objective here is optimizing water flow management, but local (cases “a” and “b”) and landscape-level alternatives (“c” and “d”) might lead to different relative strengths of metacommunity processes, emerging metacommunity archetypes, and ecosystem properties (color coding follows **Figure 2**). The strength of novelty processes (grey) is only used as a placeholder for future studies exploring this element.

Figure 5: An example of a city aiming at optimizing green space for people and biodiversity, which, depending on the local (cases “a” and “b”) or landscape perspective (“c” and “d”), might lead to different relative strengths of metacommunity processes, emerging metacommunity archetypes, and ecosystem properties (color coding follows **Figure 2**). The strength of novelty processes (grey) is only used as a placeholder for future studies exploring this element.

Figure 6: An example of a region (e.g., a nature reserve or national park) with several invasive species. To mitigate the negative impacts of invasive species on biodiversity and ecosystem services, management can concentrate on local (cases “a” and “b”) or landscape-level interventions (“c” and “d”) that might lead to different relative strengths of metacommunity processes, emerging metacommunity archetypes, and ecosystem properties (color coding follows **Figure 2**). The strength of novelty processes (grey) is only used as a placeholder for future studies exploring this element.

Boxes

Box 1 - Joint Species Distribution Models (JSDMs) and their relevance for biodiversity conservation

JSDMs are elaborations of long-utilized Species Distribution Models (SDMs). While SDMs assess how environmental factors and spatial effects related to dispersal-driven spatial patterns of individual species, they do not account for species interactions and largely overlook stochasticity, which JSDMs can address. JSDMs are implemented in various statistical packages that differ in their technical approach, undergoing rapid development to improve their utility (see e.g. Ovaskainen *et al.* 2025; Pichler & Hartig 2021; Rahman *et al.* 2024). Here we focus on their conceptual contribution to understanding metacommunity dynamics.

JSDMs provide two basic types of outputs (Ovaskainen *et al.* 2017; Pichler & Hartig 2021). The first can partition variation in the composition of sites attributable to different types of predictors: effects of environment (reflecting mostly abiotic factors), space (effects of dispersal), residual co-distribution among species (including especially species interactions), and randomness (reflecting largely the effects of stochasticity). The same can also be carried out for the contributions of each individual species. These effects can be visualized using ternary plots (Leibold *et al.* 2022b). The position of sites or species (as in **Figure B1**) in these

ternary plots can inform us of the dominant processes driving community assembly for each site or species in a metacommunity (see **Box 2**) as well as for the metacommunity as a whole (as the average of all the individual species). This can already inform conservation management about the factors that can best help conserve or control focal species (in the case of invasive or rare species). Similarly, site-based plots can help identify influential sites that are important in the distribution of species due to local environmental conditions or spatial position, serve as important 'arenas' for species interactions, or contribute with high stochasticity to species distributions. This can provide information for the prioritization of sites for biodiversity conservation.

JSDMs also estimate model parameters that can help identify which environmental gradients or spatial scales are the most important for species distribution, or which species groups share environmental responses. These parameters can further guide management with a deeper understanding of metacommunity dynamics.

It is important to understand that there are limitations to interpreting JSDMs, and e.g. unmeasured components of environmental features and spatial effects can bias and inflate the importance of co-distributions and stochasticity. There are also some important concerns regarding the robustness of pattern-to-process inference (Blanchet *et al.* 2020; Poggiato *et al.* 2021; Zurell *et al.* 2018), although this might be possible to some degree (e.g. Clark *et al.* 2018). Nevertheless, JSDMs are already a powerful tool that can deliver several types of

information relevant for conservation management and its decision-making. The rapid development of this field will likely be further boosted by machine learning and AI methods in the near future.

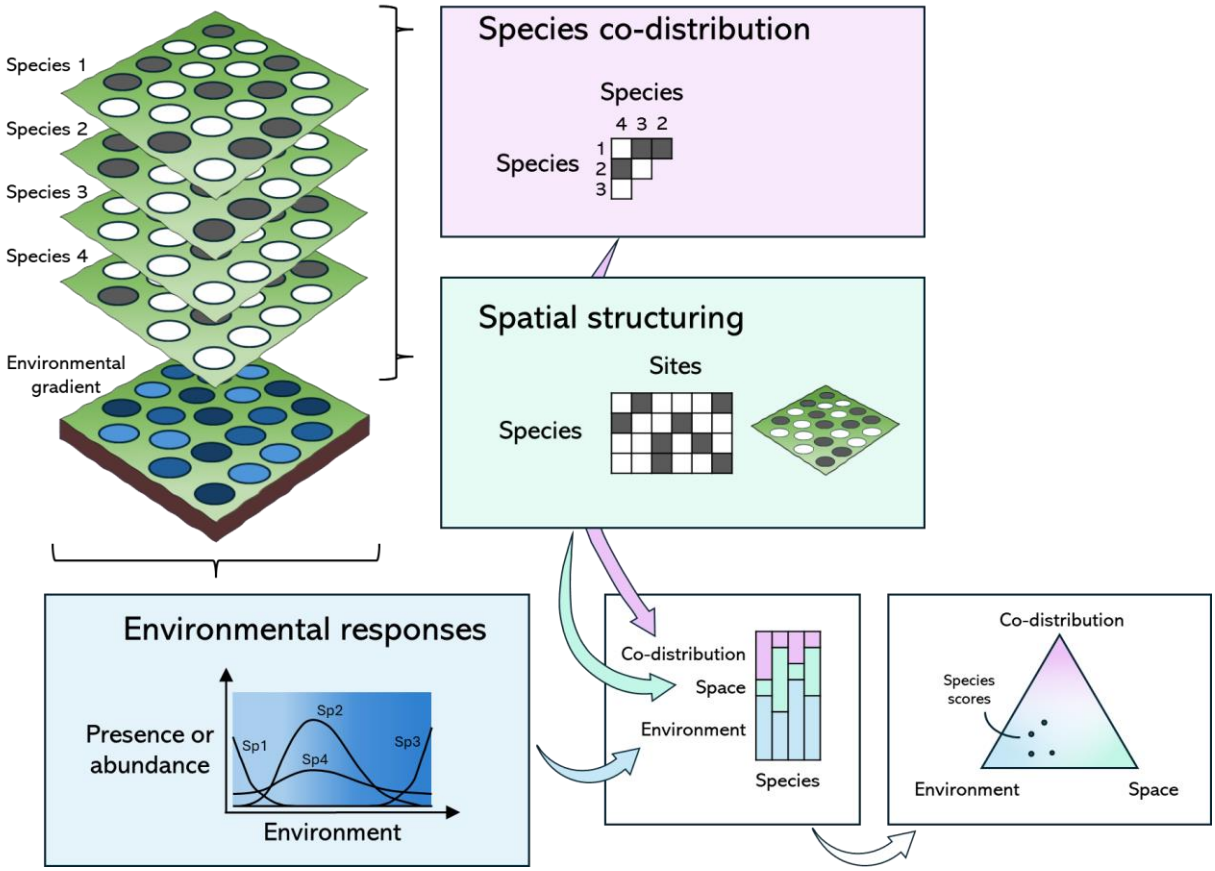


Figure B1: Decomposing landscape-level distribution patterns of members of a metacommunity into species co-distribution, environmental responses and spatial structuring with the help of JSDMs. The distribution of each species is described individually as a function of the landscape that describes the spatial location of each site and its measured environmental features (note that subsequent interpretation of these features should consider other possible but unmeasured environmental features). From this data, it is possible to hypothesize the environmental responses of each species (often as a Gaussian curve), its sensitivity to spatial structure (e.g. spatial scale, or geographic context), and an estimate of how it covaries with other species (here shown as a

correlation matrix), indicative of both direct and indirect effects of species interactions. For each species, the residual variance is also an estimate that measures how much its distribution seems to be stochastic or cannot be explained with the available data.

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Box 2 - Metacommunity archetypes and their underlying processes (Figure 2).

Metacommunity archetypes represent simplified outcomes of community dynamics that reflect different combinations of selection, dispersal, stochasticity, and species interactions. These archetypes serve as conceptual benchmarks that help identify the dominant ecological processes in a given system, even though most real-world metacommunities fall somewhere between these extremes. The six main archetypes – species sorting (SS), mass effects (ME), patch dynamics (PD), neutral theory (NT), priority effects (PE), and harlequin patch dynamics (HPD) – are described in detail in the **Supplementary Material**. Each archetype reflects distinct assumptions about the role of metacommunity processes in shaping biodiversity patterns and ecosystem function (shown in **Figure 2** and **Table S1** in the **Supplementary Material**).

The spatial patterns produced by these archetypes can be assessed using statistical tools such as JSDMs (see **Box 1**) and spatial eigenvector mapping, which can help infer which archetypes dominate within a metacommunity (**Figure B2**).

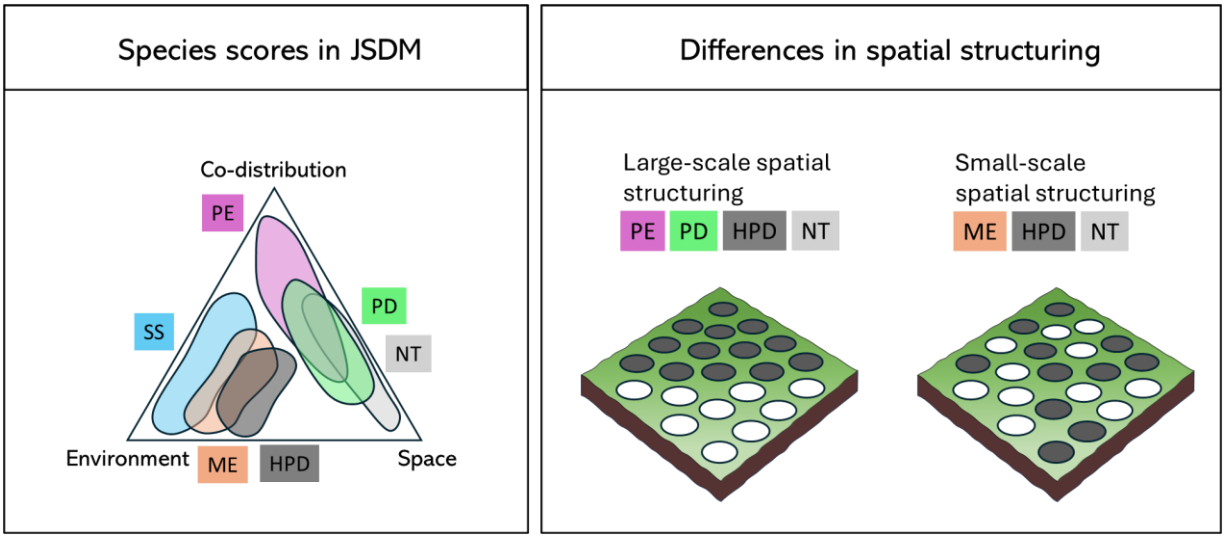

Figure B2. Detection of the dominant metacommunity archetypes (species sorting - SS, mass effects - ME, patch dynamics - PD, priority effects - PE, Harlequin patch dynamics - HPD, and neutral theory - NT) from empirical community data based on species scores with the JSDM approach (Ovaskainen *et al.* 2017; left) and analyzing spatial structuring across spatial scales (right). While a large overlap can be expected among the species score distribution of several archetypes, some of these can be teased apart by a targeted analysis looking into small and large spatial scales and at which scale spatial structuring emerges (using spatial eigenvector analyses; Legendre *et al.* 2012).

The ternary plots based on the relative contributions of environmental filtering, spatial structure, and species co-distributions (discussed in **Box 1**) can help link the distributions of species to the identification of the predominant archetype in the metacommunity. If the position of each species is plotted on the ternary plot (**Figure B2**), their contribution to SS can be determined as the range of values that have weak or zero spatial components, along the upper left side of the ternary plot. Species that contribute to NT and thus insensitive to environmental gradients will lay along the upper right side of the ternary plot. Species that

contribute to ME or HPD will have increasing spatial effects in comparison to SS. Species involved in PE will have strong co-distribution effects that position them towards the upper part of the ternary plot. Finally, species that are involved in PD will be similar to NT but with stronger co-distributions that position them also toward the top of the ternary plot.

Spatial eigenvector mapping can further clarify the spatial patterns associated with different metacommunity processes. Spatial structuring in PD and PE is typically observed at broader spatial scales, due to dispersal limitation and historical contingencies. In contrast, ME tends to produce fine-scale spatial patterns resulting from local spillover. NT and HPD can generate spatial structure across a wide range of scales, reflecting the combined influence of stochasticity, dispersal, and (in HPD) disturbance-driven niche mismatches.

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Supplementary Information

Species sorting (SS): an archetype in which each species' abundance (or occurrence) is strongly determined by variation in local environmental conditions. In this sense, optimizing selection to the abiotic environment is the main underlying process determining the local abundance of species. In natural systems, it is likely coupled with density-dependent selection as a secondary process. While dispersal is not a key driver here, sufficient rates of dispersal are implicitly assumed. In JSDMs, species that play strong roles in species sorting are thus likely to show substantial associations with environmental gradients, and possibly with the co-distributions of other species, with spatial patterning. Because of the influence of optimizing selection, production, biomass, and regional stability all tend to be high.

Mass effects (ME): a pattern in species distributions in which differences in environmental preferences (and hence the role of optimizing selection) are diminished by constant exchanges (mixing) of individuals due to high (excess) dispersal. This constant flow of individuals can also influence interspecific competition, hence density-dependent selection is also included among the basic effects behind mass effects dynamics. In JSDMs, species involved with mass effects should show weaker patterns related to environmental gradients and should show some spatial patterning that is particularly visible at smaller scales. The degree to which ecosystem properties such as production, biomass, and regional stability are reduced compared to SS archetype depends on the magnitude of the mass effect (Mouquet & Loreau 2003).

Patch dynamics (PD): an archetype in which one species is slower to colonize recently disturbed or created patches than the other, even though it is a strong competitor that will suppress the better colonizer once it arrives. The better colonizer thus exists in the metacommunity as a "fugitive" species whose distribution is always in flux. Species involved in patch dynamics should show weaker distributions that relate to environmental gradients, but instead show spatial patterning that is particularly evident at larger spatial scales. If ecosystem features, especially production and biomass are closely associated with the strength of the competition colonization trade-off and thus to the stability of regional coexistence in this model (Livingston *et al.* 2012), they should be substantially lower compared to the SS archetype.

Neutral theory (NT): an archetype in which all species are effectively identical in their ecologies. As such, the processes that determine their relative abundances are stochastic and related to stochasticity in birth, death, and dispersal events. The distribution of species involved in such dynamics should show relatively high stochasticity and possibly show spatial patterning that may occur over a wide array of spatial scales. It is hard to say how biomass and productivity would differ from the SS archetype but the regional stability should be substantially lower.

Harlequin patch dynamics (HPD): an archetype in which dispersal-limited species have different environmental preferences (as in species sorting) but are also subject to disturbances that cause extinctions. Individual sites may therefore be temporarily occupied by the environmentally disfavored species until the favored species arrives. Species involved in such

863 dynamics should show distributions related to environmental gradients but also show spatial
864 patterning over a wide span of spatial scales. As in the ME scenario, biomass and productivity as
865 well as regional stability should differ in proportion to the effects of disturbance-driven
866 extinctions (Leibold & Loeuille 2015).
867
868 **Priority effects (PE):** an archetype in which different species have different environmental
869 preferences, but there are some sites where both species have similar preferences (as in
870 species sorting) and cannot coexist because interspecific competition is stronger than
871 intraspecific competition. In this case, there is a priority effect in which the first species to have
872 arrived will monopolize the site. There is thus a strong stochastic effect that is absent in the
873 species sorting case and spatial patterning that mostly occurs over larger spatial scales (Shurin
874 *et al.* 2004). The effects on ecosystem features should be similar to those in the HPD archetype.
875
876 In general, and in the absence of direct negative interactions with their competitors (i.e. no
877 secondary compounds or interspecific aggression), species that are associated with SS will have
878 high abundance/biomass and have high stability/resilience due to their well-defined niche
879 relations (**Figure 2b**). Assuming there is enough habitat variation, mean alpha (local) diversity
880 will be lower than gamma (regional) diversity. The stability and abundance will decline as they
881 increasingly show spatial structure at the expense of such niche-structuring. This is evident for
882 species that better correspond to ME since some portion of the metapopulation will find itself
883 in habitats where they are not as well suited to them, and because their populations in well
884 suited habitats are diminished by emigration. Alpha diversity will increase as sink populations

885 maintain additional species via sustained immigration. Gamma diversity will eventually decline
886 as there is increasing homogenization and selection for species at the regional scale. This also
887 reduces their stability in the face of competition (Shoemaker & Melbourne 2016). For HPD,
888 biomass also declines as a larger proportion of the populations are found in less suitable
889 habitats. Alpha and gamma diversity are unaffected relative to SS but stability is decreased
890 (Shoemaker & Melbourne 2016). On the other side of things (weak environmental effects),
891 species that show mostly neutral interactions with other species will have low stability as their
892 overall abundances in the metacommunity show random drift. Gamma diversity can be high,
893 but local diversity can vary substantially. Similarly, species that show primarily PD interactions,
894 and thus rely on extinctions by other species, have fairly constrained populations that show
895 weak resistance to extinction from the metacommunity. Here alpha diversity can be
896 substantially lower than gamma diversity. Similarly species whose interactions with other
897 species depend on priority effects show low stability to metacommunity-wide stability unless
898 they also have environmentally-determined niches and alpha diversity can also be substantially
899 lower than gamma diversity (Shurin *et al.* 2004).
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901

902 **Table S1** - Metacommunity archetypes and their underlying processes (indicates the qualitative

903 contribution of each process to the archetypes, which was used to generate the rosette

904 diagram in **Figure 2**)

	Optimizing selection (abiotic)	Density-dependent selection (biotic)	Dispersal	Stochasticity	Novelty
Mass effects	▨	▨	▨		▨
Species sorting	▨	▨			▨
Patch dynamics	▨		▨	▨	▨
Priority effects	▨	▨	▨	▨	▨
Harlequin patch dynamics	▨	▨	▨		▨
Neutral theory			▨	▨	▨

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