



Carabidocoenoses and Fragments of Forests

Exploring the Carabid Landscape

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Carabidocoenoses and Fragments of Forests. Exploring the Carabid Landscape

Skogsfragmentens carabidocenosis. En resa genom jordlöparnas landskap

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*Für meine Großeltern, Elfriede und Robert,
ja niitä, joita en koskaan tavannut, Lilja ja Mauri.*

“The ancient city of Rome ... was eventually reclaimed by the forests, first by analogy, then in the form of forest-peoples from the north, and finally by the vegetation belt itself. The Forum became wild pasture land for Dark Age cattle. Wilderness overgrew the roads that led to Rome. The work of history fell to the ground it had tried to surmount under the auspices of god. This is the ground, or *humus*, of the ancestors. As the subterranean commandments of the dead cease to persuade the ironic generations, the forests gradually overtake the clearings and close the lid of the [eye].” (Harrison 2009:13)

Abstract

Epigeic ground beetles (*Coleoptera: Carabidae*) were sampled between 2021-06-28 and 2021-07-09 using pitfall traps in the Swedish counties Värmland and Gävleborg. The structural properties of the landscapes surrounding these points were estimated from the Swedish Environmental Protection Agency's national land cover databases and the Swedish Forest Agency's data for all formally protected and high conservation value forests using patch-based configurational metrics. Their effects on the diversity of carabids were investigated using generalized additive models.

An optimum in explanatory power and model fit was observed at around 452 ha landscapes. In accordance with area-heterogeneity trade-off principles, carabid diversity maximized at intermediate levels of patch shape complexity. No statistically significant response to patch type interspersions could be observed however. Habitat-wise core areas did not affect carabid diversity uniformly. Some increased diversity linearly positively or negatively with increased abundance, while others produced curves or waves. The ratio between total core and ecotone area affected carabid diversity negatively linearly above 1.

The results indicate that this approach is useful for investigating landscape ecological processes and therefore developing practical landscape level management strategies. Not only are the configurational parameters of habitat patches significant for carabid communities, they produce completely different responses. As the conservational values of landscape structures gain more attention, solutions to novel issues are demanded. Here I present the first steps in developing a fruitful investigative approach.

Finally, discussions on carabid ecology and improvements to both sampling and modeling are presented, and future avenues of inquiry and considerations for management recommended.

Keywords: biodiversity, Carabidae, entomology, fragmentation, Fragstats, habitat fragmentation, habitat heterogeneity, landscape, landscape ecology, landscape heterogeneity, quantifying fragmentation.

Prologue

Science and an emotion of being

Why do humans concern themselves with knowledge, and why does *scientific* knowledge specifically embody such cultural merit? These questions seem ridiculous to the modern mindset. Not because their resolutions have been determined unnecessary, rather, because they are not considered. Systematically so. By requiring the investigative purpose to contribute to any societal issue, scientific reports avoid responsibility to address metaethical critique. Referring to the benefit of humanity is easier than defending a personal romanticism to the topic of interest. Science cannot simply be valued for its own sake; modernity requires utilitarian motive. Scientific knowledge is after all considered *the truth*, its development analogous to *progress*, its state *a priori*. Knowledge is *first* scientific, *then* accessible. Prevailing any personal relationship to the world and clearly separate from the subject.

Science is not valuable, it guides value. It guides morality in an attempt to reach an ethical imperative. However, science does not justify its own application. Science does not tell us *why* progress is important. Our morals do. We value the lives of humans, so we devote our resources to developing scientific methods of saving and prolonging lives. Scientific models make complex ecosystems conceptually digestible and point to us the effects on our environment of a treatment through prediction. We then choose to regulate these treatments through policy – our practical moral guidelines. We could just as well produce scientific methods and tools with the aim of decreasing human life expectancy and standards, or to raze ecosystems as efficiently as possible. Here we find a discrepancy between the true information embedded in our universe and an interaction with it.

If science unfolds and displays *true* knowledge, how can an indulgence be considered value-less? It would be an interaction with the universe in its *true* form. Further, assuming a utilitarian purpose does not dismiss the requirement for an ethical argument. Utilitarianism is foundationally moral. So why, then, would we not consider science as the ultimate source of morality? It already guides our moral structures. Perhaps these considerations highlight the differences between *pure* (theoretical discovery) and *applied* science (technological invention), or perhaps

the core issue behind a return-on-investment research strategy. Namely, a requirement to objectively define *meaning* – or, the currency that science yields – through a value structure. Which, as already determined, science cannot. Ethics must.

So, what is utility? Investigation may highlight a vector of dimensions whose sustainable resource accesses are required for the continuation of society. Meeting these requirements would accordingly be considered the goal of utility. Its purpose: to maintain social institutions. Scientific research, thus, aims at enhancing societal resource-use efficiency. What is lost in this approach, sadly, is any ethical consideration beyond this scale. What does science mean to the individual of any organism besides humans? What mechanisms are unanimously relevant, universally causal? How is science reduced by this perspective? Can science truly investigate the world if its development is limited to human utility? I would argue no. This view is a reduction of knowledge to the practical use for humanity. Not the true fundamentals of the world. The *want* for knowledge precedes its application, simply by virtue of its *a priori* state to application. Remember, knowledge is *first* scientific, *then* accessible. Principles are *first* discovered, *then* usefully applied. In this sense, the curiosity behind scientific inquiry positions itself closer to *true* knowledge than some application of it. Reduction of the world's true complexity makes inference easier but diminishes information, whereas decryption of absolute entropy yields absolute meaning. Science is more than just human utility – it is an attempt to understand the world as it is, to everything and everyone. Simply viewing science as a method for developing something useful therefore reduces its meaning.

Detrimentially, I think, science is to most people merely a (the) tool for methodical inquiry. Not a source of purpose, meaning, nor spirituality. *Science*, through school, is something that burdens one's youth, when all thoughts revolve around avoiding embarrassment in the eyes of peers. It is a *scientific education*, and all its adversities, that separate the young adult from a decent job. To survive, an education ought to be overcome, not enjoyed. It is a lack of *scientific evidence* that hurdles progress – it is something that must be done before one can determine that a certain treatment is beneficial for the response. *Science*, therefore, must be overpowered, surmounted. It needs to be depleted of all its secrets. Preferably as efficiently as possible. It is seen as a source of information to be yielded by humanity, not as an aesthetic experience of beautiful interactivity beyond the domains of anthropogenic creation. A reduction of nature's *true* form to our utilitarian perception of it.

If to aesthetically appreciate art we must have knowledge of artistic traditions and styles within those traditions, to aesthetically appreciate nature we must have knowledge of the different environments of nature and of the systems and elements within those environments. In the way in which the art critic and the art historian are well equipped to aesthetically appreciate art, the naturalist and the ecologist are well equipped to aesthetically appreciate nature.” (Carlson 1979:273)

Knowledge enables meaning. An object only becomes a symbol once it has been provided context by an observer (arguments can be made for allowing unconscious contextualization of the object; this, however, simply reduces the influence of *conscious* knowledge, without eradicating knowledge *per se*; some unconscious knowledge is still involved). Toddlers do not see the significance in Euler's constant, and so it is meaningless to them. Language barriers, similarly, curtail communication and interpretation. Additionally, interaction with symbols yields meaning. A Christian might *know* what the Tora says yet will not produce the same response to David's star as would a Jew. Nor would a nationalist feel the same pride for any flag that is not their native. Equally, I think, any person without either knowledge or interactive experience with nature would not find as much meaning with it as an involved ecologist would. Although crucially, the symbols that produce meaningful response are always fraudulent. The Christian cross inspires visions of god, but being of human origin, does not present it truthfully. A model of interspecific interactions predicts the future and explains to the ecologist what was before a mystery, but does not absolutely capture the regulatory mechanisms behind every system. As the theologian has faith to be guided towards spiritual truth through religious symbols, so does the ecologist have faith to approximate scientific truth through the development of models. Increasing congruence between the symbols and lived experience thereafter increases the meaning underneath. As these discrepancies diminish, and the observer – in discrete steps of discovery – asymptotically reaches for the truth, the magnitude of meaning amplifies. As the experience, through our symbols, tangents *truth*, transcendence emerges. The observer is not only aware of the regulatory principles, but also what they omit. They *feel* truth approaching, and this feeling yields meaning.

During the last two years my life and world view have changed drastically through a combination of philosophic, scientific, and spiritual inquiry. In large part due to my education and a meaningful interaction with it. I have never experienced anything like this before. Examination of any domain of my life seems purposeful. As I learn more about the world I inhabit, I am continually humbled by its beautiful complexities. Both what is physically in front of me and what certain people are able to make me think and feel. This feeling radiates when an author eloquently elucidates a difficult topic through creative reasoning – or when scientific labor bears fruit through exquisite knowledge – or during revelations concerning the physical and spiritual unity of the world and its inhabitants. Science structures the entropy of the world and therefore produces meaning. Discrete moments of complete clarity bound in time by mundane experience. This sudden influx of extreme awareness illuminates my dim consciousness, exposing its endless potential. It invokes an ancient, primeval emotion of being. A transcendence of the spirit by congruence in thought. When such a feeling surfaces, it seems immoral to not worship it... *it*... This *thing*, state of being, vanishes at notice. But does not

revel in nostalgia. It is experienced in the moment yet beyond perception – metaphysically mystical. Later remembered in symbol, objects that tie our spirit to the experience of transcendence. Transcendence as beyond the physical. This is where symbols point us. Not towards themselves, but some purpose beyond what is physically perceivable, only to be experienced. This thesis is the synthesis of all such experiences I can tie to *science*. It therefore symbolizes all that has become meaningful to me during my bachelor years at university. It has become *holy*. An artefact of my being.

In contrast to this source of (to me) obvious meaning – what Tillich certainly would call *Faith* –, modernity treats science as work. Industrialized inquiry. A spiritually innocuous condition of investigation. In fact, I would go as far as to say that the world of authorship in the natural sciences (as I have experienced it) is coated in a spiritual pathogen of literary dogma. A regressive tradition of communication that has reduced an involved dialectic between written creation and read experience into talking and listening – efficiency in dictation and facultative compliance. Efficiency in the sense that “trimming the fat” and suppressing “floral” language for the purpose of disturbing personality is, categorically, considered *good* writing. Dictation in the sense that the author speaks and the reader listens, without interactive discussion nor connection. The text *should not* be meaningful, but rather, resemble a data spreadsheet and its cold analysis. Facultatively in the sense that new ideas, alternative grammar, literary structure, and novel approaches to writing and communication are repressed – tunnel visioning is normative. Compliant in the sense that the author assumes that the reader has a comprehensive understanding of the typical terminology and assumptions of the field of study. This approach is not consistent with my view of meaningful interactivity, and I cannot seem to unite them.

While working on this project, I keep being told that “word-use efficiency, without information loss, is an art-form”, as if I do not agree, nor that being an art-form categorically demands facultative compliance. It is obviously difficult to write like natural science researchers, just as it was once difficult for me to swallow food. Both activities require practice, but requiring practice is hardly an argument one should consider as ultimate in the face of determining something as subjective as appropriate writing style. And while we’re on the topic of *art*, I do not think the proponents of the earlier comment realize what they are comparing the numbing practice of research paper writing to. If any domain of humanity has ever refused templates, intellectual patterns, social requirements, or efficiency in communication, it must be *art*. Specifically how we understand the concept today.

I *truly* enjoyed researching the subject of this thesis, as well as developing the investigative design with my supervisors. As soon as I realized the limitations on my communication, however, my personal connection to this project was seriously threatened. By a virulent disease, no less. Vectored through literary tones,

manuscript templates, grammatical approach, and the attrition of personality, the regressive literary dogma of the natural sciences infested my spirit and almost destroyed my meaningful connection to this work. This happens, perhaps, spontaneously during the formal structuring of large amounts of scientific literature. As science represses expressions of the spirit, discussions concerning its core purpose diminish. *Why investigate the world at all?* I do not mean to require of science to answer such questions – I do not think it can –, but simply not to institutionally ignore the topic. As Karl Jaspers so beautifully puts it,

“Spirit lives and moves wherever our striving for clarity is a striving for fullness of insight. Without ideas there is no such insight. Ideas impel us from within and at the same time beckon to us as the goal we can never reach. Ideas unify and systematize study and research by furnishing us with hypothetical constructs, themselves only approximations to the ideas themselves. Spirit is the power of creative intuition; without imagination science remains sterile. Such imagination enables us to see what is essential and real, to understand from within, that which lies below the surface, and to make this available to scientific study.” (Jaspers 1965:44)

I wrote this thesis for me, no one else, yet was systemically coerced into making it fit a dogmatic structure. No one, except for myself, depends on the literary outcome of this work. It is therefore absurd to me to subject my project to the same structural standards as research papers aimed at producing income for researchers and publishing journals. In my view, this approach to writing theses seriously hurts creative expression and in extension the development of novel scientific perspective. The ideas, and spirit, of independent students deserve more respect.

A conduit of meaning

What makes a good landscape painting? Perhaps twisting and winding swirls of mountains, their natural sovereignty irregularly curtailed by lakes and streams, focally concealed by titan boulders and old-growth oaks of pristine forests. Asher B. Durand would likely agree. But why limit oneself to natural depictions? Consider Hieronymus Bosch’s medieval triptych of heaven and hell; the beautiful youth, ecstasy and prosperity, feasting on all of God’s earthly delights – and the torture of sinners by Satan’s unholy animal-human fusions. From heavenly hills, covered in all sorts of wondrous creatures and structures, tightly interlocking their fates – to woe and smoke, the deepest caverns of horror, where nightmare weaves sacrilege into dreadful homogeneous sludge. If not of woodlands and peaks, might these be portrayals of the landscape of morality within each human being? Perspective alters vision. From his apartment window, Camille Pissarro paints the streets below in constant flux. In parallel lanes, the step of horses carrying passengers, parking in the shades of street-lined broadleaf trees. Complex webs of people entering and

leaving cafés, crossing streets, and elusively managing the mass of bodies bound by rows of apartment buildings. Do these illustrations not depict the ecology of urbanism in the landscape of la belle époque de Paris? If all three painters have managed to portray the essence of a landscape, their juxtaposition might initiate an inquiry into what constitutes its meaning.

Within myself I find a wish for expanding ecology beyond the biological domain, to make its principles applicable to all manners of networks. No doubt, we would consider Durand's aggregates of wilderness landscapes; we imagine all the animals, plants, bacteria, and fungi interacting in webs of ebbs and flows of energy and molecule. This interactive flux to and fro and in-between, I think, is essential to our understanding of ecosystems.

Competition would, to most ecologists, mean a reciprocal loss of fitness between biological individuals. This concept can, additionally, describe the conflicting interpretations of internal and external moral guidelines – one's wish to maximize pleasure often *competes* with cultural compliance. Normative social standards arrest acts of increased life satisfaction in the margins of acceptance. Imagine how prey animals consider – perhaps consciously, perhaps not – the amplified resource availability and sexual prosperity an expansion of their local territory might bear, while acknowledging the increased risks of exposure to predators and intraspecific *competition*. In the same vein, a person would weigh – consciously or not – the benefits of challenging social norms against the cost of outcast, relative to the environment surrounding them (acceptable levels, and expression of, social idiosyncrasy varies between societies and cultures). As these nonconformist ideas are exchanged between individuals and groups, their flux through the cultural domain amplifies, and eventually changes the entire social ecosystem. Likewise, novel biological adaptation may infest a population throughout, or be extinguished in an instant. Both processes may be explained by theories of *evolution*.

The term *mutualism* typically invokes, to students of nature, memories of lectures on mycorrhizal dynamics – tree and fungi depending on each other's flux of nutrients in opposite directions. Today, these interactions are modeled as complex: nutrient transport may change in either direction, depending on conspecific condition and relationship to the environment. Comparably, the horse carriage business outside Pissarro's apartment depends both on the activity of people in the streets and their social prominence. Their movements mesh, giving form to the *mutual* flux of currency and service between economic actors. These interactive fluxes between autonomous vectors, independent of formal domain, define our ecosystems, and their dynamic complex of conduit the landscape.

Functionally, then, landscapes are the arenas of interactive change. Change as the volatilization of the current state, not necessarily continually in any direction. Change in a self-governing vector of an overwhelming amount of dimensions, unbound by their faculties. Change through the integration of collaborative

fundamental principles, endlessly wrestling with environmental entropy. An open and *truly* incorporative system, incapable of dilution and thus ultimately illuminating. Landscapes produce the meaningful interconnectedness between individuals – the sources of being – and habitats – the hosts of all life.

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Glossary

- \forall Logical operator: “for all”, appears during metric formalization and explanation.
- \cap Logical operator: *AND* or *intersect*, quantifies the conditional overlap between categories.
- \cup Logical operator: *OR* or *union*, quantifies the conditional combination of categories; both the *intersect* and the remaining amounts of all constituents.
- Activity-abundance* The interactive effect between activity and abundance of a species within an ecosystem. The likelihood of catching a species of beetle in a stationary trap depends on both its active movement and population abundance within the ecosystem in question.
- Aggregation* A clustering of categories in distinct groups, e.g. patches of same raster cell types.
- Attrition* Analogous to erosion. Used in the context of habitat fragmentation; extreme fragmentation causes a landscape-wide “erosion” of patches of the habitat of interest, to the point of attrition.
- Biocoenoses* (*Bios*) “life” and (*koinós*) “collection” in ancient Greek; a collection of life-forms.
- Carabido-coenoses* (*Carabidae*) “ground beetles” taxon and (*koinós*) “collection” in ancient Greek, a collection of ground beetles (carabids).
- Carabidology* The scientific study of the *Carabidae* family of beetles (*Coleoptera*).
- Carrying capacity* The theoretical maximum population size of any species that can be sustained in a certain environment. The limiting factor of any population growth is always resource availability for the species in question. At the carrying capacity birth rates equal death rates, however, this point is theoretically never realized in closed systems.
- Composition* A categorical description of the system in question, e.g. what habitat types are included in a landscape, or which plant species live in an environment.

<i>Configuration</i>	The intrinsic properties of <i>compositional</i> categories, e.g. the variation in patch shape complexity or dispersion of habitat categories. “The difference between landscape composition and configuration is analogous to the difference between floristics (for example, the types of plant species present) and vegetation structure (for example, foliage height diversity) so commonly considered in wildlife-habitat studies at the within-patch scale.” (McGarigal & Marks 1995:9). The species of plants in a stand describe its vegetative composition, their heights and shape its configuration.
<i>Conspecific</i>	Regarding a certain species of organism or habitat.
<i>Contagion</i>	An aggregated distribution of type, e.g. of adjacent raster cells. Often used synonymously with <i>aggregation</i> .
<i>Dispersion</i>	The distribution of one category within a boundary. For instance, a measure of aggregation of one habitat type within a landscape.
<i>Disturbance</i>	Events, discrete in time, causing destruction or severe change in parts of, or entire, ecosystems (e.g. fire, flooding, logging, or windthrow).
<i>Diversity</i>	Describes non-homogeneity as well as increased categorical richness: diverse systems are typically viewed as rich in categories, which are evenly distributed – the entropy of a system’s constituents (this is typically how <i>alpha</i> diversity is measured in ecology and biology).
<i>Ecosystem</i>	A system of autonomous and interdependent actors in a certain environment. Without clear scale, we may declare an ecosystem to be a puddle, lake, or ocean – even the Earth or entire solar system.
<i>Ecotone</i>	Areas of overlap between two ecosystems, where properties of both diffuse into each other, forming environments suspended between categories.
<i>Edge effect</i>	The effects by each ecosystem on the other at their boundaries, forming an ecotone.
<i>Epigeic</i>	Living on the soil surface.
<i>Eurytopic</i>	Environmental generalist.
<i>Generalist</i>	Organisms, at any taxonomic level, without adaptations to specific environments, e.g. broad consumers, dispersers, or acclimators. Always used as the relative opposite to a specialist.
<i>Habitat</i>	The environment where one species, or even individual, may live and survive. Comparable to conspecific ecosystems.
<i>Hyperspace</i>	Multidimensional space, specifically more than three dimensions. Briefly mentioned while presenting the area-heterogeneity trade-off

hypothesis. In niche theory the hyperspace of all parameters that regulate or are regulated by the ecosystem produce the limits between species' niches. If two species occupy the same portion of the niche hyperspace of their ecosystem, they will inevitably compete for the resources produced by those parameters. See Hutchinson (1957) for a thorough discussion on niche-hyperspace.

- Instar* Developmental phase prior to maturity in the life cycle of arthropods, many species may have multiple. The larval phase of carabids is an instar phase.
- Interspecific* Between categories, e.g. between species or habitat types.
- Inter-spersion* The distribution and intermixing of categorical constituents within a boundary, relative to each other. For instance, a measure of habitat type configuration within a landscape, for all contemporary habitat types.
- Intraspecific* Within categories (e.g. between individuals of a species).
- Littoral* Something with shore-like properties, e.g. coasts and beaches.
- Matrix* In an ecological context: the reference background to any patch type.
- Psammophile* Having a special affinity for sandy environments.
- Pyrophile* Having a special affinity for burned or burning environments.
- Specialist* Organisms, at any taxonomic level, adapted to specific conditions, e.g. to explicit moisture contents or another species. Always used as the relative opposite to a generalist.
- Stand* A homogeneous distribution of properties typical of a forested environment. Commonly used term in forestry sciences to describe a forested patch with similar composition throughout.
- Stenotopic* Environmental specialist.
- Tyrphophilic* Having a special affinity for peaty soils, i.e. moors.
- Xerophilic* Having a special affinity for dry environments, i.e. heath lands.

Introduction

A primer on landscape structure

The patch mosaic paradigm

Landscape ecology deals with the connectivity, fragmentation, and interaction of patch-like elements on different scales of area (Forman & Godron 1986:vii; Wiens 2005; Kilianová et al. 2022). These patches are differentiated by their contrast in structure or function from their surroundings. When many differing types, or categories, of patches bound each other in mosaics, landscape ecologists conventionally describe their assemblage as heterogeneous (Forman & Godron 1986:83; Turner 1987:v; Hunter 1990:80; Wiens 1995; Arroyo-Rodríguez et al. 2017; Kilianová et al. 2022). Of course, this is a relative term, since any plane covered in complexes of patches may display heterogeneity in multiple parameters, for instance: shape, size, or interspersions between types. A patch may host a network of organisms or not; when it does, we call it their habitat (Forman & Godron 1986:95–96). A patch may even *be* some organic aggregate. They may also designate pavement or buildings, or perhaps glaciers or lakes (Forman & Godron 1986:83). In theory, any spatial group or cluster can be considered a patch in any number of dimensions, but for simplicity's sake, the term “patch” henceforth refers to a static environment.

Just as heterogeneity only relatively describes the landscape, so do the categories and properties of patches. Therefore, any ontological claim concerning type differentiation needs substantive motive (Thomasson 2022). And so, before making any inquiry, I need to ask myself: *What is a category of patch? What makes the differentiation between their types meaningful? Is the separation empirically substantive?* Next, let us consider their origin.

The successional shift in patch replacement is causally regulated by mechanisms of disturbance, be it by competitive exclusion, pathogen, or catastrophe – both natural and anthropogenic (Forman & Godron 1986:84–94; Turner 1989; Hunter 1990:27; Arroyo-Rodríguez et al. 2017). Fires destroy canopies, winds knock over stands, lightning breaks stems, and logging prompts primary succession. However,

patch types aren't uniformly susceptible to all disturbances. Riparian systems are selectively disturbed and altered by beavers (Remillard et al. 1987). Swamps saturated in water might not be as severely affected by forest fires as the surrounding dry soil, neither during the disturbance nor its following restorative succession (Forman & Godron 1986:84). Similarly, response severity in biomass accumulation and species assemblage shifts, following sudden nutrient influx, depends on the prior community composition, water contents, and nutrient conditions of the system (Päivänen & Hännell 2012:181–184; Sponseller et al. 2016). In turn, these depend on topography, climate, biology, and geochemistry (Forman & Godron 1986:93–98). Depressions in geomorphology give rise to water catchment pathways, climate regulates temperature and precipitation, local biotics will realize ecological function and trophic networks, and plant available nutrition depends on soil mineralogy. These factors will simultaneously and interactively form the patch structures, and according to their relative effects, both disturbance and succession regimes are determined (Forman & Godron 1986:83–98; Arroyo-Rodríguez et al. 2017). Here we have a channel for definition; through disturbance susceptibility and successional organization, including their regulating mechanisms.

How patches form

Since patch categories often depend on long-term resource availability, e.g. local water or nutrient contents, their successional pattern post-disturbance is somewhat predictable (although stochasticity, such as immigration patterns and disturbance initiation, obviously influences succession) (Forman & Godron 1986:84–89). When a patch is disturbed to destruction, its (a)biotic architects will initiate re-construction, eventually producing a rotation time in within-patch structure. This is called patch turnover (Forman & Godron 1986:85, 93–94). Interacting with the, practically, stochastic patterns of many disturbances (of course, climate will regulate these, but predicting them is difficult [Hantson et al. 2016; McDowell et al. 2018]), landscape structures are volatilized. Patches grow and shrink, their structures are destroyed and rebuilt, their contents flushed out and replaced. As centuries mold their dynamic form, and populations manage the temporal flux, landscapes are continuously changing. They are alive.

Any landscape participant – that is, any mobile life-form – which depends on a set of particular resources for survival, cannot spend much time in patches that do not produce it (Wiens 1976). They may see the landscape as a constant, a temporally locked grid of resources. From this perspective, patch types, or categories, assume a binary state to conspecific actors. They either contribute or not. And as these binary conditions are clustered, the complex of patch dynamics forms (Wang & Cumming 2011). The participant may appreciate the aesthetics of the landscape from afar, but what matters mechanically is only their interaction within it. Alas, a discrepancy

between observation and participation. Do all observers interpret the landscape equally? Of course not. Even humans – in spite of all our methodical tools – struggle to unanimously define both their size and function (Wiens 2005).

How patches fragment

In stochastic appearance, certain patch structures are left intact post disturbance. Sometimes they cluster, form groups – remnant patches (Forman & Godron 1986:89–93; Arroyo-Rodríguez et al. 2017). Their inverse, disturbance patches, form in opposite fashion (Forman & Godron 1986:85–89); small clusters of trees are destroyed, broken, or felled. In both patch types – remnant and disturbance – the expansion of the reference background is disrupted. This is what constitutes fragmentation; a sudden, independent of form and size, spatial arrest of the reference matrix.

If one imagines fragmentation as the subdivision of a whole into multiple isolated constituents, landscapes containing heavily fragmented patch types would, in abstract terms, slide from homo- towards heterogeneity. Thus, fragmentation of patch types gives rise to heterogeneity within landscapes – it is the discrete disruption in patch type spatial distribution, leading to landscape heterogenization. Thus, patch inception causally fragments habitats by virtue of their differentiated function.

At the boundaries between the fragmented patch types *ecotones* emerge; transitional and diffuse habitats containing properties of both categories. Riparian zones along freshwater streams, or quagmires covering lakes. These range in widths depending on either habitat's influence on each other according to environmental parameters (Hunter 1990:102–107) and are typically rich in species (Shmida & Wilson 1985; Kemp 2000; Kark et al. 2007). This stimulates – to the ecotone's constituent habitats – novel interspecific interaction and structural variation (Didham 1997; Rankin-de Mérona & Hutchings H. 2001; Hossain et al. 2002). Thus, ecotones are rather unstable environments (Hunter 1990:107–108), arrested into continuously volatile states, constantly at the mercy of their architects. This fundamental anticipation of structural flux might curtail any evolutionary attempts at specialization of its inhabitants. Unsurprisingly then, specialists typically struggle in heavily disturbed habitats, while generalists prosper at their expense (de Vries 1994; Rainio & Niemelä 2003; Neumann et al. 2016). The more stenotopic a species, the more negative realized conspecific effects from fragmentation are to be expected (Cramer & Willig 2002; Kotze & O'Hara 2003; Devictor et al. 2008). Thus, some species might benefit from habitat fragmentation, others not (see Davies & Margules 1998).

Carabid beetles

Beetles, *Coleoptera*, of the carabid family, *Carabidae*, are facultatively epigeic (some fly on rare occasion and few live on trees) (Lindroth 1949:478–480; Thiele 1977:1–9). They display astonishingly uniform morphology (Thiele 1977:1–9; Evans 1994), and range in size between 1-50 mm in Europe (Sandhall & Lindroth 1976:36). Carabids are, globally, some of the most diverse groups of similar organisms, and can be found virtually anywhere on Earth (e.g. Desender 1994). The widespread use of pitfall traps has made their sampling cheap and efficient (Thiele 1977:1; Woodcock 2005), this makes them splendid subjects for ecological inquiry.

Herbivorous and carnivorous insects naturally regulate plant and animal populations (Waldbauer 2003:7–9; Joshi et al. 2007), carabids included (Šerić Jelaska et al. 2014; Cutler et al. 2016). *Carabidae* consume seeds, fruits, plant tissue, carrion, insect larvae and eggs, worms, caterpillars, snails, and other carabids, with significant dietary variation between species (Lindroth 1949:469–488, 495; Thiele 1977:3–9; Frank et al. 2010; Foffová et al. 2020; Reich et al. 2020). They are in turn consumed by foxes, badgers, shrews, hedgehogs, moles, bats, rodents, spiders, mites, rove beetles, protozoa, almost all kinds of birds, frogs and toads, sawflies and wasps, nematodes and nematomorphs, fungi (Lindroth 1949:493–495; Thiele 1977:80–100), and, unintentionally, mammal grazers (van Klink et al. 2015). Thus, carabids contribute to trophic webs of the ecosystems they inhabit throughout.

Response to landscape structure

By convention, ecologists assume that heterogeneity in both internal and external habitat parameters will influence biodiversity positively (Turner 1989; Hunter 1990:82–100; Veech & Crist 2007; Thomsen et al. 2022). Establishing such a general principle would require substantial synthetic research, but empirical evidence suggests that some heterogeneity in both within- and between-habitat structure affects carabid diversity positively (Niemelä et al. 1996; Spence et al. 1996). In contrast, using predicted landscape complexity by land use categories in agricultural landscapes, Gayer et al. (2019) did not find any significant effects on carabid assemblages. Although, these results are based on land use diversity – calculated using Shannon’s (1948) index – and forest cover, unconcerned with spatial structure. Gallé et al. (2019), however, found significantly positive effects on functional traits in carabid populations from landscape agricultural heterogeneity, inferred categorically as increased farmland edge density. These effects were observed in ≤ 27 ha fields. Fahrig et al. (2015) found similar effects at 100 ha. In circular landscapes, positive heterogeneity-effects on carabid diversity have been observed at 500 m (Woodcock et al. 2010) and 1 km radii (Palmu et al. 2014; Gallé et al. 2018). De Vries (1994) found varying effects on populations by habitat size depending on dispersal strategy: species with weak dispersal strength required 75 ha and strong

dispersers about 8-25 ha to retain stable populations. In circular landscapes, this equates to radii of 489 m and 160-282 m, respectively. Further, however inconclusive their results may be, Davies & Margules (1998) present how habitat fragment size simply is not sufficient for explaining fragmentation effects on carabid populations (although it probably should not be omitted during investigation [Hunter 1990:92–100]). They only measured species richness and changes in conspecific populations, without considering qualitative differences in assemblages or even interspecific ecology. Open-habitat specialist immigration post-disturbance, and subsequent competitive exclusion of remnant patch dependent species, will affect the realized community. Meanwhile, species richness may be unaffected. The authors also suggest a variety of edge effects; some species may increase in abundance in heterogeneous landscapes, and so core area (non-ecotone habitat) may not respond positively to carabid diversity over the whole landscape.

Modeling framework and theory

Spatial relevance

Interspecies analyses with landscape metrics invokes methodological and analytical hurdles (Wiens 1989; Li et al. 2000; Li & Wu 2004). It is not necessarily useful to compare the same spatial dataset to different species, both because species inherently interact with landscapes differently (although, biological similarities surely helps) (Wiens 1976, 1989), and because preferences for habitat properties will change, so then should the dataset (Li et al. 2000). What use is a landscape-wide habitat analysis, if the spatial data lacks ecological relevance for the taxa in question? And: how comparable are two different spatial datasets, e.g. what is the qualitative effect of changing the landscape's habitat-matrix? Spatial analyses concerned with habitat quality and interspersions crucially need to incorporate these specifics, without over-generalizing, in their spatial data (Li & Wu 2004; Harris & Sanderson 2020). This is necessary for any valuable analysis, otherwise specifics are not measured. Thus, analysis scope needs to be reflected qualitatively in data and metric calculation, as to keep relevancy (Turner 1989; Wiens 1989), while also avoiding scaling issues during modeling.

The first step would be investigating habitat differentiation (e.g. Hunter 1999:22–24). The meaning of *habitat* changes both with spatial distribution and scale (Hunter 1990:80–100). For instance, whereas carabids might conceptualize open and closed habitats as black and white areas on a plane from below, hawks might only see them diffused as gray from above, only ever noticing large aggregates (Hunter 1990:80–81). In the same vein, the landscape's functional difference to generalist and specialist carabids should be considered (Hunter 1990:81–82); habitat functionality

thus changes as well. The task during spatial modeling is, therefore, to consider the differences in habitat differentiation, functionality, and distribution. Here I tackle the first two topics, by reviewing literature identifying common carabid differentiation in habitat types.

Since there is no discrete difference between generalist and specialist – all organisms exist on a continuous and opposite spectrum (Devictor et al. 2008) –, differentiating conspecific habitat preference is not always useful. Instead, differentiation is often declared as a function of measured differences in assemblages according to environmental parameters like temperature, humidity, light conditions, and vegetation cover. It should be mentioned: many carabids are predators, and so vegetation cover might not influence their dispersal as much as prey distribution. The link here would be the prey's association to vegetation cover, the predator carabid's distribution should then follow. Generally, however, vegetation distribution should be a reasonable proxy for most carabid assemblages (Thiele 1977:45).

Empirical habitat differentiation and response to change

Essentially, what is interesting is the interspersions of target population distributions in the landscape (Wiens 1976). This distribution is qualitatively different from the habitat interspersions, since they describe different things: one, an approximate distribution of individuals, the other, their preferred environment. But they are assumed to correlate, given an adequate – that is, substantive – habitat differentiation. The habitats act as proxies for species assemblages, partly because they are easier to determine spatially, e.g. with remote sensing techniques, partly because this is how ecologists investigate spatial effects between populations and environment (Wiens 1976). Hereafter, I will attempt to assemble an empirically motivated vector of habitat categories.

Carabid assemblages seem to differ between agricultural crops and wildflower fields (Anjum-Zubair et al. 2015), as well as between agricultural crops, wild grasslands, and coniferous forests (Brigić et al. 2014; Schneider et al. 2016); clear cuts and conifer forests (Heliölä et al. 2001); wild grasslands and deciduous forests (Karsai et al. 1994; Brigić et al. 2014); and between heaths and grasslands (Vermeulen 1994).

Between forest types assemblages become very similar, yet some distinction should probably be made between coniferous and deciduous stands (Jacobs et al. 2007), as well as wetlands and forests (Thiele 1977:22–25, 37–40; Ludwiczak et al. 2020). Lindroth (1949:495–499) also argues for an ecologically motivated separation of wetlands, and further between wetland forests and open bogs. He lists species typical for hardwood forests yet makes no distinction to coniferous carabid species. Whether Lindroth considers coniferous forests as referential or “neutral” to most

species is not clear, but importantly, its value to carabids is not stated. However, since carabids, in fact, do inhabit coniferous forests (Heliölä et al. 2001; Schneider et al. 2016), the conifer-deciduous split seems warranted. Neither spruce and spruce-pine mixtures (Oxbrough et al. 2012) nor conifer and coniferous-deciduous mixtures seem to produce differing carabid assemblages (Oxbrough et al. 2012; Neumann et al. 2016), although the literature is diminutive. This could either suggest significant overlap to both coniferous and deciduous forests from the mixes, or that conifer inclusion reduces dominance of hardwood species in assemblages, or simply that further elucidation of the topic is required. Either way, the results are inconclusive.

Similar assemblages have been found between moors, meadows, and moist forests, suggesting some resemblance between habitats with high moisture contents (Thiele 1977:37–38). These overlap somewhat with typical agricultural compositions in moist environments (Thiele 1977:32, 38, 45), although some species seem to be specifically tyrphophilic (Thiele 1977:39; Müller-Kroehling 2019). Old-growth forests are crucial for certain species (Niemelä et al. 1996, 2007; Spence et al. 1996), but not necessarily important for whole assemblages (Stenbacka et al. 2010). Urban land-use environments, e.g. roads, contain some specialists (Neumann et al. 2016). Young (<20 years) and medium (20–60 years) aged forests do not seem to vary in carabid assemblages (Niemelä et al. 1996). And finally, a distinct – from forests and wetlands – composition of carabids seem to converge in littoral environments (Thiele 1977:40–43).

Thus, there are empirical motives for the following habitat differentiation:

1. *Agricultural crops*
2. *Wild grasslands/fields*
3. *Heaths*
4. *Clear cuts*
5. *Conifer forests*
6. *Conifer forests on wetland*
7. *Deciduous forests*
8. *Deciduous forests on wetland*
9. *Wetlands*
10. *Littoral shores*
11. *Old-growth forests*
12. *Urban areas*

Conclusively, conspecific carabid habitat preferences overlap (Lindroth 1949:384–396, 495–502; Thiele 1977:18–48). The habitat types investigated will most likely not present the true scope of habitat preference in investigated species – this, however, has more to do with formal categorization (Thomasson 2022). Habitat choice in *Carabidae* is not uniformal (Niemelä et al. 1987; Worthen & Merriman 2013). All the habitats are assumed to increase diversity, but many carabids benefit

from several. Therefore, their populations overlap, and so some loss in predictive power between habitat categories is to be expected.

I fundamentally require that the current landscape estimates carabid dispersion effectively and accurately, which completely depends on the rotation times of assemblages post habitat changes. Thus, I assume that carabid assemblages change in a quick manner post habitat changing-disturbances, and that assemblage replacement is continuous during periods without them. As it turns out, carabids are known to respond quickly to environmental changes (Rainio & Niemelä 2003; Sipos et al. 2017), and seem to require about 1-4 years until post-disturbance assemblages are realized (Skłodowski 2017; Koivula et al. 2019). Further, community structures vary continuously (Skłodowski 2017), although changes in functional diversity might be somewhat dynamic (Sipos et al. 2017). This might be a point of contention, but is something I am willing to accept for the purpose of this thesis. The rationale behind the arbitrary nature of the assumption is simply to avoid making claims that are too specific and indefensible.

Any concerns about the non-restriction to a specific biome in studies cited can largely be neglected. Since only few species specialize in European boreal environments (Lindroth 1949:379), investigation may cover most of Sweden while relevancy is maintained.

Landscapes as heterogeneous habitats

Jarmer's (1973) results indicate that homogeneous habitats (agricultural fields and *Sphagnum* zones) contain fewer carabid species with a greater discrepancy in relative abundance, than heterogeneous habitats (shrubs and eutrophic shores). Thiele (1977:46) argues increased environmental heterogeneity to be the cause, echoing Thienemann's (1920) biocoenotic principles,

“... the more variable the conditions in a particular environment the greater the number of species occurring at this site. The more extreme the conditions become, the more impoverished is the biocoenosis with respect to number of species, but the greater the number of individuals occurring within each species.” (Thiele 1977:46)

What happens when habitat heterogeneity increases? Given that: (1) certain species benefit more than others in equal environments, (2) some require stable habitat conditions (e.g. specialists), and (3) interspecific competition increases closer to adjoined habitat edges (Thiele 1977:50–51); the relationship between carabid diversity and landscape heterogeneity should not be expected to be linear. Rather, certain habitat types would benefit diversity more than others (e.g. Kotze & O'Hara 2003; Woodcock et al. 2010), and thus, less heterogeneity might actually benefit diversity if, either, beneficial habitat sizes increase, or detrimental habitat sizes decrease in the landscape. The benefiting parameter being diversity. Empirical

studies support this heterogeneity hypothesis (Allouche et al. 2012; Chocron et al. 2015). The expected decrease in diversity in heterogeneous habitats post intermediate unimodal peak is typically explained as amplified stochastic effects on the relatively small residual populations (Allouche et al. 2012; Ben-Hur & Kadmon 2020). Increased niche partitioning and weaker environmental filtering explains the increase in diversity in fragmenting homogeneous habitats (Allouche et al. 2012; Thomsen et al. 2022). However, as more and more resources are partitioned, the carrying capacities will diminish, populations go extinct, and consequently diversity plummet (Chocron et al. 2015). Therefore, carabid diversity might peak before landscape heterogeneity maximizes (see the different responses to disturbance in Niemelä et al. [1996] and van Klink et al. [2015]). This synthesis of island biogeography (MacArthur & Wilson 1967) and niche-hyperspace (see Hutchinson 1957) is typically referred to as the area-heterogeneity trade-off (AHTO) hypothesis.

Some level of intermediacy in landscape heterogeneity should yield sufficiently stable habitats for specialists, while providing room for interspecific overlap without competitive exclusion by generalists (Cramer & Willig 2002; Chocron et al. 2015). Conclusively, by treating the landscape as *the* heterogeneous habitat, I may investigate its spatial effects on carabid diversity as an AHTO.

Landscapes as parameterized planes

Given an adequate habitat differentiation, what else is there to measure? Really, any dimension of spatial structure, e.g. size, shape, edge length or density, interspersion, aggregation, and so on... There is a multitude of landscape metrics (McGarigal & Marks 1995), which importantly co-vary due to their similar formalism and estimation (Riitters et al. 1995; Cushman et al. 2008). Broadly, one could categorize them into two quantitative groups: one that measures patch shape complexity, and one that measures interspersion of patch types (another group also measures areas, but this correlates strongly with shape [Riitters et al. 1995]). Plotting paired variables of these two categories on a two-dimensional plane produces a diagram, which, in theory, could cover the complexity of any landscape – as a measure of the two patch parameters mentioned. This conceptualization of a landscape – as a two-dimensional plane – makes inference regarding its heterogeneity relatively easy to digest. We would simply have to plot the response variable on a third axis, producing a three-dimensional diagram.

Certain drawbacks accompany this model (see Figure 1): B can be interpreted as homogeneous, as the patch interspersion is continuously similar – as in D. This, however, has more to do with the relative nature of our notions of “hetero-” and “homogeneity”. It is true that B could be *more* heterogeneous if patch size also varied within it. But one would still claim that B is the “most” heterogeneous landscape on the plane presented (Figure 1), since both patch shape complexity and type

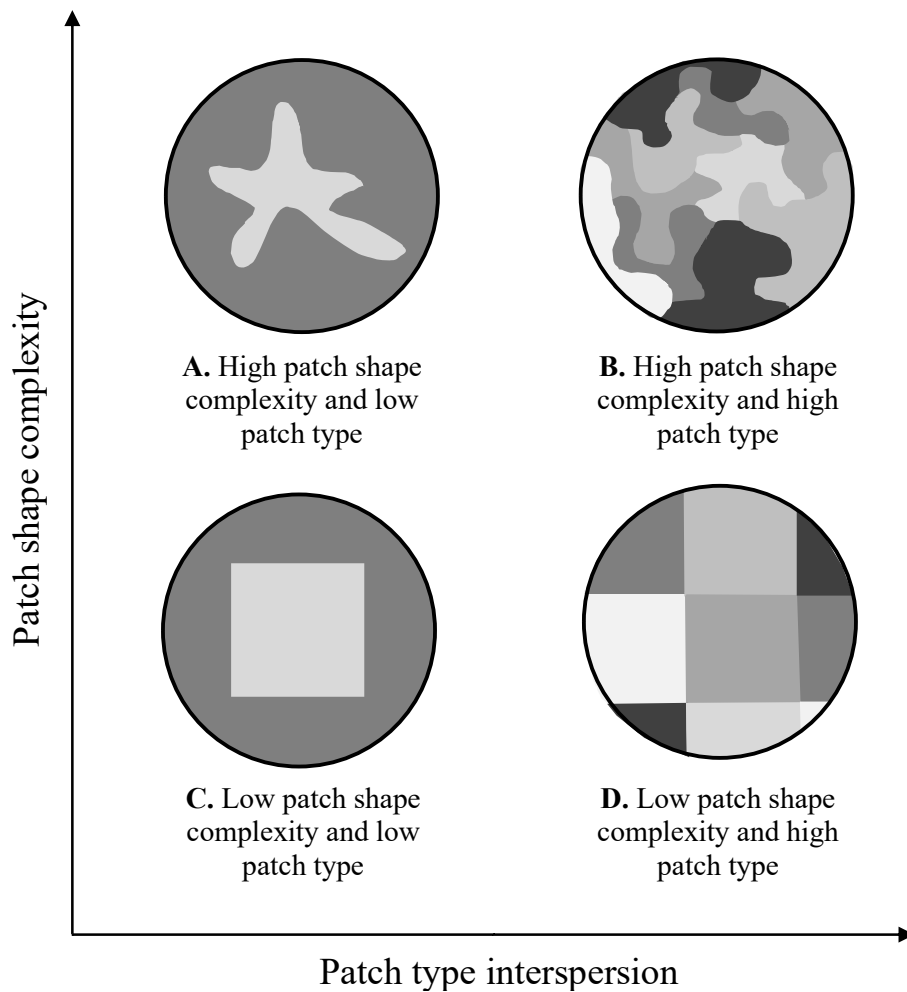


Figure 1. Conceptual structure of landscape heterogeneity along two axes. Each circle (A, B, C, and D) represents a landscape. *Vertical axis:* increased patch shape complexity – a measure of perimeter to area ratio, this estimates the complexity of patch shape and therefore increased edge density. *Horizontal axis:* increased patch type interspersions – as this parameter maximizes, the distribution of patch types becomes less aggregate, or more uniform; both interpretations suffice. This two-dimensional space does not completely account for patch size however (although, size will influence shape complexity), which might be an important factor for some species and not others (Hunter 1990:92–100). Any point on a map could fall somewhere in this plane, and as the points move further towards B, the landscapes become more heterogeneous.

interspersions are large (relative to A, C, and D). Fundamentally, these critiques illuminate some core issues with the patch mosaic paradigm, which will become obvious in the discussion. What is more interesting, for now, is how the two-dimensional landscape plane constructed (Figure 1) affects the response variable.

As suggested by Riitters et al. (1996), parameters beyond area, such as contagion (broadly defined as aggregation) of habitats within landscapes and their shapes, might be required to explain the complex effects of spatial heterogeneity. These processes should also be expected to amplify in frequently disturbed landscapes

(Turner 1989), such as Sweden's forests historically, naturally (Östlund et al. 1997; Kivinen et al. 2012), and also likely in the future (Senf & Seidl 2021).

One should, in conclusion, consider that patch shape complexity might not include patch size as desired, and patch type interspersions inherently require increased habitat richness. What is important then, is finding appropriate landscape metrics. As stated, there are many, and they measure similar things. Producing candidates and selecting low co-variant pairs will therefore be the main subject of modeling.

Investigative purpose and aim

Background

Most of the aforementioned studies investigated *compositional* parameters, e.g. area and edge density classes, land-use types (Davies & Margules 1998; Palmu et al. 2014; Fahrig et al. 2015; Gallé et al. 2018, 2019; Gayer et al. 2019), or tree age groups (Niemelä et al. 1996; Spence et al. 1996). Woodcock et al. (2010) did attempt to quantify landscape heterogeneity using Shannon's index as a function of different habitat area proportion. However, first, they assumed a landscape radius of 500 m to be adequate for carabid ecology, second, they did not consider spatial heterogeneity precisely. Their proxies were heterogeneity estimates based on landscape composition. That is, patch types and their proportional cover of the landscape. These estimates do not consider the influence of patch shape or interspersions (e.g. edge to area ratio, or dispersion of types between each other within the landscape), and therefore lose information regarding core areas and ecotones. Which are, as already established, sensitive to fragmentation and regulate assemblages through environmental filtering.

Instead of only looking at categorical land-use or classes of habitat parameters, I aim to investigate spatial *configuration* (the spatially quantitative properties of the categories, as opposed to the categorical *composition* of a landscape [McGarigal & Marks 1995:9; Fahrig 2005]). Given the substantive importance put on patch configuration (e.g. shape, size, and interspersions) (Forman & Godron 1981, 1986), landscape scaled ecological modeling requires consideration for these properties. Including both relevant patch type and quantified configuration should yield enhanced models which may enlighten what scales populations interact with landscapes and their structures at.

Research questions

Land-use categories are defined by humans for human land use, without much consideration for their natural populations. Response by carabids to habitat

configuration will therefore depend on the categorical view of the habitats in question. This thesis, necessarily, needs to consider the landscape from the perspective of carabid communities (Wiens 1976). Accordingly, the study will adopt a functional view regarding the structure of their assemblages.

The purpose of this study is to provide a basis for contextual large scale spatial modeling, and thereby improve the approach to ecological investigation in boreal forest landscapes. I will attempt to reach this goal by answering the following questions:

1. *How can one quantify spatial heterogeneity in landscapes?*
2. *How does carabid diversity react to spatial heterogeneity?*
3. *Do habitats and their abundance affect carabid diversity uniformly?*
4. *What is a carabid landscape?*

Hypotheses

In order to answer the four research questions and produce meaningful discussions on their topics, this thesis will test the following hypotheses:

I

Considering the landscape as a circle from any point, the heterogeneity effect will maximize carabid diversity, within the circle, at a certain radius. This should be somewhere between 200 and 1000 m (see de Vries 1994; Woodcock et al. 2010; Palmu et al. 2014; Fahrig et al. 2015; Gallé et al. 2018, 2019).

II

Carabid diversity will increase when homogeneous landscapes become more heterogeneous and vice versa, effectively maximizing at an intermediate level of forest fragmentation. This can be investigated at the optimal landscape size (see hypothesis I).

III

All habitat categories will reduce forest carabid diversity equally linearly as their core areas increase.

IV

Core area and ecotone abundance increase carabid diversity equally and maximally interactively, since stenotopic species prefer core areas and eurytopic species ecotones (de Vries 1994; Rainio & Niemelä 2003; Neumann et al. 2016). An equal ratio of the two within a forest landscape yields the highest alpha diversity.

Methods

Data and design

Carabid sampling

Carabids were caught using pitfall traps at 40 different locations split evenly throughout two Swedish counties, Värmland and Gävleborg (Figure 2). Each site included three circular sample plots with 15 m radii: one on an older clear cut (20-30 years old at the time), one in a free standing retention patch (remnant tree patch in the center of a clear cut) with similar tree composition to the previous stand, the third in a woodland key habitat (set-aside forest stand) with similar tree composition and within 5 km from the retention patch. The distance between plot perimeter and patch edge was at least 15 m in all instances. The plots were selected from a list of candidate locations, with the purpose of producing a gradient from spruce-dominated

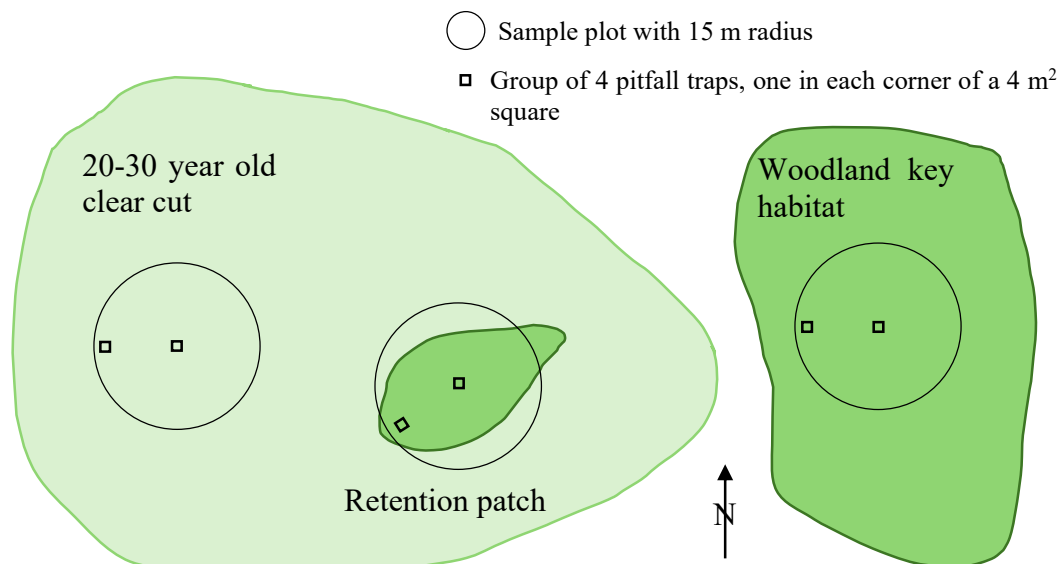


Figure 2. Conceptual pitfall trap sampling design, older clear cut in lighter and remaining trees in darker green.

to pine-dominated stands. Each sample plot contained two sets of four pitfall traps, one in each corner of a 4 m² square (Figure 2). One set placed in the center of the sample plot, one on the western edge. Where the soil was suboptimal for trap placement, the edge group was moved either clock- or counter-clockwise, whichever direction seemed the most suitable. In total 960 pitfall traps, in 120 sample plots, at 40 locations, in 2 counties. Each trap had an opening of about 75 mm, volume of 2-3 dl, a 10 cm² plastic or metallic roof, and was filled from the bottom up with 5 cm colorless propylene glycol, diluted to 50 percent. The solution kills and preserves the specimen (Woodcock 2005).

Naturally, some traps were lost, this negatively affects catch rates and thus skews the results. Sample plots with more than 1 lost trap (12.5 percent) will be omitted during data analysis, so that only relatively intact trap groups are kept.

During sampling, the contents of all four traps in each group were pooled and stored in either alcohol or a freezer. This was done about once a month starting mid-May to mid-August during 2021 – pitfall traps are typically only sampled in the summer due to low winter activity (Woodcock 2005). This comfortably falls within the recommendations of Niemelä et al. (1990).

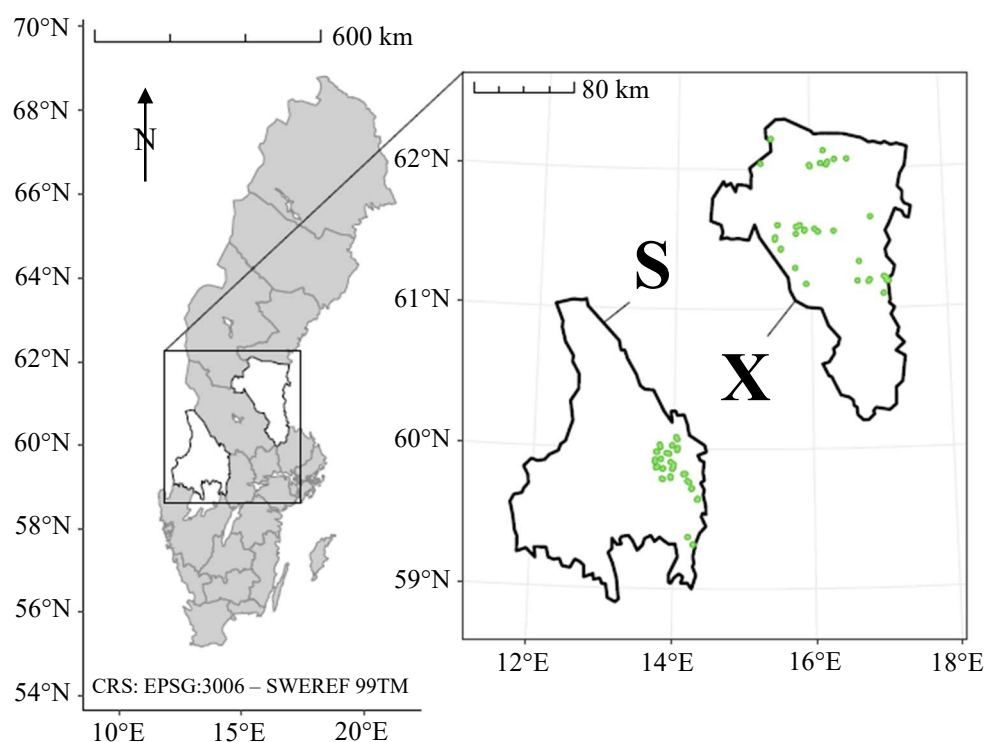


Figure 3. Regional map of Sweden and the two counties of interest, Värmland (S) and Gävleborg (X). All 120 sample plot locations and their corresponding 2 km radii circles are marked in green. In total, 74 504 ha will be included in the analysis. Since 120 circles with 2 km radii equals 150 796 ha, the maximum overlap between samples will be about 50 percent.

The relative similarity in latitude and longitude between the sample plots (about $SE_{\circ N}=0.2$ percent and $SE_{\circ E}=1.4$ percent from SWEREF 99TM coordinates) (Figure 3) is favorable, since climatic factors are largely responsible for conspecific distributions of carabids (Lindroth 1949:538–541). However, forestry practices might vary between the counties due to differences in legislative and cultural practices. Forest management affects both carabid abundance and species richness (Roberge & Stenbacka 2014), and so including county and plot placement as categorical terms in modeling should be beneficial (more on this during statistical modeling).

Spatial data

The Swedish Environmental Protection Agency's (SEPA) national land cover database (NMD) keeps raster data for categorical land use (Naturvårdsverket 2022a). Data gathering for the current NMD was conducted between 2017-2019 and provides raster maps with 10 m resolution, produced from combining satellite imagery with laser mapping. These should be sufficient for landscape metric calculation (Wickham & Riitters 1995). The forest land use classes require more than 70% modeled volumetric content of the species in question, e.g. a 10 m² plot with >70% relative *Pinus sylvestris* volume would be considered a pine forest raster. All forest raster classes cover an area with a canopy cover of more than 10% where trees were taller than 5 meters during the measurements, as per the FRA 2020 definition (FAO 2018). Where the canopy was shorter, the raster is considered a clear cut. Wetlands are considered areas with high water contents close below, in, or above the surface soil layer (Löfroth 1991).

The Swedish Forest Agency (SKS) and SEPA keep national polygon data for all formally protected and high conservation value forests (Skogsstyrelsen 2020a, b, c, d, e; Naturvårdsverket 2022b, c, d, g, e, f, h) – many of these overlap. This data was rasterized in QGIS (2023) version 3.22.16-Białowieża and integrated with the NMD data by raster reclassification to create the *Old-growth forest* (OF) and *Old-growth forest wetland* (OFW) classes (see the finished habitat differentiation in Table 2). Any non-forest class from the NMD data overlapping with OF or OFW was categorically associated with its preliminary NMD class. This is important, otherwise OF and OFW will include non-forest habitats – this is not their purpose (more on this soon). Finally, batch buffering functions with specific lengths were used as masks around the sample plot coordinates to create circular landscape raster maps for radii in 100 m intervals between 100-2000 m.

Spatial modeling

Modeled habitats

Deciduous trees other than *Betula* spp., *Populus tremula*, and *Alnus* spp. account for about 1 percent tree volume in southern Norrland and 1.8 percent in Svealand (SLU 2022). This motivates merging all deciduous classes from the NMD.

The NMD combines old pastures, non-forested heaths, and herbaceous fields into one category, which I have reclassified as *Grass and shrubs* (GS), and meadows with agricultural crops into what I call *Agriculture* (A). Alas, separation of heaths and wild grasslands is not possible. Even though Thiele (1977:34–37) argues for their differentiation, he also notes a strong overlap in most species. Some, however, are xerophilic, and thus specialized for dry heath lands. The spatial data limits me in this regard.

Even though Oxbrough et al. (2012) and Neumann et al. (2016) suggest similar communities in coniferous mixes, I have decided to keep separate any conifer species, coniferous from deciduous forest, and the mixes from the NMD. These differentiations need to necessarily be empirical, and there is a lack of data (basing the modeling on one non-replicated study is dubious at best). For this particular differentiation, I have to resort to avoid making assumptions – such as “carabid assemblages do not differentiate between pine and spruce habitats” – without clear backing. Since *Pinus sylvestris* and *Picea abies* dominated stands are normatively – with good reason – assumed to be quite different in most ecological dimensions (for instance, Lindroth [1945] notes that some xerophilic carabids tolerate moderate shading in pine but not spruce forests, and tyrphophilic species prefer spruce over pine cover), this compromise seems appropriate.

Table 1. Datasets, from SKS and SEPA, included in the old-growth habitat categories.

SKS and SEPA data	Source
<i>Skogliga värdekärnor 2016</i>	Naturvårdsverket (2022b)
<i>Natura2000, SCI, SAC</i>	Naturvårdsverket (2022c)
<i>Natura2000, SPA</i>	Naturvårdsverket (2022d)
<i>Nationalparker</i>	Naturvårdsverket (2022e)
<i>Naturminnen</i>	Naturvårdsverket (2022f)
<i>Naturreservat</i>	Naturvårdsverket (2022g)
<i>Naturvårdsområden</i>	Naturvårdsverket (2022h)
<i>Biotopskydd</i>	Skogsstyrelsen (2022a)
<i>Naturvårdsavtal</i>	Skogsstyrelsen (2022b)
<i>Nyckelbiotoper</i>	Skogsstyrelsen (2022c)
<i>Nyckelbiotoper storskogsbruket</i>	Skogsstyrelsen (2022d)
<i>Objekt med naturvärden</i>	Skogsstyrelsen (2022e)

Table 2. All the defined habitats and their merged NMD classes. See descriptions for noteworthy remarks.

NMD ID	NMD class	Final ID	Final class	Description
51	<i>Exploaterad mark, byggnad</i>			Urbanized areas without vegetation, can be roads and parking spots, as well as buildings, but also flattened hardened surfaces.
52	<i>Exploaterad mark, ej byggnad eller väg/järnväg</i>	1	Urban (U)	
53	<i>Exploaterad mark, väg/järnväg</i>			
2	<i>Våtmark</i>	2	Wetland (W)	Non-forested land with tall water tables.
3	<i>Åkermark</i>	3	Agriculture (A)	With or without permanent crop, meadows included.
61	<i>Sjö och vattendrag</i>	4	Freshwater (FW)	Includes artificial streams and dams.
62	<i>Hav</i>	5	Ocean (O)	Includes aquatic vegetation. The only class considered background in <i>Fragstats</i> .
111	<i>Tallskog utanför våtmark</i>	6	Pine (P)	Includes stands dominated (>70% volume) by <i>Pinus sylvestris</i> and <i>Larix</i> spp.
112	<i>Granskogs utanför våtmark</i>	7	Spruce (S)	Includes stands dominated (>70% volume) by <i>Picea abies</i> .
113	<i>Barrblandskog utanför våtmark</i>	8	Mixed coniferous (MC)	P-S mixes.
114	<i>Lövblandad barrskog utanför våtmark</i>	9	Mixed (M)	Coniferous-deciduous mixes.
115	<i>Triviallövskog utanför våtmark</i>			
116	<i>Ädellövskog</i>	10	Deciduous (D)	Includes stands dominated (>70% volume) by non-conifers.
117	<i>Triviallövskog med ädellövinslag utanför våtmark</i>			
121	<i>Tallskog på våtmark</i>	11	Pine wetland (PW)	Same as P, but on wetland soil.
122	<i>Granskog på våtmark</i>	12	Spruce wetland (SW)	Same as S, but on wetland soil.

Table 2. (continued)

NMD ID	NMD class	Final ID	Final class	Description
123	<i>Barrblandskog på våtmark</i>	13	<i>Mixed coniferous wetland (MCW)</i>	Same as MC, but on wetland soil.
124	<i>Lövblandad barrskog på våtmark</i>	14	<i>Mixed wetland (MW)</i>	Same as M, but on wetland soil.
125	<i>Triviallövskog på våtmark</i>			
126	<i>Ädellövskog på våtmark</i>	15	<i>Deciduous wetland (DW)</i>	Same as D, but on wetland soil.
127	<i>Triviallövskog med ädellövinslag på våtmark</i>			
		16	<i>Old-growth forest (OF)</i>	Formally protected forests and woodland key habitats.
		17	<i>Old-growth forest wetland (OFW)</i>	Same as OF, but on wetland soil.
118	<i>Temporärt ej skog utanför våtmark</i>			
128	<i>Temporärt ej skog på våtmark</i>	18	<i>Clear cut (CC)</i>	Windthrown and burned stands, as well as overgrown wetlands can be included.
41	<i>Övrig öppen mark utan vegetation</i>	19	<i>Bare soil (BS)</i>	Soil without vegetation or shores.
42	<i>Övrig öppen mark med vegetation</i>	20	<i>Grass and shrubs (GS)</i>	More than 5 year old pastures, non-forest heath and shrub lands, and small herbs.

Protected areas and woodland key habitats contain higher volumes of large living trees and dead wood in all diameters larger than 10 cm, in all decay stages, for both conifers and deciduous, and in total (Kyaschenko et al. 2022). Considering the conservation purpose – to maintain remnant populations of habitat sensitive species in a landscape of intensively managed environments – of the protected forests in Sweden, these function as proxies for *proto* old-growth forests in ecological study. Merging the data in Table 1 and separating the class into wet and dry soil categories will produce the *Old-growth forest* and *Old-growth forest wetland* classes.

Since freshwater may benefit carabid diversity in small fragments (Neumann et al. 2016) and as riparian buffer zones (Sprössig et al. 2022), it seems unreasonable to omit *Freshwater* from metric calculations. Comparatively, seawater (not all salt water) seems only to disrupt dispersion and a detriment for habitation (Lindroth 1949:525–529, 533–535). Therefore, *Ocean* will be disregarded during modeling (Table 2). The landscape modeling software *Fragstats* (version 4.2.598, McGarigal & Ene 2014) allows for classifying certain raster values as background, this will effectively remove *Ocean* from any metric calculations. *Freshwater*, however, will be included.

Differentiating *Bare soil* (which accumulates along land-ocean borders and on the edges of larger lakes) from *Grass and shrubs* (which are more frequent deeper into the landscape, around clear cuts, agriculture, and inside power grid lines) in the NMD (Naturvårdsverket 2022a), allows the model to discriminate between shore soil habitats and general grassland types. This should also be beneficial, as certain carabid species specifically live on ocean shores, others in grass and shrub habitats (Thiele 1977:34–37, 40–43).

A matrix model for calculating core area

Habitat core areas represent the habitat area unaffected by edge effects from adjacent habitats. Core areas can be useful during ecological modeling, as they describe non-ecotone environments efficiently (Temple 1986). By modeling edge effects between habitats, total core area (TCA) can be estimated as the sum of unaffected areas within patches.

Before TCA calculation, the transgressive interactions must be established. *Fragstats* incorporates them as a matrix of interspecific habitat interactions. That is, the transgressive effect on one habitat by all others, for all habitat types. This is a huge benefit of *Fragstats*, but it invites some technical considerations. (1) Estimating detailed core areas would require empirical species-specific edge-sensitivity models (Laurance & Yensen 1991), and therefore rerunning of the model with different edge depth matrices for isolated taxa. Although, general analysis of diversity (e.g. Shannon 1948; Simpson 1949) of aggregated taxa would not necessarily be bound

Table 3. The matrix model for transgressive edge effects on each row by each column. Edge depths in meters. For instance, the *Agriculture* row displays the edge effects on itself by the habitat in each column. Green = forested habitat, yellow = non-forested habitat, blue = water, grey = insignificant interaction, bold = wetland environment. The colors inside the matrix cells describe the transgressive habitat, the colors in the rows describe the transgressed habitat.

Edge depth matrix	U	W	A	FW	O	P	S	MC	M	D	PW	SW	MCW	MW	DW	OF	OFW	CC	BS	GS
<i>Urban (U)</i>	0	10	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	0	0	0
Wetland (W)	20	0	20	0	20	20	20	20	20	20	10	10	10	10	10	20	10	10	10	10
<i>Agriculture (A)</i>	0	20	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	0	0	0
<i>Freshwater (FW)</i>	20	20	20	0	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
<i>Ocean (O)</i>	20	20	20	0	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	20
<i>Pine (P)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
<i>Spruce (S)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
<i>Mixed Coniferous (MC)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
<i>Mixed (M)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
<i>Deciduous (D)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
Pine wetland (PW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
Spruce wetland (SW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
Mixed coniferous wetland (MCW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
Mixed wetland (MW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
Deciduous wetland (DW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
<i>Old-growth forest (OF)</i>	20	20	20	20	20	0	0	0	0	0	10	10	10	10	10	0	10	20	20	20
Old-growth forest wetland (OFW)	20	10	20	20	20	10	10	10	10	10	0	0	0	0	0	10	0	20	20	20
<i>Clear cut (CC)</i>	0	0	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	0	0	0
<i>Bare soil (BS)</i>	0	0	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	0	0	0
<i>Grass and shrubs (GS)</i>	0	0	0	20	20	20	20	20	20	20	20	20	20	20	20	20	20	0	0	0

to such specifics. (2) Very detailed models would, similarly, require empirical comparisons between all combinations of habitats. Which, necessarily, invites k^2 assumptions for k habitats. Instead, applying a single default edge effect for all interactions only makes one assumption: namely, that an approximation for all interactions adequately describes an average measure of edge effect transgression.

It is not unreasonable to me to consider allowance for random error more acceptable than making an incommensurate amount of assumptions.

Next, a default value must be established. Research suggests that carabid species assemblage, diversity and activity-abundance may be affected significantly about 15 meters into forests and open habitats from their boundaries in boreal, temperate, and tropical biotopes (Heliölä et al. 2001; Magura 2002; Matveinen-Huju et al. 2009; Brigić et al. 2014; Cividanes et al. 2018; Knapp et al. 2019). To account for the raster widths of 10 meters in the NMD, the default value of the *edge depth* parameter (calculates the transgressive depth of edge effects at interspecific habitat boundaries) in *Fragstats* will be adjusted to 20 meters between open and closed habitat types to avoid unwanted rounding. As suggested by literature however, there is significant overlap in assemblage preference between wet habitats (Thiele 1977:37–38) and forested habitats (Jacobs et al. 2007; Oxbrough et al. 2012; Neumann et al. 2016). The model could therefore benefit from making one additional assumption: different wetland environments are similar enough in configuration to reduce the transgressive edge effects between habitats.

The *edge depth* matrix (Table 3) in *Fragstats* will accordingly apply the following conditions: (1) forested, non-forested, and water habitats affect each other maximally (20 m) between and minimally (0 m) within; (2) edge depth is increased by 10 m between wetland and non-wetland habitats; (3) edge depth is reduced by 10 m between wetland habitats; (4) freshwater and ocean always maximally affect land habitats.

Measuring diversity

Since pitfall trap results are useful abundance-estimators for carabids (Baars 1979), they become really useful when investigating relative population sizes. One might not be able to accurately estimate specific populations (Karsai et al. 1994), but instead the proportional evenness between them. This, in turn, is very useful during *alpha* diversity – local diversity (Whittaker 1972) – index calculation.

Shannon’s (1948) diversity index (H') incorporates richness and evenness in relative abundance between categories, without upper limit, as

$$H' = -\sum_{\forall i} p_i \cdot \ln(p_i)$$

where p is the proportional abundance of species i of the whole community ($\forall i$).

Statistics

Response and multiple comparisons

Carabid diversity might maximize at a certain level of heterogeneity and not increase indefinitely (see the theoretical approach). It would therefore be relevant to investigate how carabid assemblages react dynamically as landscape configuration varies. An appropriate statistical model should therefore reflect nonlinear responses. For nonlinear model parameter testing, one can use general additive models (GAMs) (Hastie & Tibshirani 1986). To fit my landscape parameterization (Figure 1) and data, GAMs are formalized as

$$\eta(\mu(y_i)) = \alpha + \gamma_i + \lambda_i + f_1(x_1)_i + f_2(x_2)_i$$

where η is a link function for the mean, μ , of the response variable y , of any exponential distribution. α is the model intercept, γ and λ are the categorical effects of sample plot county (Värmland and Gävleborg, see Figure 3) and group (older clear cut, retention patch, or woodland key habitat, see Figure 2), respectively. f are smoothing functions for the patch shape variable, x_1 , and patch type interspersion variable, x_2 , for sample plot i (Wood 2006:121–122). GAMs are similar to GLMs, they simply apply a penalized smoothing function (f) to the explanatory variables (x). Thin plate splines (Wood 2003, 2006:128–130, 154–160) will produce the smoothing functions. Calculation of GAMs – and all other statistical work – will be done in *R* version 4.1.2 (R Core Team 2021; RStudio Team 2022) with the *mgcv* package (Wood 2022).

All comparative p -values will be adjusted using Holm’s (1979) method, which works similar to Bonferroni’s but eases the requirement for significance sequentially from lowest to highest, comparing p to

$$\frac{\text{significance level}}{n}, \frac{\text{significance level}}{n-1}, \dots, \frac{\text{significance level}}{1}$$

where n is the amount of hypothesis tests. Effectively, this punishes p decreasingly on abundance and scale. The assumed significance level is 0.05 for all tests hereafter.

Model and variable selection

Partitioning the spatial data by landscape radii and comparing explanatory power between models can estimate optimal radius length. Akaike’s (1974) information criterion (AIC) offers an efficient term for model comparison as the discrepancy between *truth* and *approximated truth*, under the assumption that no model describes any system perfectly. Since it is fair to assume that we do not measure

every single parameter of all investigated systems, the AIC becomes appropriate for biological inquiry (Burnham & Anderson 2002:284). Theoretical information loss (as the aforementioned discrepancy) can be estimated with maximum likelihood functions for response variable (y) data paired to different explanatory variables (x) (Burnham & Anderson 2004). Formally,

$$\text{AIC} = -2 \log(\mathcal{L}(\theta|Y)) + 2K$$

where \mathcal{L} is the likelihood function of the modelled parameters, θ , given the data Y , and K the amount of estimable parameters of the model, without any nestedness in θ required (Burnham & Anderson 2004). For practical purposes, AIC can be interpreted as: the absolutely smallest value (AIC_{\min}) is always the best fitting, to the data given, model (Burnham & Anderson 2004). This means: any models, independent of structure, can be compared, as long as all explanatory variables (x) are paired to the same set of response variables (y). To avoid overfitting on sample size, n , the conservative estimate

$$\text{AIC}_c = \text{AIC} + \frac{2K(K+1)}{n-K-1}$$

will always be used for model comparison.

Since many common landscape metrics are known to co-vary (Riitters et al. 1995; Cushman et al. 2008), model selection should prioritize low correlation between paired variables (x_1 and x_2). Sets of candidate variables will be constructed for both x_1 and x_2 (see Appendix A), the most frequent (in all landscape radii) least correlative pair will be chosen for all models. This selection process seems a reasonable strategy for scrutinizing co-variance and maximizing model predictability, while maintaining ecological relevance and analytical contingency.

Results

Caught carabids and their environments

8061 individual carabids were caught. All species were of *Least Concern* (see the whole list in Appendix B), and so discrepancies in functional contribution to *diversity* between Shannon's index and alpha diversity is not necessarily an issue. All species are common and none prioritized for national conservation. Forest and eurytopic humid and wet species were very common (e.g. *Agonum fuliginosum* [9 percent of total catch], *Carabus violaceus* [35 percent], and *Pterostichus oblongopunctatus* [9 percent]), xerophiles and open dry habitat species were noticeably rarer (e.g. *P. melanarius* [0.21 percent], *Leistus ferrugineus* [0.14 percent], and *Notiophilus germinyi* [0.10 percent]). Even single individuals of specialist pyro- (*Sericoda quadripunctata*) and psammophiles (*A. quenseli*) were caught. The list of species caught and their environmental requirements does not seem to deviate from what should be expected (see Niemelä et al. 1987, 1996, 2007). I see no reason to consider the carabid data as non-representative of the communities studied.

In total, 45 different species were caught in the 103 sample plots included during analysis (<2 traps lost), 34 species in Gävleborg, 25 in Värmland, and 24 in both. The catch was similar between counties, and differences between sample plot locations are probably due to conspecific habitat preference. Some species seem frequent in the same plot type in both counties (e.g. *C. hortensis* and *P. oblongopunctatus*), others' preferences indicate some interactive effect between location and species (e.g. *P. niger* and *L. terminatus*). Keep in mind however, no tests have been conducted in this regard. The significance of the γ and λ terms are without interest to my investigations, they simply isolate expected variance.

Landscape modeling

Hypothesis I

Model integrity seems sensitive to landscape area – shape complexity (x_1) and type interspersion (x_2) correlation decreased seemingly linearly with landscape radius (Figure 4). This might, however, simply be caused by raster size. The influence of patch *grain* reduces as landscapes grow (or grain diminishes), proportionally reducing the stochastic effects from edge estimation (Wiens 1989). Producing equivalent models with smaller cells might falsify scale dependence on model parameter co-variance.

As the co-variance diminished, a pattern in model explanatory power emerged: R^2_{adj} increased and AIC_c decreased in parallel until they both reached a peak in maximum and minimum, respectively, around a 1100-1200 m radius (Figure 4).

The absolute difference in deviance (D , see Appendix A) between the models at 1100 m and 1200 m was 0.11849 with 0.13075 estimated degrees of freedom. At a 0.05 significance level, a χ^2 distribution returns an insignificant p -value (for D_{diff}

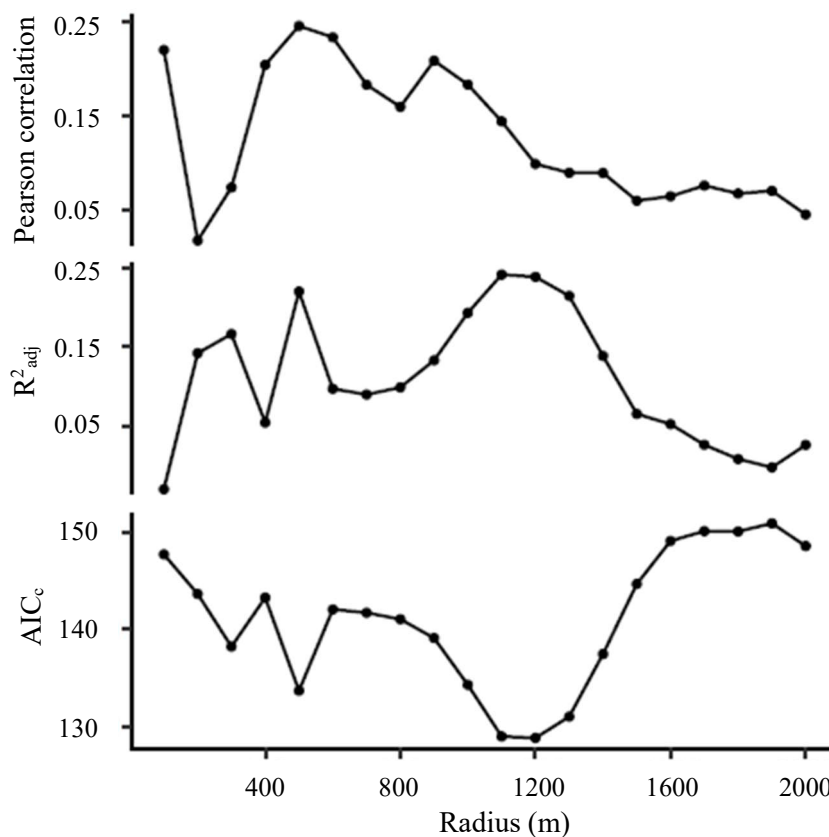


Figure 4. Pearson correlation between x_1 and x_2 , R^2_{adj} , and AIC_c for models at all landscape radii. Pearson correlation maximizes at 500 m (0.24), R^2_{adj} at 1100 m (0.24), and AIC_c minimizes at 1200 m (128.93).

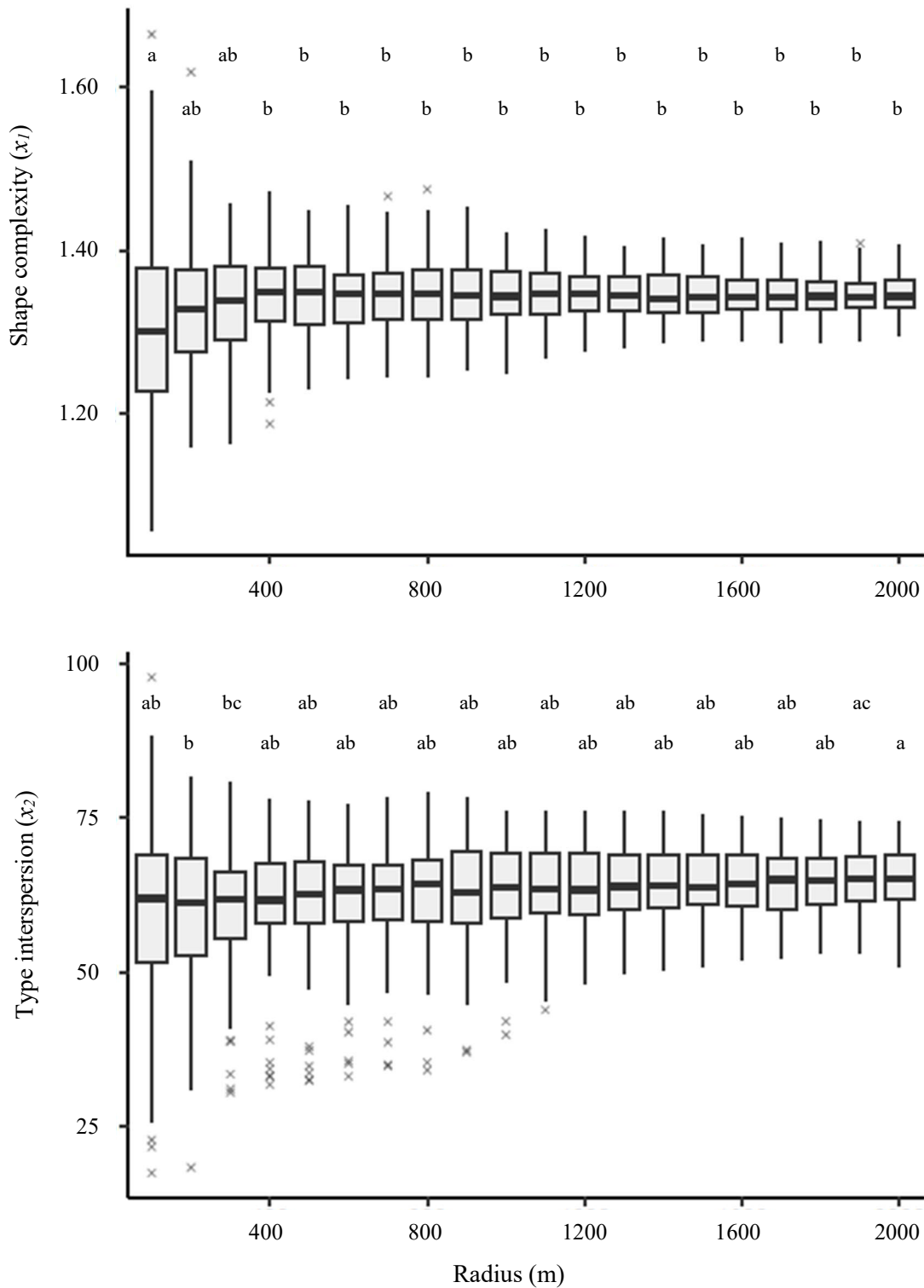


Figure 5. Distribution of shape complexity (MSI) and type interspersion (IJI) over all landscape radii as boxplots. See Appendix A for variable formulas. At a 0.05 significance level, Kruskal & Wallis' (1952) rank sum test indicates significant differences in distributions for both variables. Conover & Iman's (1979) multiple rank sum comparison produced the *post-hoc* test results. Significant differences in distributions of both shape complexity and type interspersion between radii are indicated with letter labels – shared labels infer insignificant ($p_{adj} > 0.05$) differences in distributions.

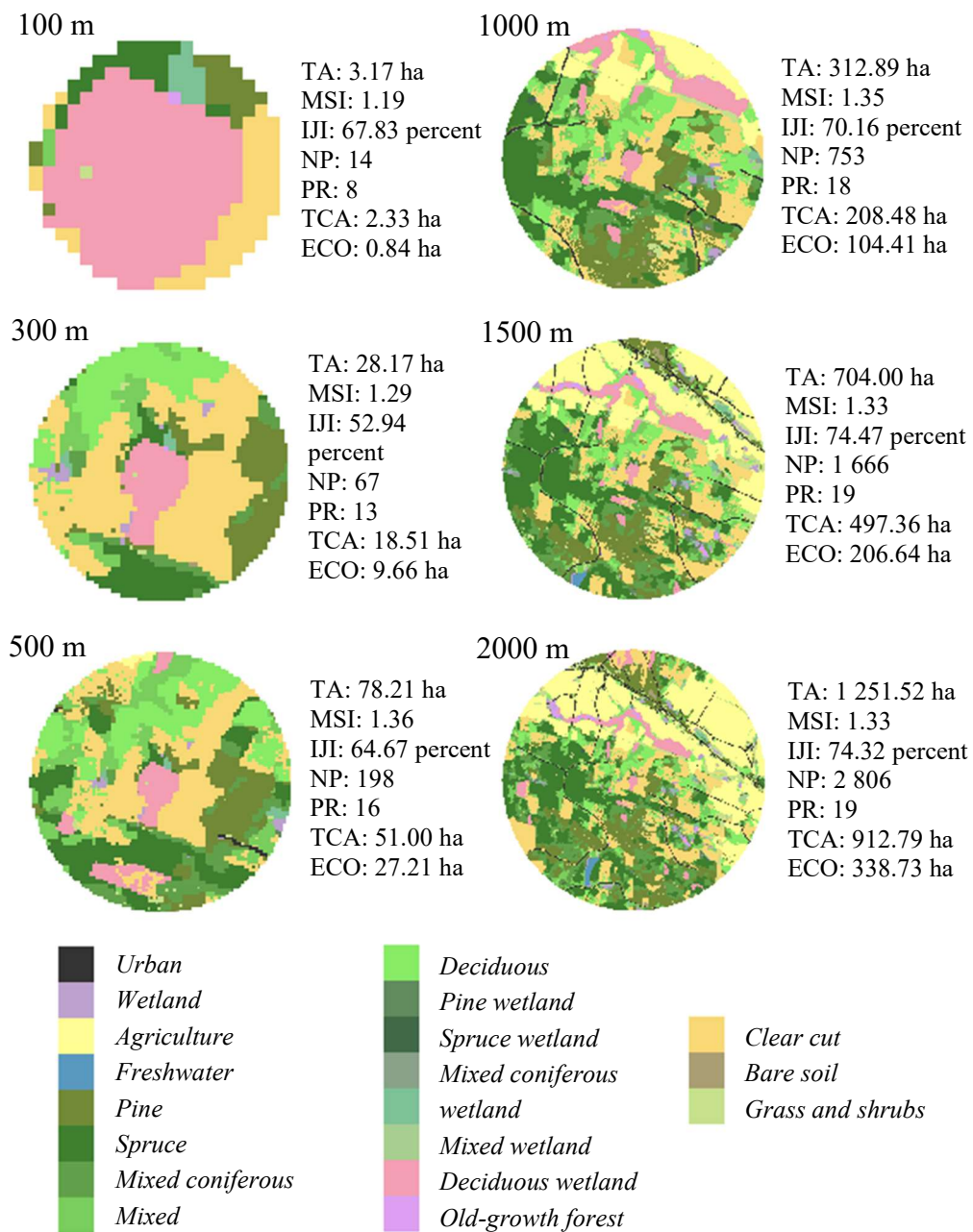


Figure 6. Different radii and their corresponding landscape metrics for site 23 at 61°20'8.07" N and 16°42'38.52" E, south of Glössbo between Bollnäs and Söderhamn. Note that *Ocean* is not included in this landscape. H' at this site was 1.74. NP = number of patches, PR = patch richness.

≥ 0.11849). Either model could therefore be chosen as the best fitting. Since 1200 m produced the lowest AIC_c and variable co-variance (Figure 4), it seemed the theoretically best choice for subsequent habitat analysis. Realistically however, carabid diversity was affected similarly by landscape configuration at both radii. In the context of hypothesis I, there was an optimum circular landscape size at 1200 m radius (about 452 ha). The smaller landscapes – specifically below 600 m radius

– seemed to vary much more than the larger. This might, again, be due to raster scale.

Further, and clearly, the shape and interspersion metrics (the MSI and IJI) were similarly sensitive to either landscape or raster size (Figure 5). Both decreased in variance as landscape size increased and differed significantly between some radii. Since the IJI, mathematically, is insensitive to patch scale (it only accounts for perimeter proportions), the effect on x_2 in Figure 5 has to be a condition of relative raster size (see Figure 5 and Figure 6). In addition, the MSI is sensitive to patch scale, that is, the relationship between patch and landscape area. Despite the raster bias correction (see Appendix A), some influence should be expected (McGarigal & Marks 1995:36).

Conclusively, the co-variance of the explanatory variables between 400-1000 m radii (Figure 4), and their increase in variance between 100-300 m radius (Figure 5) might affect model strength, reducing both reliability and predictability. Finding other appropriate model selection strategies that punish collinearity, and minimizing raster size could potentially reduce the differences between distributions at smaller radii. This is worth noting for the future.

Hypothesis II

The smoothing function of x_1 (f_1) was statistically significant ($p < 0.05$) at a 1200 m radius but not for x_2 (f_2) (Figure 7). Both models between 1100-1200 m seemed similar, even in response (see Appendix C). In fact, from 600-1700 m a pattern emerged: f_1 produced a peak towards the optimum, with some interaction with f_2 as the radius decreased towards 600 m and increased towards 1700 m (see Appendix C). The influence of shape complexity seems to overshadow that of type interspersion at optimum radius. As landscape size – either increasingly or decreasingly – “moves away” from this optimum, both parameters lose effective power and stochasticity plays a larger role.

The maximal response in the diversity of carabid activity-abundance (H'_{\max}) was produced in patches with intermediate complexity in shape, and at the lowest levels of patch type interspersion (Figure 7). This partly follows the prediction of hypothesis II. The predicted response to heterogeneity in landscape structure necessarily assumes ecological relevancy to the metrics used. Accordingly, the reason for the non-significant response to f_2 may be a lack of ecological consideration. Simply, type interspersion (or at least the way it was estimated here, as the IJI) is not undoubtedly relevant to carabid ecology. The parameters chosen function as *general* descriptors of landscape spatial configuration. Therefore, the model might be more appropriate when investigating taxa *generally* than carabids *specifically*.

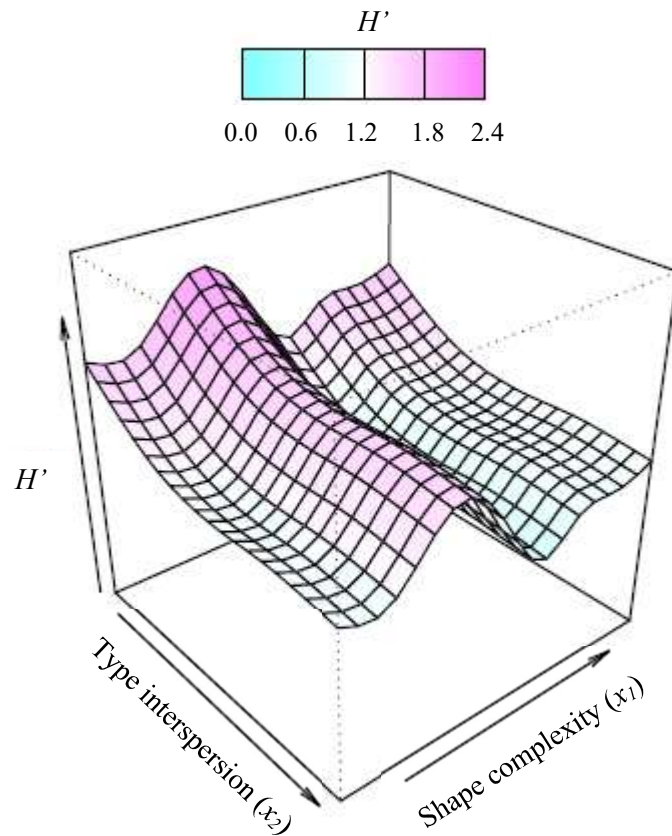


Figure 7. General additive model of Shannon's diversity index (H') of carabid activity-abundance as a function of shape complexity (MSI) and type interspersions (IJI) of patches in 1200 m radii landscapes. Significant f_1 ($p < 0.05$) but not f_2 ($p \approx 0.08$) and $R^2_{adj} \approx 0.24$.

Hypotheses III and IV

Responses to core areas varied between habitats (Figure 8). Two produced statistically significant ($p_{adj} < 0.05$) linear relationships with H' post p -value adjustment (D and MCW, modeled as GLMs). Three complex relationships were almost statistically significant post p -value adjustment, two wave-like and one convex (OFW and PW, and DW, respectively, modeled as GAMs). 7 of the 11 GLMs produced negative coefficients (FW, P, MC, SW, MCW, MW, and OF), the others positive (M, D, CC, and BS) (see Appendix E). Since the response was not uniformly linearly negative between habitat categories, hypothesis III could not be supported. The habitat-wise response seems more complex than primarily assumed. Although, the differences in observed habitat-wise core areas were relatively large (e.g. $DW_{max} \approx 15$ ha and $PW_{max} \approx 37$ ha, or $MCW_{max} \approx 6$ ha and $D_{max} \approx 36$ ha, Figure 8).

Since the TCA/ECO ratio was always larger than 1 ($TCA/ECO_{min} \approx 1.05$), hypothesis IV could not be completely answered. Measuring the relationship

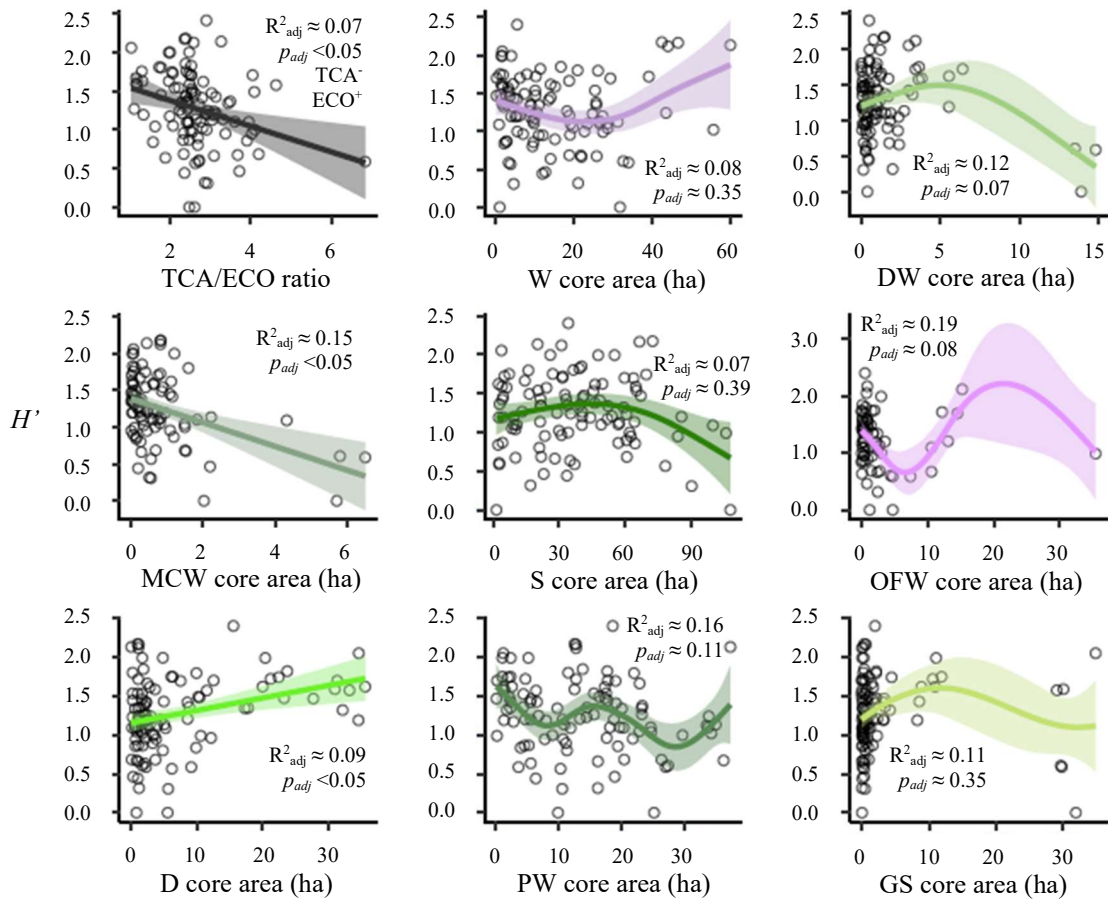


Figure 8. The relationships between H' and the ratio of total core area to ecotone (TCA/ECO), as well as the core areas of *Wetland* (W), *Deciduous wetland* (DW), *Mixed coniferous wetland* (MCW), *Spruce* (S), *Old-growth forest wetland* (OFW), *Deciduous* (D), *Pine wetland* (PW), and *Grass and shrubs* (GS) at 1200 m radii landscapes. TCA had a significant ($p_{adj} < 0.05$) negative (-) effect on H' , ECO was significantly positive (+). The lines are the modeled means (μ) and bands their 95 percent confidence intervals, the circles are observations. See Appendix D for residual distributions and E for all models. The models in the left column are GLMs, the others are GAMs. All were statistically significant ($p < 0.05$) prior to p-value adjustment.

between the two, without producing this bias, should improve inference. Although, carabid diversity seems to behave as predicted in the range above 1 (Figure 8).

Discussion

Carabids and their landscapes

Landscape size

As radii shrink, one might expect both patch shape complexity (x_1) and their interspersion (x_2) to vary more due to stochastic effects. However, this reasoning is based on the patch paradigm from a human perspective. Again, the raster size in the spatial dataset (10 m²) is partly arbitrary, and partly technology and economy limited. If carabids interact with their environments at smaller scales than 10 m² (which they probably do), aggregates of trees and shrubs at these scales should be considered patches (see some realized patch sizes and morphology in Figure 6). So, the distribution of patch parameters should stay constant, given that raster scale accommodates to landscape size. Additionally, claiming that the patch mosaic paradigm absolutely explains landscape structure is false at best (see McGarigal et al. 2009). This has, technologically, simply been the most efficient way for us – humans – to model landscapes.

Hypothesis I predicted a unimodal pattern in model fit along a landscape radius gradient. The results (Figure 4) indicate that this prediction fits observation. What stands out, however, is the uncertainty in the comparative model metrics at smaller radii. Collinearity between explanatory variables is large at these scales (Figure 4), and their distributions vary significantly (Figure 5). Redundancy in explanatory power might be the cause. Alternatively, some ecological processes may only emerge as significant factors for carabid diversity at specific scales. First, these would be impossible to determine through spatial analysis alone. Second, this conclusion is contentious, as ecological processes are typically relevant at multiple scales. Only losing influence continuously (Wiens 1989). Although, the radius intervals might be too large to capture their smooth transitions. Perhaps single species influence the model increasingly with stochasticity as a consequence of narrowing spatial scale. Whatever the case, the relatively high R^2_{adj} at 300 m and 500 m (Figure 4) potentially points to a foundational modeling problem. Landscapes ought perhaps not be considered as absolute distances or areas from a point. Birds, for instance, can benefit from the structural heterogeneity in

landscapes at multiple scales (Katayama et al. 2014). The resulting peak in R^2_{adj} and dip in AIC_c at 300 m and 500 m (Figure 4) might indicate that this is the case for these carabids. Effectively, they may be interacting with processes at different scales simultaneously, producing layers of landscapes of interactions.

The peak in model fit around 1200 m radius (Figure 4) indicates that a large part of the ecological processes relevant for carabid diversity are strongest at these radii. The landscapes were unexpectedly large; none of the studies cited in the introduction had considered these scales (Niemelä et al. 1996; Fahrig 2005; Woodcock et al. 2010; Palmu et al. 2014; Gallé et al. 2018, 2019; Gayer et al. 2019). Although, some were close at 1000 m radii (Palmu et al. 2014; Gallé et al. 2018). Palmu et al. (2014) noted larger increases in diversity from agricultural field boundary lengths in the least intensively managed crop types. They attributed two processes to this increase: larger overlap zones of the habitat properties (what I call ecotones), and stable population sources (both for carabids and their prey). Gallé et al. (2018) also highlight the importance of habitat edges for overwintering in agricultural landscapes. They present data that indicates significant overlap between functional groups, and stenotopic and eurytopic species, in field margins. Since forests and wetlands have considerably longer rotation times, it seems reasonable to suggest an amplified effect in forest landscapes. Comparably, these habitats are extremely stable, in theory producing population spill-over for longer periods and over larger areas than those in agricultural landscapes.

Effectively, adequate measurements of processes such as carabid migration patterns (Mader 1984; Wessels & Sundermann 2022), habitat quality (Smit et al. 1997; Pétilion et al. 2008), and temporal shifts in habitat selection along seasons and life stages (Thiele 1977:40–41; Niemelä et al. 1996) may require scales around 452 ha (circles with 1200 m radii). The peak does not tell us what the configuration of the patches do to carabids, but that their influence is strongest at these scales. Additionally, some habitat types require larger core areas than others to maintain their populations (see Figure 8). The quality in these habitats may perhaps only be realized at a certain landscape size. If it is too small or large, the positive influence of all habitat types may not be captured by the model. Without this foundation, the populations – and therefore their habitats – would not interact enough to produce response. In this view, it might even be false to assume that all habitat types function at the same scale.

Heterogeneity and metapopulations

Carabid diversity produced an intermediate peak in response to varying degrees of patch shape complexity, but not their type interspersion (Figure 7). Either type interspersion plays no role in landscape structural heterogeneity, or carabid communities do not respond to this parameter statistically significantly. Keep in mind though, the model variables were not chosen based on explanatory power, but

as a measure to limit variable collinearity. Other interspersion/aggregation metrics (e.g. CONTAG or the AI, see Appendix A) might have produced significant responses. These results do not refute the importance of interspersion of patches in landscapes to community ecology, they simply indicate that other parameters (or at least metrics) might be more useful when modeling *specifically* for carabids.

The AHTO hypothesis predicts the response in shape complexity as a consequence of shared habitability between stenotopic and eurytopic species. Given that the shape complexity estimates spatial heterogeneity as a function of the relationship between patch perimeter and area, the position of the peak in diversity along the axis is regulated by two dominating factors. (1) Environmental filters (Le Provost et al. 2020) exclude eurytopic species in homogeneous environments where stenotopics dominate their niches. It is assumed, then, that homogeneous environments are either spatially or temporally stable, which benefits specialists over generalists. (2) In heterogeneous environments, core areas are reduced due to fragmentation. Every patch can only host a certain number of stenotopic individuals or species (e.g. Niemelä et al. 1987). If these patches become too small and too fragmented, stochastic extinctions due to diminishing populations are predicted (Samways 2005:66–67). In this sense, the AHTO builds on the paradigm of the specialist-generalist spectrum, as even specialists eventually will be filtered out in increasingly homogeneous environments. It merges ideas from niche-theory and island biogeography to predict where and when biodiversity and functional redundancy, and therefore ecosystem resilience (Tilman & Downing 1994), maximizes (Allouche et al. 2012). Hypothesis II is accordingly partly supported by the data.

There should be some concern over the effect on dispersal; heterogeneous landscapes might not allow for sufficient internal dispersion between populations of animals to produce strong enough responses (Grant & Morris 1971; Samways 2005:67–68). Immigration exceeding extinction rates post-disturbance might be a requirement for biodiversity to maximize in heterogeneous landscapes (see Forman & Godron 1986:91). In the homo-heterogeneity paradigm, any homogenization of the landscape necessarily introduces attrition of the excluded habitat types (this is how one habitat type homogenizes the landscape). The opposite nature of these terms should produce similar responses in either direction on the configurational spectrum, and in the intermediary one finds the maximum richness of species and evenness in abundance (Figure 7).

Space and time and behavior

The question regarding an appropriate threshold for habitat differentiation is both difficult to answer and paramount to this modeling strategy. Choosing not to continue was due to lack of spatial data, potential loss in model explanatory power, lack of ecological relevance, analytical contingency, and scale.

For instance, typical littoral carabid species are generally found within most shore types, but the environment's structural and seasonal properties will still make the habitat inhospitable during instar phases (Thiele 1977:40–42). Even when habitats seem similar, conspecific habitat dependence (Thiele 1977:45), local population dynamics, habitat size and isolation, and stochastic effects might cause community composition and configuration to vary significantly (Niemelä et al. 1987). Given that it's possible, would it be valuable to continue the differentiation for the sake of a single species? Certain carabids do require old-growth forest environments (Spence et al. 1996), but assemblages do not necessarily respond statistically significantly in a larger context (Stenbacka et al. 2010). Would either an extended or reduced differentiation help answer any questions regarding landscape heterogeneity-effects on carabid diversity, or would it simply increase explanatory redundancy or reduce predictive strength? One would have to quantify the effect of omitting such details, which requires an entire thesis itself.

Similarly to littoral compositions (Thiele 1977:40–41), assemblages will differ in agricultural fields depending on the crop (Palmu et al. 2014) and within-field structural diversity (Fahrig et al. 2015; Gayer et al. 2019; Knapp et al. 2019). Carabid assemblages also change in parallel to crop rotations and soil scarification (Thiele 1977:31–33; Pihlaja et al. 2006). As with the carabid sampling, however, the landscape data only considers space. Since niche-theory makes no analogous exclusion of time, considering temporally caused heterogeneity, e.g. seasonal shifts (Thiele 1977:41; Cramer & Willig 2002) or stochastic migration (Thompson et al. 2021), would most likely be desirable. In fact, besides habitat dependency, assemblage turnover is known to depend on both time and space (Thompson et al. 2021). Comparing permanent sampling plots in time intervals might reveal uncovered processes.

The symbolic purpose, to the investigator, of the habitats is limited by time. Two individuals of the same species will prefer different habitats depending on their geographical positions (e.g. *Carabus glabratus* or *Dicheirotichus cognatus*, and many others in Lindroth [1945] and Thiele [1977]). Additionally, and as discussed earlier, landscape structure affects dispersal patterns. For instance, assemblages in power grid corridors seem similar to surrounding forests (Lindholm et al. 2019). Grüm's (1994) findings suggest this is not due to interspecific competitive dominance by the forest species. Instead, the power grid corridors might simply be too fragmented to maintain heathland carabid populations (Lindholm et al. 2019). These seem to lack dispersal strength for small and fragmented habitats (de Vries 1994).

Conspecific behavior will thus – always – introduce some stochasticity, as a function of both space and time. Mathematically weighing these patterns (as perhaps activity-abundance or landscape configuration) might improve model strength, while introducing a new assumption. Namely: “behavior affects

sensitivity to landscape configurational properties in space *and* time, which can be approximated by some ecologically motivated mathematical weight.” The layers of interactions within the landscapes assume another dimension: time. Overlap in spatially determined ecological processes (such as life history traits, habitat preference, or migration), relevant to both the individual carabid and their entire assemblage, merge and separate to the tune of the seasons.

Carabid habitats, core areas, and ecotones

The nature of the edge effect estimation requires mention. The 20 m maximum was based on empirical evidence (Heliölä et al. 2001; Magura 2002; Matveinen-Huju et al. 2009; Brigić et al. 2014; Cividanes et al. 2018; Knapp et al. 2019). The additional conditions – dissimilarity between forested and non-forested, and wetland and non-wetland habitats – considered relevant observations in assemblages (Thiele 1977:37–38; Jacobs et al. 2007; Oxbrough et al. 2012; Neumann et al. 2016). However, the dissimilarity thresholds and consequent edge effect strengths were simply guessed. Here the opponents of my matrix model will surely find much to critique. For instance, it might seem strange that *Pine* and *Pine wetland* transgress each other more than *Pine* and *Deciduous* do (Table 3). This, of course, is a consequence of the applied conditions, and therefore an example of how empirically backed estimates have affected the outcome. I expect this model to be improved significantly through discussions on assemblage scaled ecology and novel evidence. Although, since some core areas did produce statistically significant coefficients, even following considerable *p*-value adjustments (Figure 8), I do recognize the matrix model as reasonable. The low variance explained ($R^2_{\text{adj}} \approx 0.07$) in the TCA/ECO ratio model indicates that either the core areas and ecotones could be estimated better, or that there are other significant factors determining diversity at 1200 m radii. The relationship does seem to be negative, however. There is obviously room for improvement.

What determines the positive response of carabid diversity to *Deciduous* (D) core area and the negative to *Mixed coniferous wetland* (MCW) (Figure 8)? Deciduous forests are known to be important diversity drivers for carabids (Marrec et al. 2021) and other taxa (Heilmann-Clausen et al. 2005). Historical land use and forestry practices, e.g. replacing natal deciduous forests with spruce, *Picea abies*, plantations (Lindbladh et al. 2014) and suppressing natural disturbance regimes like wildfires (Edenius et al. 2011), are assumed to have largely negatively affected deciduous dependent species in Sweden (Angelstam et al. 2017). If anything, the increase in carabid diversity with D core area validate these concerns (although remember, all caught species were of *Least Concern*). The mechanism behind the positive relationship may be explained as the disparity between deciduous species habitat demands and the cover of deciduous habitats in the landscapes. Species extinctions do not necessarily follow habitat destruction in parallel, remnant

populations may survive outside optimal environmental conditions (Snäll et al. 2004), producing a time lag between habitat and population collapse. So called, *extinction debt*. An increase in the abundance of core areas of these kinds of habitats would, in theory, allow affected species to reclaim niche dominance. If deciduous core area increases in excess, non-deciduous stenotopic species would effectively become locally threatened, again reducing diversity.

Deciduous wetland (DW) and *Pine wetland* (PW) core areas almost produced statistically significant ($p_{adj} < 0.05$) non-linear relationships to carabid diversity. D might as well if the deciduous forest cover reaches higher relative levels (Figure 8). In the realized landscapes however, these results point to clear functional differences in the context of carabid diversity. MCW core area behaved as predicted, reducing diversity negatively linearly. Again, this is assumed to be caused by an “instability” between the ratio of core area to ecotone, as the negative linear relationship of TCA/ECO in Figure 8 indicates. The saturation of carabid diversity in the balance between core area and ecotone might differ between habitat types. MCW has perhaps reached it at lower levels of core area cover, whereas at might take >30 ha for D to reach a point of diminishing returns in diversity. Such as seems to have been the case for DW and *Spruce* (S). The larger the core area at H'_{max} , the more beneficial (in comparative terms) the habitat type for carabid diversity, given a convex or negative linear response.

Any explanation for the response in carabid diversity to *Pine wetland* (PW) core area eludes me (see the wave-like response in Figure 8). The model might simply be overfitting, although it hardly seems like it. Is this a consequence of some interdependency? Perhaps PW is especially sensitive to interactions between other habitats, say through a shared (or maybe absent?) stenotopic species composition. If carabid assemblages typical of PW overlap with DW, and the majority of carabids prefer the latter, the effect from PW core area on diversity will diminish in landscapes with large amounts of DW. Should PW share such overlap with other habitats, the response will not be predictable without interactive terms. These responses should, however, not produce patterns, but seem random. Additionally, if PW carabids depend heavily on another organism typical of these environments, which can only occupy the habitat at a certain level of core area, the response in diversity should change dynamically. Whatever the case, I have no clear answer.

The complex relationships between carabid diversity and *Old-growth forest wetland* (OFW) core area depends very much on a single observation at a large value. This sample point is close to a formally protected wetland nature reserve (*Andersvallsslätten*) established to primarily protect rare birds, vegetation, and wetland habitats. The traps and the nature reserve are separated by a road, which do, in fact, inhibit migration of forest and wetland type carabids (Mader 1984). These were the only types caught here (*Carabus* spp., *Pterostichus oblongopunctatus*, *Leistus ferrugineus*, and *Amara brunnea*). Omittance of this

point would produce a smooth concave response (in a smaller interval, no less). In this case, an anthropogenically defined border (the nature reserve) has influenced the relationship between explanatory and response variables, without consideration to carabid ecology (the nature reserve boundaries do not necessarily mean anything to the populations within it, only to the humans without). Carabids might accordingly not respond to this environment. However, there might simply be some threshold in diversity gain from larger OFW core areas. Since this observation is very isolated, denying the possibility that such a threshold exists seems unreasonable. In this sense, the saturation point in carabid diversity might be “delayed” until OFW reaches larger core area sizes (around 20 ha). We should also consider the purpose of formally protected land areas. They are not always established to increase alpha diversity as H' estimates it, but instead to protect single or few threatened species. The response of H' to increased OFW core area therefore highlights a modeling issue. Namely that using protected land areas as proxies for old-growth forest – even if carabids typical for old-growth habitats would respond to them – necessarily introduces human influence, and therefore modeling stochasticity.

Just as habitat core area abundances (Figure 8) do not affect carabid diversity uniformly, one cannot assume that ecotones do either. Without an appropriate incorporation into configurational models, the regulatory mechanisms behind nutrient and population fluxes across habitat boundaries necessarily increase random error (Wiens 1992). Hansen & di Castri put it, really, beautifully analogously to molecular biology,

“Studying landscapes without consideration of ecotones may be as fruitless as trying to understand cellular behavior without knowledge of cell membranes.” (Hansen & di Castri 1992a:vi)

The synthesis of core areas and ecotones in the landscape model depends on their conceptualizations. If one views ecotones – in the context of species assemblages – as separate from core areas (Johnston et al. 1992), their inclusion might merit isolation in raster or polygon category as “novel” habitats. If, instead, ecotones are to function as the realized inertia in the flow of biomass, energy, and molecule between core areas (Wiens 1992), their differentiation as specific pairwise habitat interactions could be weighed using contrast values. In this case, the term *ecoclines* might be more appropriate (Hansen & di Castri 1992b). Both approaches should probably be considered, but the one most in line with ecological theory and investigative purpose may be more appealing during modeling.

Landscape paradigms

In an attempt to isolate the effect from landscape size on carabid diversity, its shape was kept constant. No evidence suggested the circle as the optimal option, this

geometry was chosen solely on the grounds of avoiding bias against rasters at the boundaries of spatial influence. Some arguments for the use of a square might be raised, considering that it is the least complex shape of both raster cells and their patches (MSI_{\min} produces a perfect square). In landscapes with frequent dispersal barriers, such as montane regions or archipelagos, the appropriate geometry might be more complex. Due to a lack of investigation into functional carabid landscape geometry, however, options are limited (although, gradient approaches [e.g. Cushman et al. 2010:86–87] might uncover these details). Other geometries could produce different R^2_{adj} and AIC_c curves (see Figure 4).

At the root of most systematic issues in my modeling we find the patch mosaic paradigm. It is perhaps the reason why the conceptualization of ecotones becomes difficult (Forman 1995:4), as well as finding appropriate landscape metrics (McGarigal et al. 2009). In the view of patch mosaics, it is impossible to quantify the spatial configuration of boundary-less gradients – even the spatial overlapping between habitat types is ignored (e.g. canopies covering freshwater streams, or mixed forests). In fact, configurational parameters might be redundant when modeling continuous change. A distance, or edge, requires a beginning and an end. The habitat gradient paradigm (Cushman et al. 2010) is therefore, in theory, incompatible with patch-based approaches. Should their synthesis be impossible, discrepancies in their comparisons might still produce theoretically important results.

Conclusively, any investigator will have to decide which landscape paradigm fits their interest best, based on habitat configurations. Due to the human dependency on systematic structure (for instance when determining the owner for any space of land, e.g. of Swedish forests), anthropogenically exploited landscapes typically fit the patch mosaic well (Forman & Godron 1981). In contrast, rarely disturbed pristine forests with significant habitat overlapping and no obvious boundaries (Forman & Godron 1986:211–216; Forman 1995:4) might require continuous gradients. Metrics have been developed for both (McGarigal & Marks 1995; McGarigal et al. 2009).

Ethical considerations and application

The approach to practical implementation of these results depends on the purpose of the implementation's function. Landscape manipulation or management necessarily assumes either anthropogenic responsibility or rights of exploitation of the affected ecosystems and their populations (I echo Samways 2005:4–6). Any exploitative attempt needs to evaluate how these responsibilities or rights are expressed ethically. Whether the aim is sustainable utilitarianism or essentialist conservation, or some synthesis of both (see Samways 2005:3–15), this approach to landscape modeling presents a method of quantifying realized effects on scales

foresters rarely consider. This is useful, since landscape spatial structure, in some cases, may be more valuable for conservation of biodiversity than within-habitat management (Noss 1983; Marrec et al. 2021). The significance of landscape composition and configuration to local ecology have been recognized by policymakers (FSC 2020; PEFC 2022), but its practical implementation – specifically for industrial Swedish forestry – remains without convention. At what scales *ought* one consider forest ecology and what *ought* to be done to conserve its, either utilitarian or essential, values? If my findings are determined valuable, regarding forest and wetland type carabids in central Sweden: at about 452 ha and manipulation of habitats in the context of their effective responses.

Habitats affect diversity unequally (Figure 8 and Appendix E), this might depend both on assemblage composition and landscape size. However, populations of threatened species may not produce response in the short term, or at all, due to an already established local extinction debt and conspecific environmental demand (Samways 2005:99–102). Again, all species caught in the data analyzed in this thesis were common, of *Least Concern*. In this sense, time also influences the practical usefulness of this model. Therefore, no standardized management plan seems practically reasonable, given that the conservation of threatened species is a foundational value to human land-use. Landscape management, for the purposes of biological conservation, needs to consider each case of application in the context it is to be applied. Restoring and managing require entirely different approaches (Ludwig 2005).

Additionally, since these models provide a general measure of quality in landscape configuration, its manipulation may be optimized for any ecological property in managed environments by fitting different response variables. For instance, the landscape may be manipulated to the detriment of migration and carrying capacities of populations of common insect pests. These are sensitive to migratory patterns and substrate distribution (Berryman 1986:60, 146–147). Pre-emptively managing outbreaks (Wiens 1992). The model's potential use thus expands beyond conservation and might, in the future, provide ecosystem managers with a generally useful tool for optimizing landscape-wide resilience in addition to within-habitat options.

The reader should remember that this thesis only aimed for a *natural* understanding of measurements of landscapes, being systematically unconcerned with their social and spiritually meaningful aspects. Landscapes are obviously important beyond the natural sciences (Samways 2005; Wiens 2005). Implementation of these models should therefore only succeed through discussions on the ethics behind ecological exploitation and management, specifically on large scales.

Modeling concerns for the future

Study design

The carabid sampling design was originally developed for investigating the response in epigeic assemblages in clear cuts, retention patches, and woodland key habitats. Its purpose was to collect data for empirical analysis of retention patch functionality as long-term habitat remnants in Swedish forestry. This means that the sampling incorporates bias towards these three categories. For my purposes, sampling all the eventually defined habitats – or a random selection of them – would have been more appropriate.

Furthermore, carabids were sampled between 2021-06-28 and 2021-07-09. Thus, there is an expected time lag of 2-5 years between spatial data gathering and carabid sampling. This issue will amplify in areas where new clear cuts (post 2017) have not been included in the spatial data. The gathering of carabids, or any other taxa, should in the future preferably occur as close to planned spatial land-use estimations (e.g. the NMD) as possible. Alternatively, be accompanied by one.

Residuals

Since the data collection was not designed for my purposes, overlap in landscapes between sample plots could not be avoided without significant loss in observations. This is without a doubt the biggest concern for my entire investigation, since it introduces definite violations of the independence assumptions of all models. These results do not necessarily reject my findings categorically however. No autocorrelation could be observed (see Appendix D), which should be expected, as sample index was based on plot location (Chatterjee & Hadi 2006:87). Alas, this does not reduce the influence on inference. One must consider the effect on model fit; the variance explained should not be inflated. In the future, this issue is easily solvable, simply by sampling taxa in points separated by the maximum landscape diameter. Conclusively, the modeling indicates that some response in landscape configuration is worth investigating.

To my successors

(a) This modeling approach seems sensitive to raster size (Figure 4 and Figure 5), future inquiries should attempt to reduce them. This, however, requires large scale and detailed spatial inventory. (b) Since the spatial structures of legally protected land areas depend on human categorization (e.g. land owner borders), some bias in patch parameter calculation is to be expected. In my case, OF and OFW might require to be merged or entirely removed. This might also be true for other similar habitat types. (c) Incorporating ecotones as the interactions between habitat types should improve the model, but their methodical introduction remains uncertain.

Experimental designs would surely help in this regard (e.g. Wiersma 2022). (d) Since the IJI could not produce a significant response in H' , either another metric or a principal component analysis might be required to measure heterogeneity in spatial distribution (e.g. interspersion or contagion). Additionally, using a metric, for either parameter, developed for patch size sensitivity (e.g. AWMSI or AWFrac, or CONTAG or AI) might improve the model. Both metrics used only produce the arithmetic mean of all patches, it might be appropriate to weigh interspersion by patch types as the aggregation of that type within the landscape. One patch type might be heavily aggregated, the other heavily interspersed, the mean would then produce an intermediate that is not representative. Instead, I suggest the IJI should be penalized habitat-wise by increased aggregation or contagion. (e) Finally, this modeling approach should, in theory, work with any taxa that can be sufficiently sampled in positions. The necessary steps are as follows:

1. *Sample the taxa of interest in positions, e.g. in single or groups of traps in small areas (relative to landscape size).*
2. *Compile habitats relevant to the taxa of interest and produce maps with spatially inventoried categorical data.*
3. *Calculate response variables from the sampling data, and explanatory variables from relevant metrics for the two parameters (and perhaps core areas and ecotones as well) from the spatial data.*

Conclusions

There are two conventionally accepted approaches to landscape modeling: the patch mosaic and gradient paradigms. Landscapes significantly affected by human exploitation merit the use of the former, whereas very stable environments with frequent overlap between habitat types fit the latter. Due to the relative ease of modeling, the patch perspective was adopted in my case. Accordingly, parameter estimation through patch-based metrics aimed at quantifying shape complexity and type interspersions within the landscapes observed. On a two-dimensional plane, these two parameters produce a significant proportion of what ecologists consider configurationally relevant for landscape processes. However, heterogeneity in patch size should also be considered. Thus, introducing metrics specifically sensitive to patch size, e.g. area-weighted shape metrics, could improve my approach. This, then, requires some considerations: (1) the metrics are sensitive to raster size, they might therefore not be very useful in small landscapes, and (2) since landscape metrics are known to co-vary, limiting one's choice during variable selection might aggravate collinearity. Both demand attention.

Carabid diversity peaked at intermediate levels of shape complexity but did not react statistically significantly to interspersions. More thorough investigations on the usefulness of the metric are required, as well as exploring other options of estimating interspersions or aggregations.

Not all habitats affect diversity positively, some seem beneficial as core areas increase, some detrimental, others complex. These are regulated by their ecological differences in the context of carabid biology. In the view of the area-heterogeneity trade-off hypothesis, there should be some diversity saturation point in the balance between core area and ecotone. Some habitat types might require larger core area cover to reach saturation due to their ecological functionality. Comparing core area cover at this point can uncover functional habitat benefits for ecosystem management. However, the exact effects from each habitat type can only be determined when their interactions are understood, and differentiation optimized.

Considering the landscape as a circle from any point on the terrestrial plane, the diversity of forest and wetland type carabids in central Sweden seems to be statistically significantly affected by the spatial configuration of their habitats maximally at a radius of about 1200 m. This translates to landscape sizes of 452 ha. Some ecological processes may only be relevant at specific scales. Accordingly,

452 ha landscapes do not explain all configurational influences on carabid communities. They were the largest at these scales, however. These environments are heterogenized by natural disturbance and human activity, mainly logging and sometimes agriculture. Not only are novel habitats established in clear cuts and artificially regenerated stands, but their form and magnitude affect both the shapes and interspersion of forest and wetland habitats. This, in turn, influences which populations may be maintained or flourish throughout the landscapes. Ecological theory posits these dynamics to be regulated by conspecific habitat preferences, specifically by the discrepancies between what are considered generalist and specialist species. The former preferring unstable habitats rich in colonizable niches (ecotones), the latter, in contrast, stable habitats with predictable properties, where their niche-dominance continues (core areas). If one wishes to maintain these populations, ecosystem management needs to accommodate to the scales at which they are regulated.

The literature on the significance of landscape processes for conservation efforts is clear: they cannot be ignored. Property-level and stand-wise management is not enough to conserve the populations of forest landscapes. Both the patch shape and interconnectedness of high value stands, such as formally protected forests, and the habitats that make up their reference matrix, need management in the context of conservation. Additionally, forestry operations need to manage heterogeneity thresholds at large scales – not only within properties as current Swedish environmental laws and practices demand. Investigations into where these thresholds lie are required. Combining landscape modeling with samples of taxa, whose sustainable populations are determined important conservation goals, can point at what scales we might want to define “landscapes” and accordingly consider our environmental integration or impacts.

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Appendices

A

Patch shape metrics

McGarigal & Marks (1995) apply Patton's (1975) shape index to raster format while reducing its area bias. Averaging the shape index by patch amount gives us the mean shape index (MSI) for all patches within the landscape. Formally,

$$\text{MSI} = \frac{\sum_{\forall j} \left[\frac{0.25 p_j}{\sqrt{a_j}} \right]}{N}$$

where p is the perimeter and a the area of patch j of all N patches in the landscape, where $\text{MSI} \geq 1$ without upper limit. The 0.25 coefficient and square root adjusts the metric for rasters. Larger MSI therefore indicates longer perimeter, which necessarily makes the patch shape more complex. MSI can be weighted with patch area by replacing the denominator with a term within the summation as

$$\text{AWMSI} = \sum_{\forall j} \left[\frac{0.25 p_j}{\sqrt{a_j}} \cdot \frac{a_j}{A} \right]$$

where a_j is the area for patch j , and A the total landscape area. As the second term equals $1 \forall j$, it functions in the same way as N . Due to the sensitivity to changes in area, a growing square will decrease the ratio p/a , even though the shape stays constant. This is the bias.

The fractal dimension index (FRAC) measures patch shape complexity just like the MSI. Although, FRAC overcomes the area bias by log-transformation,

$$\text{FRAC} = \frac{\sum_{\forall j} \frac{2 \ln(0.25 p_j)}{\ln a_{ij}}}{N}$$

where $1 \leq \text{FRAC} \leq 2$. Approaching 2 maximizes patch shape complexity. FRAC can be area-weighted just as easily as MSI,

$$\text{AWFRAC} = \sum_{\forall j} \left[\left(\frac{2 \ln(0.25 p_j)}{\ln a_j} \right) \cdot \left(\frac{a_j}{A} \right) \right].$$

Patch type interspersion metrics

McGarigal & Marks (1995) developed the interspersion and juxtaposition index (IJI) for quantifying landscape patch interspersion, that is, a measure for adjacencies of categories (e.g. habitats). IJI compares the proportional perimeters of all other types to one habitat and calculates the overall mean, as

$$\text{IJI} = \frac{-\sum_{\forall i} \sum_{\forall k} \left[\frac{e_{ik}}{E} \cdot \ln \left(\frac{e_{ik}}{E} \right) \right]}{\ln(0.5[m(m-1)])} \cdot 100$$

where e is the total edge length between habitat types i and k , E the total edge length, and m the amount of different habitat types in the landscape. IJI therefore measures patch adjacencies, and is relatively insensitive to patch size (McGarigal & Marks 1995:53), perhaps unfavorably. This is a version of H' , where the denominator produces an upper limit of 1, and the coefficient 100 converts the units to percent, $0 < \text{IJI} \leq 100$.

Fragstats also allows for calculation of Li & Reynolds' (1993) contagion index (CONTAG), which measures the *contagion* of like-adjacency raster cells. CONTAG is therefore a measure of clustering of individual cells within types, rather than patches between them. Formally,

$$\text{CONTAG} = \left[1 + \frac{\sum_{\forall i} \sum_{\forall k} \left[\frac{P_i g_{ik}}{\sum_{\forall k} g_{ik}} \cdot \ln \left(\frac{P_i g_{ik}}{\sum_{\forall k} g_{ik}} \right) \right]}{2 \ln(m)} \right] \cdot 100$$

where P is the proportion of the landscape occupied by patch type i , g the amount of adjacent patch type rasters of type i and k (using the double-count method – both patches may be counted twice), and m the total amount of patch types in the landscape. P weighs the contagion of all patch types against their abundance, and the 100 coefficient converts the unit to percent, so that $0 < \text{CONTAG} \leq 100$. IJI and CONTAG are therefore opposite measurements, although CONTAG incorporates patch area.

He et al.'s (2000) aggregation index (AI) also counts adjacent cell types (using the single-count method however – both patches may only be counted once),

$$\text{AI} = \left[\sum_{\forall i} P_i \left(\frac{g_{ii}}{\max \rightarrow g_{ii}} \right) \right] \cdot 100$$

where g_{ii} is the number of adjacent rasters of type i and $\max \rightarrow g_{ii}$ its maximum value, given any landscape composition. This means: the theoretically maximum amount of aggregation ($\max \rightarrow g_{ii}$) scales the observed aggregation (g_{ii}) weighed by type (i) abundance (P) and is converted to percent with the 100 coefficient, so that $0 \leq \text{AI} \leq 100$. Therefore, AI and CONTAG both measure the clustering of types, with respect to patch size (as maximum raster adjacency).

All landscape metric calculations were done in *Fragstats* version 4.2.598 with the 8 cell neighborhood rule: adjacencies *and* diagonals are counted as neighbors (McGarigal & Ene 2014).

Deviance

Every GAM the *mgcv* package produces is accompanied by a deviance (D) value. Using D instead of R^2_{adj} for model comparison is often preferred for non-linear regressions (Wood et al. 2016). It is calculated as

$$D_i = 2 \left[\mathcal{L}(\theta_{\max})_i - \mathcal{L}(\theta)_i \right] \varphi$$

where \mathcal{L} are likelihood functions of saturated, θ_{\max} , and fitted, θ , model parameters, and φ a scaling factor for observation i . φ depends on the distribution family of the modeled residuals, thus its formula varies. See Wood (2006) for in-depth discussions on deviance, and GLMs and GAMs generally.

B

Table 4. Pitfall trap results. All the species, their caught amount, and where they were caught. National conservation status of all species is *Least Concern* (as of 2020). OCC = older clear cut, RP = retention patch, WKH = woodland key habitat. In total 45 species, 34 in Gävleborg, 35 in Värmland, and 24 in both, with a 0.53 similarity coefficient, calculated with Jaccard's (1912) index (\cap/U). The habitats in the far-right column are SLU Artdatabanken's (n.d.) data made to fit my habitat differentiation (C = coniferous, see Table 2 for the other abbreviations), these should not be misconstrued to be SLU Artdatabanken's environmental categorization. Cells have been crossed out when the source did not distinctly mention conspecific environmental demand.

Species	Gävleborg				Värmland				Sum total	Lindroth 1945	Environmental adaptation	
	OCC	RP	WKH	Total	OCC	RP	WKH	Total			Thiele 1977	SLU Artdatabanken n.d.
<i>Agonum ericeti</i>					1	5		6	6	Tyrphophilic	Oligotrophic bogs	W
<i>A. fuliginosum</i>	61	32	252	345	148	123	152	423	768	Eurytopic	Eurytopic	FW, W
<i>Amara aenea</i>	2	1		3					3	Xerophile	Grassland dry, A	GS, U
<i>A. brunnea</i>	2			2					2	Forest D	Grassland dry, A	C, GS, D
<i>A. lunicollis</i>		1		1					1	Eurytopic	Eurytopic	GS, C, D, U
<i>A. quenseli</i>		1		1					1	Open dry	Psammophile	GS, U
<i>Calathus fuscipes</i>						1		1	1	Eurytopic	Grassland dry	GS, U, A
<i>C. micropterus</i>	85	61	122	268	58	111	77	246	514	Forest D and C	Forest	C, D, GS
<i>Carabus coriaceus</i>	31	18	154	203	46	54	59	159	362	Forest D and C	Eurytopic	C, D
<i>C. glabratus</i>	20	10	43	73	6	6	11	23	96	Forest S and C ¹	Forest	C, D, GS
<i>C. hortensis</i>	68	138	315	521	89	133	224	446	967	Forest D and M	Forest	C, D
<i>C. nemoralis</i>	5	3	12	20	4	9	13	26	46	Eurytopic	Eurytopic	D, GS, A
<i>C. problematicus</i>					5	13	50	68	68	Xerophile	Forest	GS, C, D
<i>C. violaceus</i>	200	324	343	867	708	696	542	1946	2813	Eurytopic	Eurytopic	C, D, GS
<i>Cychnus caraboides</i>	42	110	83	235	57	78	83	218	453	Forest D and M	Forest	C, D, GS
<i>Cymindis vaporariorum</i>						1		1	1	Xerophile	Forest	GS

Table 4. (continued)

Species	Gävleborg				Värmland				Sum total	Environmental adaptation		
	OCC	RP	WKH	Total	OCC	RP	WKH	Total		Lindroth 1945	Thiele 1977	SLU Artdatabanken n.d.
<i>Trechus quadristriatus</i>		1		1		1		1	2	Xerophile	Open dry, A	GS, A
<i>T. rivularis</i>	1			1			4	4	5	Wet forest D and S	Open dry, A	W
<i>T. rubens</i>						1		1	1	Eurytopic humid	Open dry, A	W, CW, DW, GS
<i>T. secalis</i>	7	3		10	4	5	3	12	22	Forest D and S	Meadows humid	C, D, A, GS

* Refers to Lindroth (1945). ¹ Also common in the Swedish mountains, where it is not limited to forests, but mostly occurring in open land. ² As *Trichocellus cognatus*. ³ As *Trichocellus placidus*. ⁴ As *Harpalus quadripunctatus*. ⁵ As *Harpalus pubescens*. ⁶ As *Leistus rufescens*. ⁷ As *Notiophilus pusillus*. ⁸ As *Agonum obscurum*. ⁹ As *Agonum ruficorne*. ¹⁰ As *Pterostichus cupreus*. ¹¹ As *Pterostichus vulgaris*. ¹² As *Agonum quadripunctatum*. ¹³ Thiele notes that they are also found in ravine shrubs in the southern Russian steppes.

The reader should note that these are my interpretations of the literature cited – especially the information produced by Thiele (1977) required contemplation, since he did not aim to produce a list of conspecific ecological traits like Lindroth (1945). No species is absolutely limited to one *type* of environment (Lindroth 1949:495–499; Thiele 1977:45–48), this list is a gross estimation based on empirical – not *true* – categories.

Table 5. Similarity coefficients for habitat preference in all species caught, calculated as Jaccard's (1912) index (\cap/U) – effectively the inverse of Whittaker's (1972) beta-diversity between two habitat categories. Bold percentages in the diagonal are the proportion of caught carabids which the environment in question hosts. Since any species may live in multiple habitat types, the sum of the diagonal is larger than 1. Conspecific habitat preference from national data (SLU Artdatabanken n.d.) was fit to my categories as adequately as possible. Note that there are no *Pine*, *Spruce*, nor *Mixed coniferous* categories. Since SLU Artdatabanken (n.d.) does not isolate them, these three have been compiled into one category, *Coniferous*. Further, SLU Artdatabanken (n.d.) considers clear cuts human induced environments, and so it is not obvious when habitat type should be *Urban* or *Clear cut*. They also consider multiple grassland types: dry, mesic, and moist, whereas I grouped heaths, grasslands, and fields together in *Grass and shrubs*. The habitat types that are not considered in the national database are left grey.

Overlap between habitat types	U	W	A	FW	O	C	D	CW	DW	OF	OFW	CC	BS	GS
<i>Urban</i> (U)	14.89%													
<i>Wetland</i> (W)	0.00	34.04%												
<i>Agriculture</i> (A)	0.27	0.04	21.28%											
<i>Freshwater</i> (FW)	0.00	0.33	0.00	14.89%										
<i>Ocean</i> (O)														
<i>Coniferous</i> (C)	0.04	0.03	0.08	0.00		31.91%								
<i>Deciduous</i> (D)	0.03	0.18	0.21	0.00		0.56	48.94%							
<i>Coniferous wetland</i> (CW)	0.00	0.12	0.00	0.00		0.06	0.04	2.13%						
<i>Deciduous wetland</i> (DW)	0.00	0.41	0.06	0.00		0.05	0.25	0.29	14.89%					
<i>Old-growth forest</i> (OF)														
<i>Old-growth forest wetland</i> (OFW)														
<i>Clear cut</i> (CC)														
<i>Bare soil</i> (BS)	0.00	0.11	0.00	0.25		0.00	0.00	0.00	0.00				6.38%	
<i>Grass and shrubs</i> (GS)	0.26	0.20	0.35	0.00		0.24	0.50	0.03	0.19				0.03	51.06%

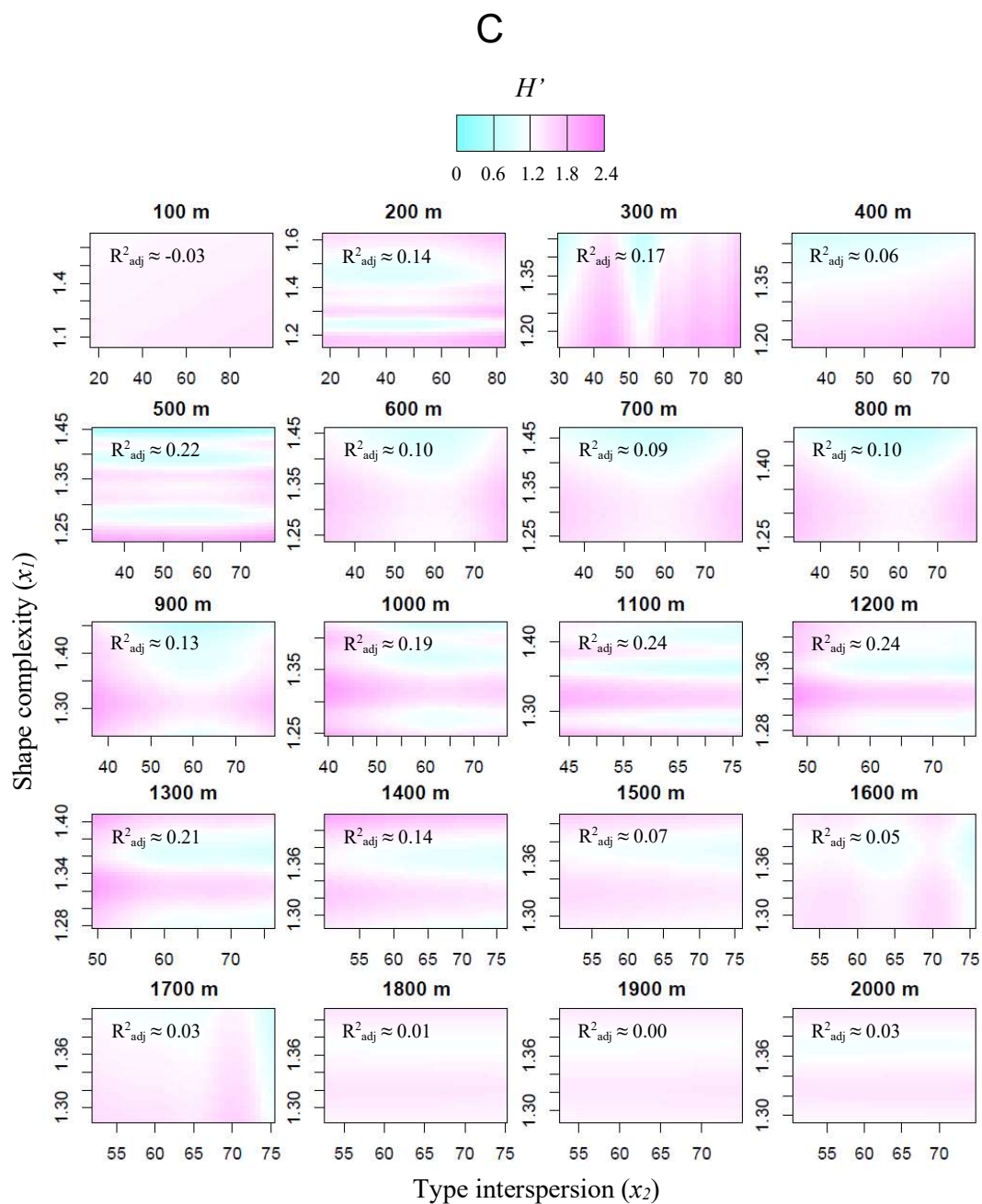


Figure 9. Shannon's diversity index (H') of carabid activity-abundance as a function of shape complexity (MSI) and type interspersion (IJ) of all landscape radii. See Appendix A for variable formulas and D for residual distributions. 99 observations at 100 m, 103 at all others.

D

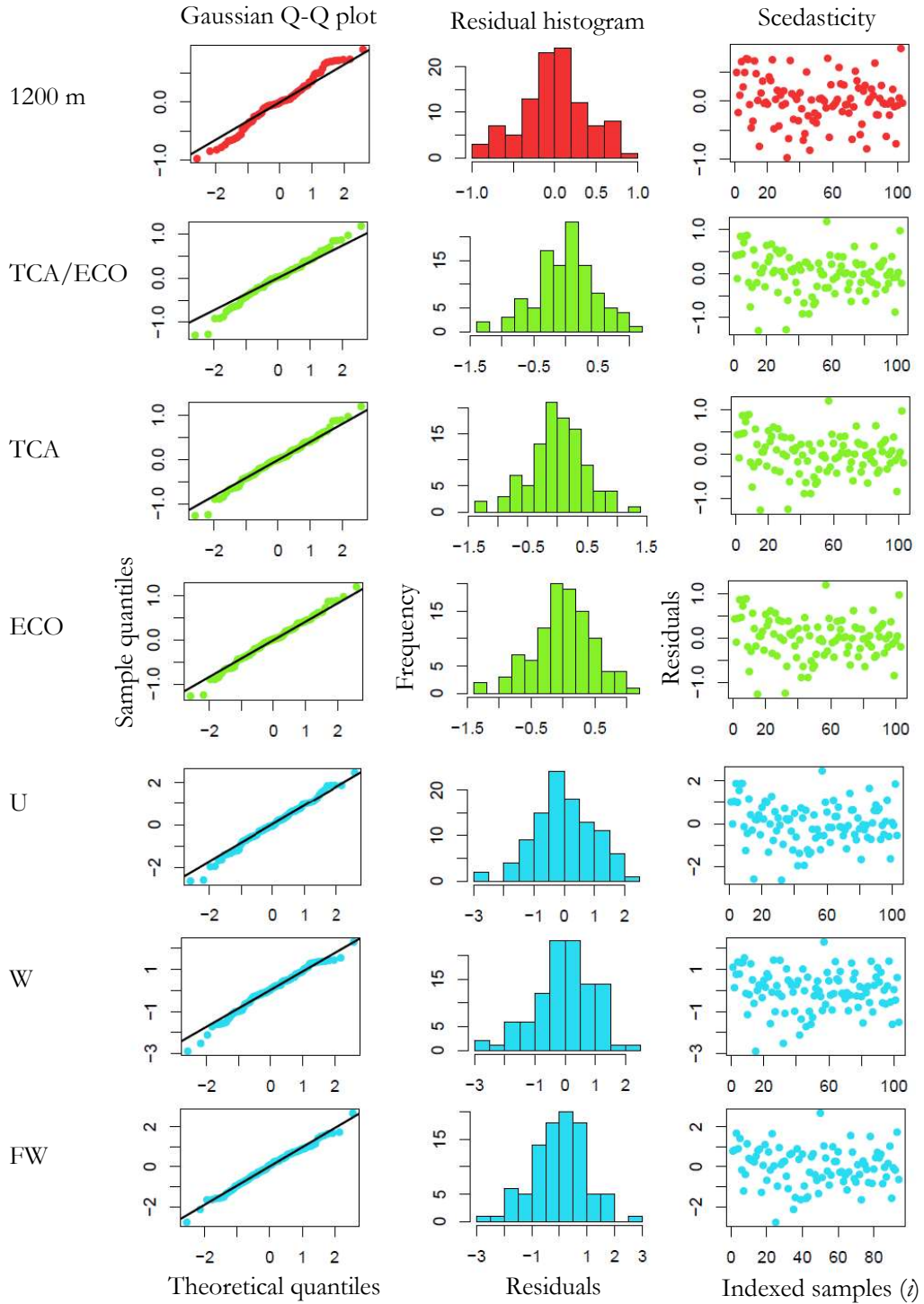


Figure 10. Residual distributions of all the models: the landscape at 1200 m (in red), TCA, ECO, and the TCA/ECO ratio (in green), and all the habitat-wise core areas (in blue).

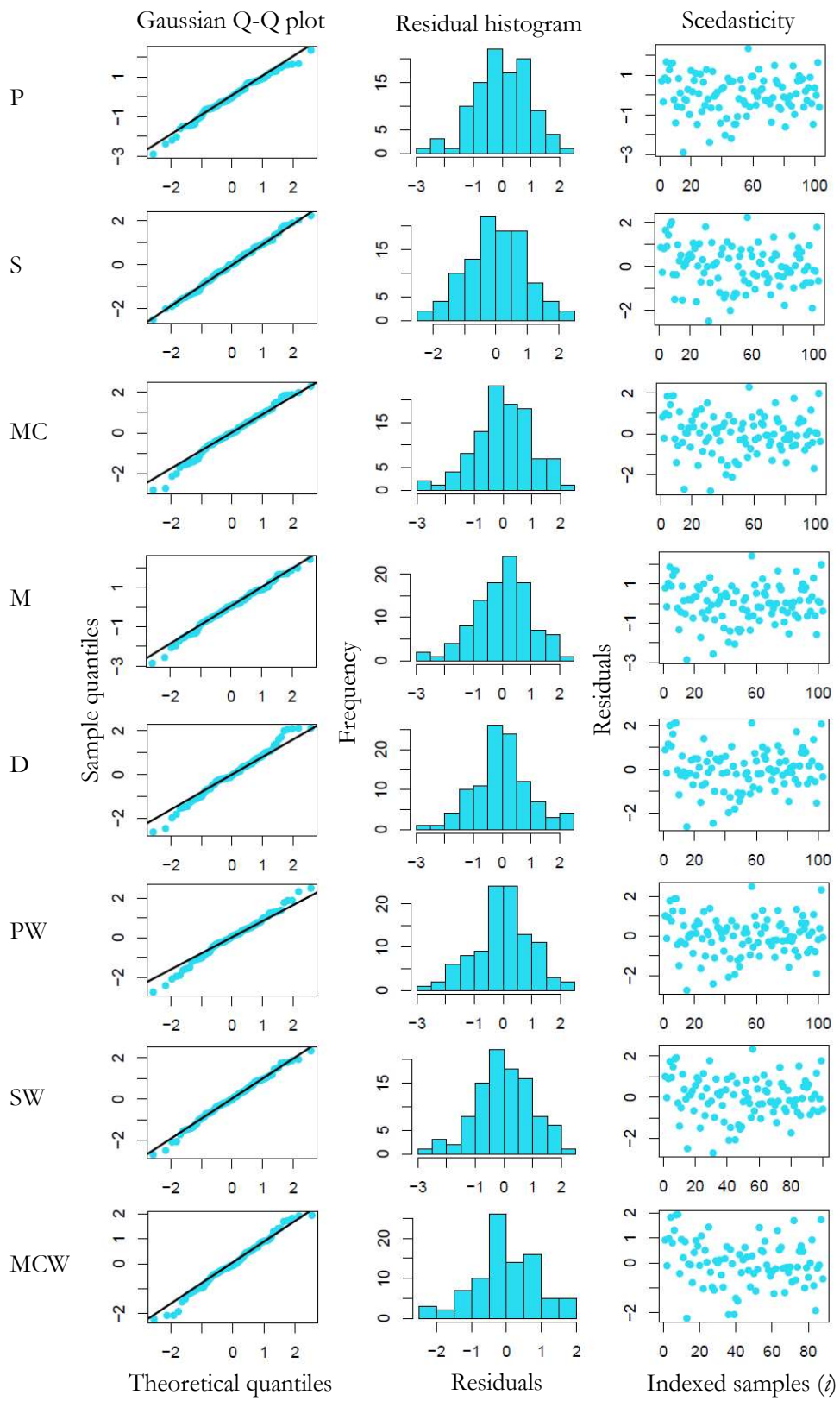


Figure 10. (continued)

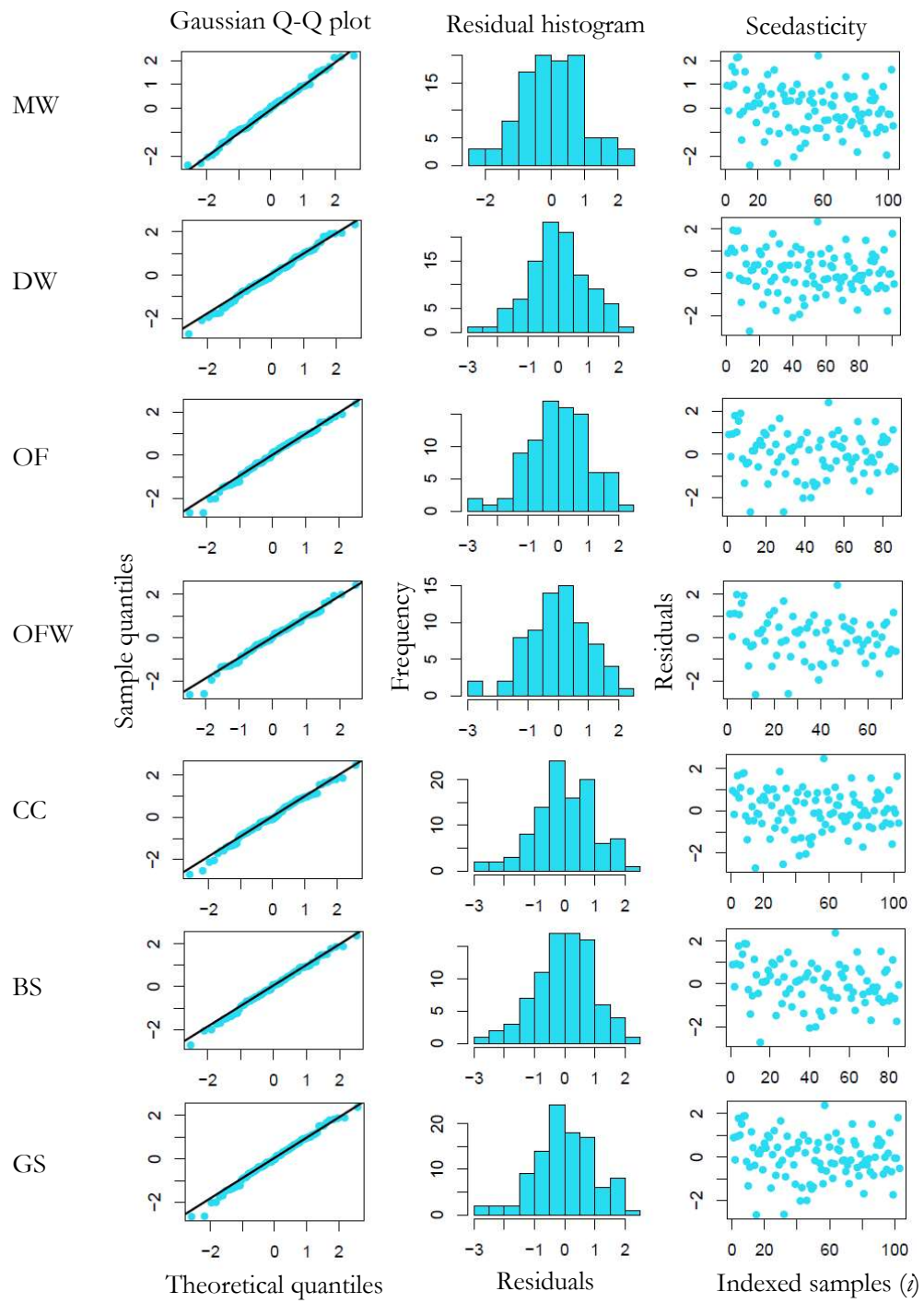


Figure 10. (continued)

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