RESEARCH ARTICLE

Refining intra-patch connectivity measures in landscape fragmentation and connectivity indices

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Abstract

Context Measuring intra-patch connectivity, i.e. the connectivity within a habitat patch, is important to evaluate landscape fragmentation and connectivity. However, intra-patch connectivity is mainly measured with patch size, which can conceal diverse intra-patch connectivity patterns for similar patch size distributions.

Objectives We suggest a method to refine the intra-patch connectivity component of fragmentation and connectivity indices. This method allows for distinguishing different intra-patch connectivity patterns for similar patch size distributions.

Methods We used normalized patch complexity indices to weight patch size in common fragmentation and connectivity indices. Patch complexity indices included two existing geometrical indices (SHAPE and FRAC), and a new index derived from spatial network analysis, the mean detour index (MDI). We analyzed the behaviours of adjusted fragmentation and connectivity indices theoretically and empirically on both artificial and real landscapes.

Results While maintaining the mathematical properties of fragmentation and connectivity indices, our method could distinguish landscapes with identical patch size distributions but different spatial configurations. The mean detour index had a different response than geometrical indices. This result indicates that, at the patch level, topological complexity can exhibit different patterns from geometrical complexity.

Conclusions Measuring intra-patch connectivity with patch size in fragmentation and connectivity indices cannot distinguish landscapes having similar patch sizes distribution but different spatial configurations. This paper introduces a method to distinguish such patterns relying on geometrical and topological indices and shows to which extent it can impact conservation planning.

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Introduction

Habitat loss and degradation due to anthropogenic land-use change are the primary causes of ecosystem collapse and biodiversity decline (Haddad et al. 2015; Díaz et al. 2020). Habitat loss often leads to

fragmentation, which is the process during which large patches of habitat are separated into a higher number of smaller patches (Wilcove and McLellan 1986), and to a loss of connectivity, which defines as the ability of species to migrate or disperse between (*inter-patch connectivity*) or within (*intra-patch connectivity*) habitat patches (Taylor et al. 1993). At the landscape scale, fragmentation and connectivity are evaluated through spatial patterns metrics that are useful to assess land-use change impacts and to inform conservation planning.

Many indices have been developed to describe fragmentation, such as the number of patches, the habitat edge length, or the habitat amount (Forman and Godron 1986; O'Neill et al. 1988; Li and Reynolds 1993; McGarigal et al. 2012; Jaeger 2000). Indeed, fragmentation encompasses various patterns that cannot be measured with a single and universal index. Moreover, as the impacts of fragmentation per se (i.e. independent of habitat loss) on biodiversity are more intricate than those only related to habitat loss (Fahrig 2003, 2017; Vieira et al. 2018), fragmentation indices must be used carefully and related as much as possible to biological processes and focal species ecological requirements (Hargis et al. 1998; Rutledge 2003; Li and Wu 2004).

Regarding the analysis of connectivity patterns, graph-theoretic connectivity indices have been applied to a wide range of applications (Urban and Keitt 2001; Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007; Saura and Rubio 2010). In such indices, the landscape is represented as a network (or graph) of habitat patches that are connected according to structural or functional parameters reflecting focal species' movement and dispersal capabilities, such as inter-patch distances or least cost path analysis (Galpern et al. 2011). The integral index of connectivity (IIC, Pascual-Hortal and Saura 2006) and the probability of connectivity (PC, Saura and Pascual-Hortal 2007) are two commonly used graph theoretic connectivity indices. They both combine topological network analysis with patch size distribution as the intra-patch connectivity component. Recently, a new graph-based connectivity measure was also introduced, ProNet, which is easier to compute than IIC and PC (Theobald et al. 2022).

The intra-patch connectivity is an important element in all of these measures. Indeed, only measuring inter-patch connectivity leads to interpreting the connectivity as null when the landscape consists of a single habitat patch. Similarly, dismissing intra-patch connectivity can indicate an increase in connectivity along with increased fragmentation (Tischendorf and Fahrig 2000a, b; Laita et al. 2011; Spanowicz and Jaeger 2019). Consequently, fragmentation and connectivity indices that are currently the most robust are those that incorporate an intra-patch connectivity component, such as MESH, IIC, or PC. Yet, the question of how to measure intra-patch connectivity has been much less explored than inter-patch connectivity. In the vast majority of cases, patch area is the proxy measure of intra-patch connectivity and, therefore, represents the amount of habitat available within the patch (e.g. Fahrig 2013; Shanthala Devi et al. 2013; Reza et al. 2018; Xu et al. 2019; Shao et al. 2021).

However, the area alone cannot reflect all patterns of intra-patch connectivity. Indeed, it cannot discriminate similar patch size distributions with different spatial configurations. For example, two landscapes with a single patch of the same size, compact in the first case and elongated in the second, can be expected to have different effects on species movements within the patch (see Fig. 1), especially on species that have limited movement capabilities outside the habitat patch. In landscapes with several patches, with the same patch size distribution and the same isolation level (i.e. the minimum distance between patches), the spatial configuration of patches should also impact how species can move from one patch to another. We illustrated this case in Fig. 2, where the middle patch, although having the same area in both examples, does not involve the same intra-patch dispersal distance between the two other patches. On the other hand, shape indices such as the shape index (SHAPE, Patton 1975; McGarigal et al. 2012) or the fractal dimension (FRAC, Mandelbrot 1983; Kenkel and Walker 1993; McGarigal et al. 2012) can discriminate different spatial configurations using patches' geometrical properties, but they will not distinguish large patches from small ones. Area-weighted geometrical indices (McGarigal et al. 2012) take into account the area of patches to give an overall picture of patches' complexity over a landscape, but two landscapes with the same habitat abundance, the same patch isolation, similarly shaped patches, and different patch sizes distributions will not be distinguished (see Fig. 3).

Fig. 1 Two landscapes containing a single patch of equal size and different shapes

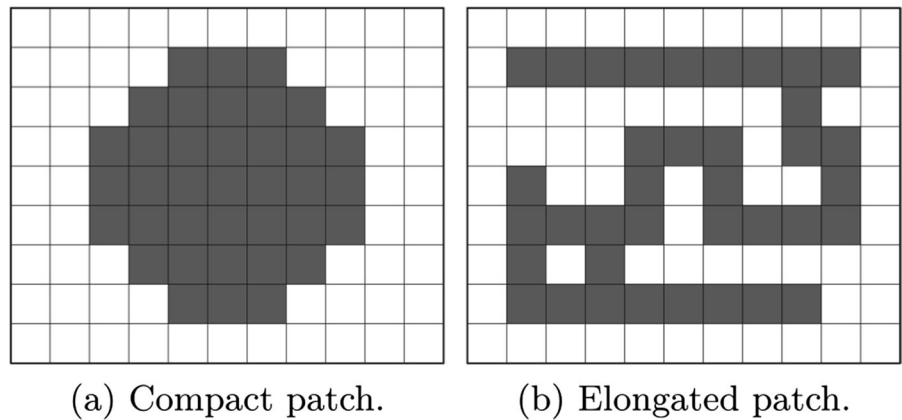(a) Compact patch.   (b) Elongated patch.

Fig. 2 Two landscapes with the same total habitat amount, same patch size distribution, and same patch isolation. The middle patch is a stepping stone whose spatial configuration can affect species migration and dispersal fluxes between other patches
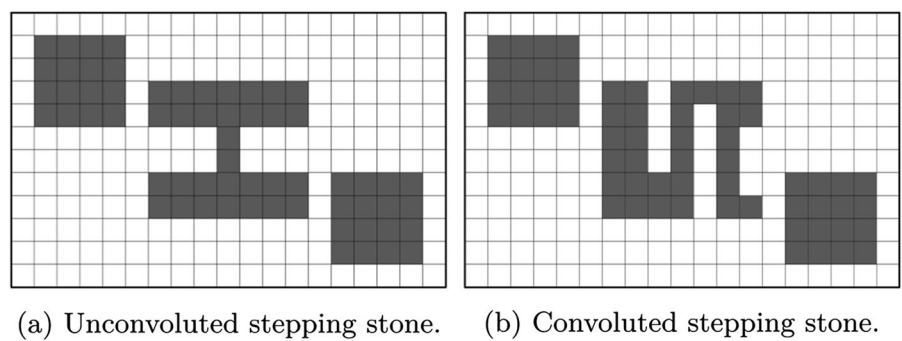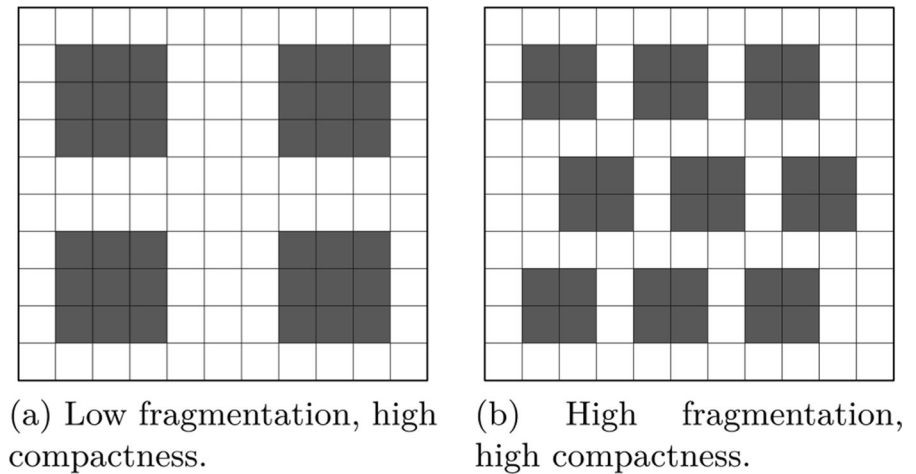

(a) Unconvoluted stepping stone.   (b) Convoluted stepping stone.

Fig. 3 Two landscapes with the same total habitat abundance, high patch compactness but different patch sizes distribution

(a) Low fragmentation, high compactness.   (b) High fragmentation, high compactness.

In this article, we introduce a method to refine intra-patch connectivity measures into fragmentation and connectivity indices (e.g MESH, IIC, PC). By combining patch area and normalized patch complexity indices, this method improves fragmentation and connectivity analyses by introducing a new family of "topo-ecological" patch attributes (Ricotta et al.

2000). We illustrate this method using two existing geometrical indices, SHAPE and FRAC, and introduce a new index derived from spatial network analysis, the mean detour index (MDI, Barthelemy 2010). After showing that our method preserves the mathematical properties of fragmentation and connectivity indices, we evaluate its response on both artificial

and real landscapes, show how it allows distinguishing identical patch size distributions with different spatial configurations, and investigate its implications on patch prioritization. In the following, we rely on a raster representation of the landscape, as it is currently the most common data type for landscape indices calculation (McGarigal et al. 2012; Hesselbarth et al. 2019). However, all the methods described in this article can be applied to other spatially-explicit landscape representations such as vector data or hexagonal grids.

Methods

Complexity-weighted patch area (CWA) as a measure of intra-patch connectivity

One of the main reasons that can explain why patch area is the most common measure of intra-patch connectivity is that it is a simple measure with a strong ecological foundation: patch area represents the total amount of habitat which is accessible within a patch (Fahrig 2013). On the other hand, we have seen that patch area alone cannot distinguish patch complexity patterns and that patch complexity indices do not integrate the notion of habitat amount (see Figs. 1, 2, and 3). To overcome this limitation, we suggest a refined measure of intra-patch connectivity that combines patch complexity with the amount of habitat accessible within a patch. Let C be a patch complexity index having a predefined range of variation between 0 (excluded) and 1 (included), such that 0 correspond to an infinite complexity (asymptotic bound) and such that 1 corresponds to an optimal (low) complexity (e.g. a perfect disk if the complexity is 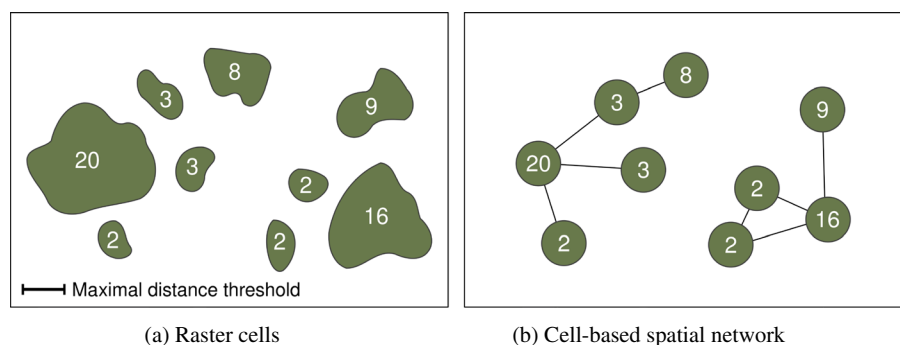defined geometrically). If A_p is the area of patch p, and C_p the measure of C for the patch p, then we propose to measure intra-patch connectivity with the *complexity-weighted patch area*, given by:

$$\text{CWA}(p) = C_p \times A_p \tag{1}$$

This measure expresses in area units, varies between 0 (excluded) and A_p (included), and corresponds to an adjusted measure of the available habitat area within the patch. If the patch has an optimal complexity (according to the definition of C) then $\text{CWA}(p) = A_p$, any two locations in the patch can be joined with an optimal path (i.e. shortest, or least cost) entirely included in the patch. The higher the patch complexity is, the lower $\text{CWA}(p)$ is, which tends to 0 as the complexity increases. Although the infinite complexity is an asymptotic bound, it can be interpreted as the hypothetical case when it is impossible to move within the patch, then the accessible area within the patch is null, regardless of its area.

Many patch complexity indices can be used with CWA. In this study, we considered the usage of two existing geometrical indices, the shape index (SHAPE, Patton 1975; McGarigal et al. 2012) and the fractal dimension (FRAC, Mandelbrot 1983; Kenkel and Walker 1993), and we introduce the mean detour index, a new topological complexity index derived from spatial network analysis which measures the efficiency of a spatial network (MDI, Barthelemy 2010). This third index rely on graph-based representation at the patch level, where patches are represented as a network of interconnected cells (see Fig. 4). Its value corresponds to the average ratio between the "natural" (i.e. optimal) and the "route" (i.e. within the patch) distance between all pairs of cells in the patch (see Fig. 5). MDI varies between 0 (excluded) and 1 (included) and is highly robust to changes in spatial

Fig. 4 Representation of three patches as raster cells (a) and the corresponding cell-based spatial network representation with the four-connected neighbourhood
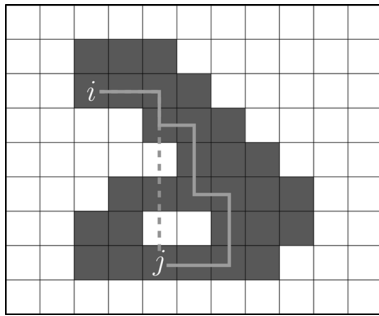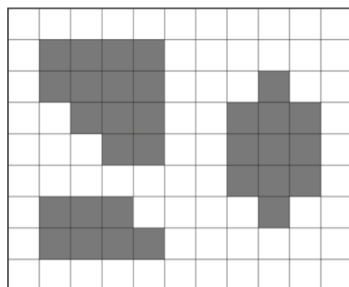

(a) Raster cells   (b) Cell-based spatial network

Fig. 5 Illustration of the best possible shortest path (Manhattan path, dashed line) and the actual shortest path (plain line) between i and j in a patch. The Manhattan path has a length of 7 and the actual shortest path has a length of 11

scale (see robustness assessment in Appendix A.1.4). It can therefore be used as is in CWA. SHAPE varies between 1 (low complexity) and increases without limit with increased complexity, and FRAC varies between 1 (low complexity) and 2 (high complexity). The ranges of variation of 1/SHAPE and 1/FRAC are both included in]0, 1] and can therefore be used in CWA. More details about SHAPE, FRAC, and MDI are given in Table 1 and Appendix A.1.
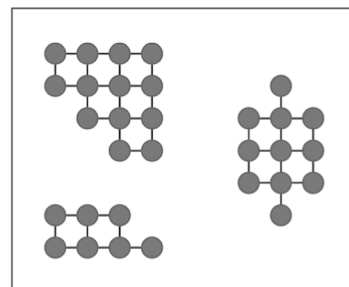
Integration of CWA into fragmentation and connectivity measures

In most fragmentation and connectivity indices, the intra-patch connectivity component is taken into account through the patch area. The complexity-weighted patch area constitutes a new

"topo-ecological" patch attribute (Ricotta et al. 2000) that can be seamlessly integrated into such indices by using CWA instead of the patch area. As for a given patch p, $CWA_p \leq A_p$ always hold, CWA conserves most mathematical properties of fragmentation and connectivity indices. In this study, we considered the integration of CWA into the effective mesh size (MESH), the integral index of connectivity (IIC), and the probability of connectivity (PC). The first index, MESH, is a fragmentation index based on the habitat patch areas distribution within the landscape (Jaeger 2000). On the other hand, IIC (Pascual-Hortal and Saura 2006) and PC (Saura and Pascual-Hortal 2007) are both connectivity indices based on a spatial network (or graph) representation of patches in the landscape. In such a representation, the landscape is represented by a network $G = (V, E)$ with V the set of nodes (patches) and $E \subseteq V \times V$ the connections between patches (edges). Two patches are connected if they satisfy a given condition, which users must determine according to the use case (Galpern et al. 2011). In practice, the condition is either structural (e.g. distance threshold) or functional (e.g. species dispersal capacities) and chosen according to focal species. In Fig. 6, we depict an example of such a network representation with a maximum distance threshold. The main difference between IIC and PC is that PC uses a probabilistic connection model where each edge is labelled with a probability (e.g. probability of dispersal between two patches), whereas IIC uses a binary connection model. More details about MESH, IIC, PC, and the integration of CWA in these indices are given in Table 1 and Appendix A.2 and A.3. In

(a) Landscape with patches of different sizes

(b) Network representation of (a), with size as node attribute

Fig. 6 Network representation of a landscape: each patch corresponds to a node, and any two patches are connected if they satisfy a structural (e.g. distance threshold) or functional (e.g.

migratory path of focal species) condition. Here, the landscape in (a) is represented in (b) as a spatial network with a maximal distance threshold as the connectivity condition

Table 1 Summary of landscape indices presented in this study

Index name (acronym)	Description	Formula	Notations
Complexity-weighted patch area (CWA)	New intra-patch connectivity index where the habitat amount is weighted by a normalized patch complexity index	$C_p \times A_p$	C_p: any normalized patch complexity measure of patch p (between 0 and 1). A_p: area of patch p.
Effective mesh size (MESH)	Fragmentation index based on the habitat patch areas distribution within the landscape (Jaeger 2000)	$\dfrac{1}{A_L}\displaystyle\sum_{p\in V} A_p^2$	A_L: total landscape area. V: set of habitat patches. l_{pq}: shortest path length between patches p and q (number of edges in a landscape network representation).
Integral index of connectivity (IIC)	Connectivity index based on a network representation of the landscape (see Fig. 6) with a binary connection model (Pascual-Hortal and Saura 2006)	$\dfrac{\sum_{p\in V}\sum_{q\in V}\frac{A_p A_q}{1+l_{pq}}}{A_L^2}$	p_{pq}^*: maximum product probability of all paths between patches p and q.
Probability of connectivity (PC)	Connectivity index based on a network representation of the landscape (see Fig. 6) with a probabilistic connection model (Saura and Pascual-Hortal 2007)	$\dfrac{\sum_{p\in V}\sum_{q\in V} A_p A_q P_{pq}^*}{A_L^2}$	P_p: perimeter of patch p. $\min P_p$: minimum possible perimeter for a patch of area A_p. N_p: number of cells in patch p.
Shape index (SHAPE)	Geometrical patch complexity index based on patch perimeter (Patton 1975)	$\dfrac{P_p}{\min P_p}$	$Q_p(i,j)$: detour index between cells i and j in patch p, given by the ratio between a "natural" (i.e. optimal) and a "route" (i.e. within the patch) distance from i to j (see Figs. 4 and 5)
Fractal dimension (FRAC)	Geometrical patch complexity index based on fractal theory (Kenkel and Walker 1993)	$\dfrac{2\ln(0.25P_p)}{\ln(A_p)}$	
Mean detour index (MDI)	Topological patch complexity index computed from a cell-based network representation of patches (see Figs. 4 and 5) and derived from spatial network analysis (Barthelemy 2010)	$\dfrac{\sum_{(i,j)/i\neq j} Q_p(i,j)}{N_p(N_p - 1)}$	

The complexity-weighted patch area (CWA) is a new measure of intra-patch connectivity that can be integrated into classical fragmentation and connectivity indices (e.g. MESH, IIC, PC) by replacing the patch area (A_p) by CWA(p). The complexity index C_p within CWA can be any normalized patch complexity index (e.g. 1/SHAPE, 1/FRAC, MDI). Regarding notation, we suggest specifying the complexity index with square brackets (e.g. CWA[MDI]) and the adapted fragmentation and connectivity measures with subscripts (e.g. MESH$_{\text{CWA[MDI]}}$). More details about these indices are given in Appendix A

the following, we respectively denote the modified version of these indices by MESH$_{CWA}$, IIC$_{CWA}$, and PC$_{CWA}$.
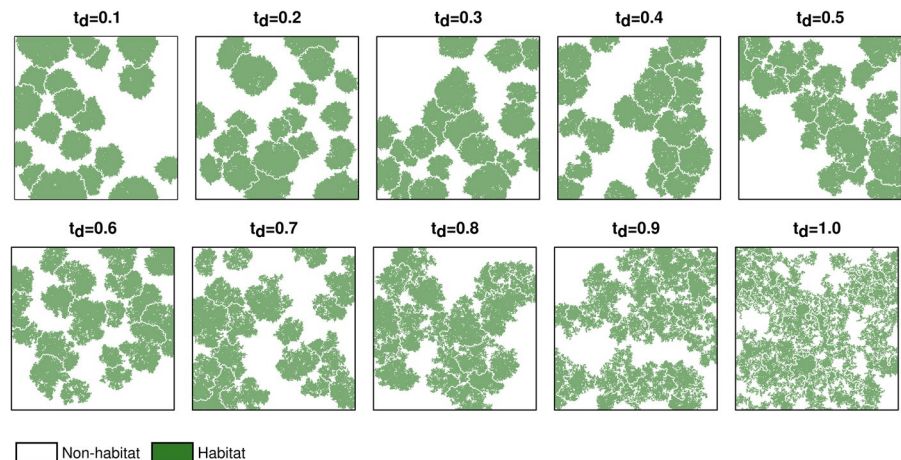
The `intra` R package

We developed the `intra` R package to provide the necessary tools to compute CWA using SHAPE, FRAC, or MDI as patch complexity indices. Although existing software packages are available to compute SHAPE and FRAC (e.g. McGarigal et al. 2012; Hesselbarth et al. 2019), there is no existing software package to compute MDI from a cell-based representation of patches. Since MDI requires the computation of the shortest path between all pairs of cells within all patches, which is a computationally expensive task, we implemented `intra`'s algorithms in C++ taking advantage of parallelization with OpenMP (https://www.openmp.org/). We relied on Rcpp to integrate our C++ code with R (Eddelbuettel 2013). The `intra` package provides functions to compute MESH$_{CWA}$, and functions to export a raster landscape as a vector layer with CWA as a patch attribute. Such vector layers can be used along with software packages such as `Conefor` (Saura and Torné 2009), or `Makurhini` (Godínez-Gómez and Correa Ayram 2020) to compute IIC$_{CWA}$ or PC$_{CWA}$. The `intra` R package is distributed as open-source software on Github: https://github.com/dimitri-juste au/intra.

Evaluation on artificial landscapes

First, we used artificial landscapes to evaluate the ability of CWA to discriminate identical patch size distributions having different spatial configurations when the index is used as the intra-patch connectivity measure within a fragmentation. We illustrated the impact of using CWA in fragmentation measure through the MESH fragmentation index. We generated a landscape series where all landscapes have the same patch sizes distribution, thus the same MESH value, but different spatial configurations. To this end, we used the `rflsgen` software (Justeau-Allaire et al. 2022) to generate a non-spatially-explicit landscape structure, and we generated artificial neutral landscapes varying the terrain dependency parameter t_d of `rflsgen` from 0.0 (low spatial complexity) to 1.0 (high spatial complexity) with a step of 0.01. For each t_d value, we generated 10 different landscapes, resulting in a total of 1010 artificial landscapes. The four-connected neighborhood was used to define patches. A subset of these generated landscape series is depicted in Fig. 7. For each of these landscapes, we computed MESH$_{CWA}$ using SHAPE, FRAC, and MDI as patch complexity indices. We evaluated the ability of each index to discriminate the different spatial configurations and we compared how complexity indices alter the available habitat area within CWA. Notably, we tested the monotony of MESH$_{CWA}$'s response to the spatial complexity using the Spearman rank correlation coefficient.

Fig. 7 Landscape series of ten landscapes having the same patch sizes distribution, but different spatial configurations. This landscape series was generated with the `flsgen` neutral landscape generator, with a terrain dependency (t_d) varying from 0.1 (low spatial complexity) to 1.0 (high spatial complexity). Patches were defined with the four-connected neighborhood

Patch prioritization on a real landscape

To evaluate the behaviour of CWA on real data, we conducted a case study on the forest landscape of New Caledonia, a tropical archipelago located in the South Pacific, and the smallest biodiversity hotspot in the world. New Caledonian forests are threatened by nickel mining activity, fire, and invasive alien species. Moreover, forest fragmentation is known to have adverse effects on local tree communities (Ibanez et al. 2017). Forest conservation and restoration challenges are notably critical in mining areas because they host many threatened narrow-endemic plant species (Lannuzel et al. 2022). Accordingly, we focused on one of these mining areas, the Koniambo massif,

located in the north part of the main island (Grande Terre). The forest cover data is a vector layer digitized by hand from aerial images (Birnbaum et al. 2022, see Fig. 8). First, we rasterized this vector data at high resolution (7.5 ms) to compute intra-patch connectivity indices with the intra R package. Then, we vectorized back the results and used the Makurhini R package (Godínez-Gómez and Correa Ayram 2020) to compute the probability of connectivity index (PC, Saura and Pascual-Hortal 2007,), successively using patch area (AREA), CWA[SHAPE], CWA[FRAC], and CWA[MDI] as patch attribute. We used the default probability threshold, based on the inverse of the mean distance between patches, and computed the contribution to PC of each patch (dPC). We then
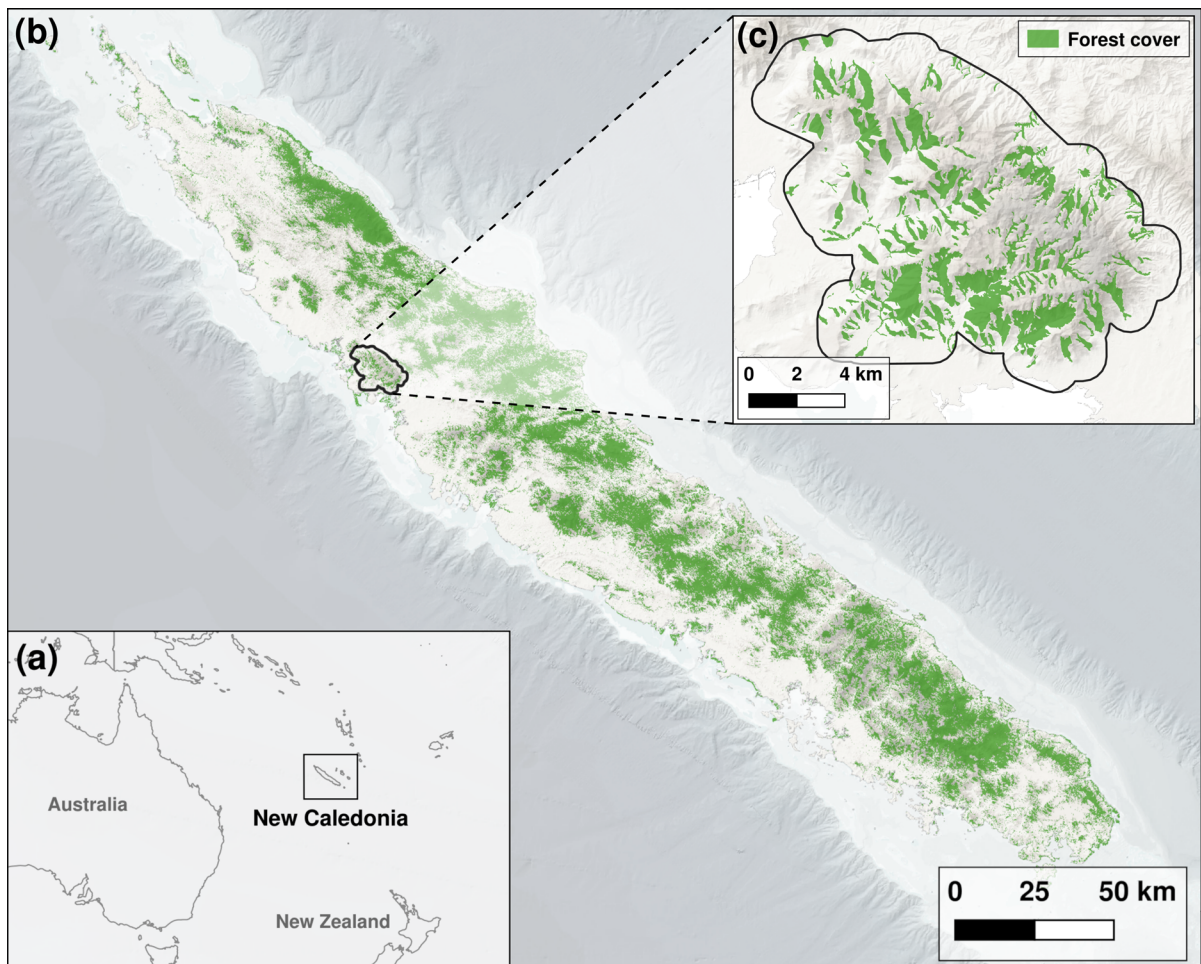

Fig. 8 (a) Location of New Caledonia, (b) Grande Terre, New Caledonia's main island, and (c) forest cover of the Koniambo mining area (digitized by hand from aerial images)

produced a patch prioritization for each patch attribute, according to their corresponding dPC value. We first tested the monotony of the CWA-based prioritizations related to the AREA-based one using the Spearman rank correlation coefficient. Then, we examined the extent to which CWA-based rankings locally varied relative to the AREA-based ranking, by computing the difference between the CWA-based ranks and the AREA-based ranks for each patch.

Results

Response to identical patch sizes distributions with different spatial configurations

We illustrated the response of the effective mesh size (MESH) and its $MESH_{CWA}$ variants to identical patch sizes distributions with different spatial configurations in Fig. 9. As expected, MESH had the exact same response with every artificial landscape, as it only considers patch areas but ignores their spatial configuration. In comparison, $MESH_{CWA}$ reacted to different spatial configurations and showed a strong monotonic response for each of the three complexity indices (see Table 2). The choice of the patch complexity index also significantly impacted the response of $MESH_{CWA}$. First, the use of SHAPE and FRAC produced a low value compared to MESH when $t_d = 0$ (respectively about 28.1% and 74.1% of MESH

Table 2 Result of the Spearman correlation tests between $MESH_{CWA}$, with SHAPE, FRAC, and MDI as patch complexity indices, and landscape spatial complexity, corresponding to the t_d parameter used for artificial landscape correlation

Fragmentation index	ρ	p-value
$MESH_{CWA[SHAPE]}$	− 0.9959493	< 0.001
$MESH_{CWA[FRAC]}$	− 0.9964736	< 0.001
$MESH_{CWA[MDI]}$	− 0.9929258	< 0.001

The Spearman rank correlation coefficients (ρ) and their associated p-values indicate a strong monotonic relation for every patch complexity index

on average). In comparison, MDI preserved a value very close to MESH when $t_d = 0$ (about 99.7% of MESH on average). In addition, the response curves induced by SHAPE and FRAC are comparable and nearly linear, whereas MDI induced an exponential decay curve. Consequently, the use of MDI produced values relatively close to MESH when $t_d \in [0, 0.8]$ and increasingly lower values than MESH when the spatial complexity is high ($t_d > 0.8$).

Impact of the intra-patch connectivity measure in patch prioritization on a real landscape

In Table 3, we depicted the overall PC values for each patch attribute (AREA, CWA[SHAPE], CWA[FRAC], and CWA[MDI]) and the Spearman rank correlation between the ranked contributions

Fig. 9 Response of MESH and $MESH_{CWA}$ (used with SHAPE, FRAC, and MDI) to different landscape spatial configurations, for a fixed landscape composition over artificial neutral landscapes generated with `rflsgen`. The t_d parameter of `rflsgen` represents the spatial complexity of the landscape, ranging from 0 (low complexity) to 1 (high complexity)
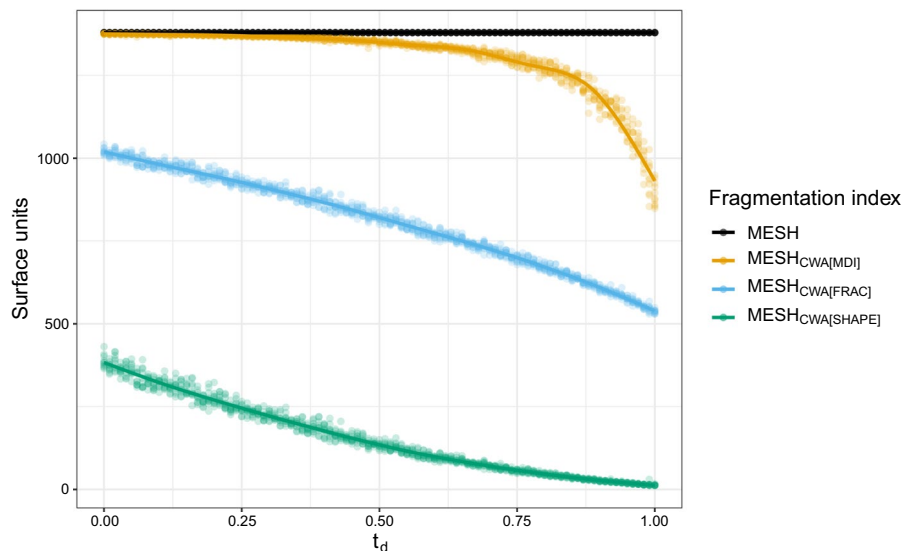
Table 3 Probability of connectivity (PC) in the forest landscape of the Koniambo massif in New Caledonia with patch area (AREA), CWA[SHAPE], CWA[FRAC], and CWA[MDI] as patch attributes

Patch attribute in PC	PC	ρ	p
AREA	0.0209	–	–
CWA[SHAPE]	0.0018	0.9844156	< 0.001
CWA[FRAC]	0.0148	0.9958258	< 0.001
CWA[MDI]	0.0176	0.9955439	< 0.001

The index was computed using the inverse of the mean distance between patches as the probability threshold. Spearman rank correlation coefficients (ρ) and associated p-value were computed by comparing the ranked patch contribution (dPC) when CWA[SHAPE], CWA[FRAC], and CWA[MDI] are used as patch attributes with the ranking produced with AREA as patch attribute

produced using CWA-based patch attributes and AREA as the patch attribute in PC. First, we observed that CWA-based patch attributes resulted in lower

overall PC values than AREA. CWA[SHAPE] produced the lowest (lower by a magnitude of 10), while CWA[FRAC] and CWA[MDI] respectively produced 30% and 16% lower values. The ranked contributions of CWA-based patch attributes all presented a strong monotonic correlation with the ranked contribution of AREA as the patch attribute. However, as illustrated in Fig. 10, there are many local differences in the prioritizations, especially for large and medium-sized patches. First, CWA[SHAPE] produced the greatest differences in the prioritization, with medium-sized patches being ranked up to 21 positions better and large patches 28 worse than the AREA-based prioritization. Among the 209 patches of the landscape, 175 were ranked differently ($\approx$84%), and only 34 achieved the same rank as the AREA-based prioritization. Differences in the prioritization produced by CWA[FRAC] and CWA[MDI] were smaller with respectively 106 ($\approx$51%) and 86 ($\approx$42%) patches ranked differently, up to respectively 4 and 3
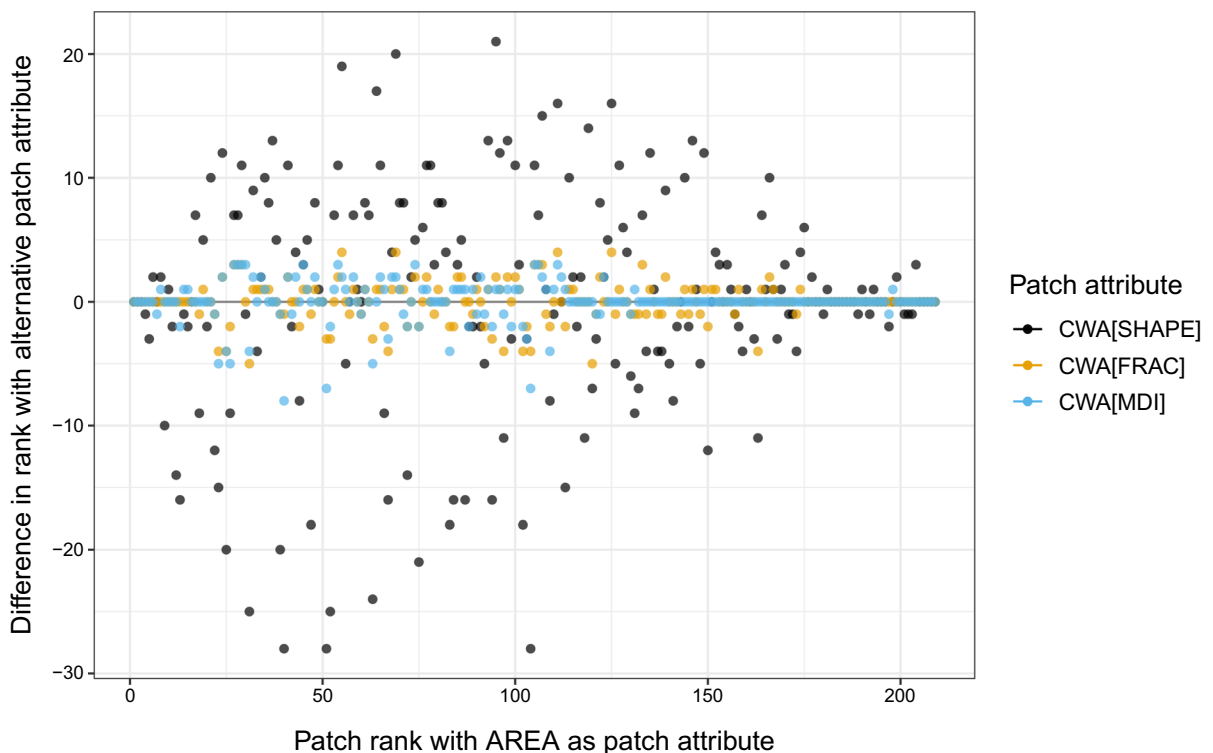

Fig. 10 Impact of using CWA (with SHAPE, FRAC, and MDI) as patch attribute in the probability of connectivity index (PC) on patch prioritization, all compared to the patch prioritization with AREA as patch attribute. Patches are ranked according to their contribution to the overall PC index (dPC). PC was computed in the forest landscape of the Koniambo massif in New Caledonia, using the inverse of the mean distance between patches as the probability threshold

positions better, and 5 and 8 worse than the AREA-based prioritization.

Discussion

Patch area cannot alone reflect the diversity of intra-patch connectivity patterns

Patch area has been the most used intra-patch connectivity measure to date. There is a strong ecological justification for this choice: patch area measures the amount of available habitat within a patch (Fahrig 2013). However, we have shown in this study that the patch area suffers from a major limitation: it cannot distinguish different spatial configurations. Therefore, using patch area as the intra-patch connectivity measure in landscape fragmentation and connectivity indices can lead to biased interpretations: landscapes with similar patch area distributions but different spatial configurations cannot be distinguished. We notably illustrated this pitfall with artificial landscapes (see Fig. 7). In response to this limitation, we suggested using normalized patch complexity indices to alter the amount of available habitat within a patch according to its spatial complexity, which gives us the complexity-weighted area (CWA). We have shown that, regardless of the patch complexity measure, using CWA instead of patch area preserves the mathematical properties of common fragmentation and connectivity indices such as the effective mesh size (MESH, Jaeger 2000), the integral index of connectivity (IIC, Pascual-Hortal and Saura 2006), or the probability of connectivity (PC, Saura and Pascual-Hortal 2007). Using both artificial and real landscapes, we have shown experimentally that using CWA in landscape indices such as MESH, IIC, or PC allows distinguishing between different spatial configurations and that refining intra-patch connectivity measures with CWA can impact both overall landscape indices values and patch prioritization. The approach proposed in this study thus introduces a new family of topo-ecological intra-patch connectivity attributes (Ricotta et al. 2000).

The many facets of patch complexity

The abstract definition of CWA offers virtually infinite ways of characterizing intra-patch connectivity through the free-of-choice normalized patch complexity measure. Several geometrical complexity indices are already available, such as the shape index (SHAPE) or the fractal dimension (FRAC) that we both considered in this study (Patton 1975; Kenkel and Walker 1993; McGarigal et al. 2012). In addition, we proposed a topological complexity index derived from network analysis, the mean detour index (MDI). In our experiments on both artificial and real landscapes, we have shown that, although preserving monotonic responses, the path complexity measure can significantly impact CWA. For example, using SHAPE instead of the patch area considerably reduced the value of MESH (see Fig. 9). The same applied to FRAC but to a lesser extent. The reduced range of variation of the inverse of FRAC between 0.5 and 1 is a possible explanation for this result. By contrast, using MDI instead of patch area in MESH mainly affected landscapes with high spatial complexity. In practice, the selection of the patch complexity measure should be contextual and supported by ecological evidence, such as focal species' movement and dispersal abilities. As landscape indices' objective is to describe landscape patterns, but a single one cannot alone reflect the diversity of ecological processes, we thus believe that it is essential to provide landscape ecologists with a wide variety of indices. The most difficult challenge, yet the most exciting, is to associate observed intra-patch connectivity patterns with ecological processes. In particular, it would be particularly relevant to investigate which intra-patch connectivity patterns best reflect species-specific dispersal and movement abilities. Can we accurately take into account plants' dispersal mode (e.g. barochoric, anemochorous, zoochorous) within a patch? How to represent animals' perception of patch topography according to their locomotion mode? We believe the high degree of freedom of CWA to be an asset to such fundamental questions of landscape ecology.

On the representation of patches as spatial networks

Spatial networks are often used in landscape ecology to describe inter-patch connectivity. Indeed, such data structures are well adapted to describe connectivity in general as they draw on established theoretical foundations that provide many ways to analyse a network qualitatively and quantitatively. However,

very few studies considered spatial network representations at the patch level for quantifying intra-patch connectivity (Tischendorf and Fahrig 2000a; Wu and Murray 2008). In this study, we introduced a new way to evaluate intra-patch connectivity by representing a patch as a network of interconnected locations and by using a classical measure of spatial network analysis, the mean detour index (MDI), which measures the efficiency of a spatial network (Barthelemy 2010). In our experiment on artificial landscapes, we have shown that MDI's response to landscape patches' spatial configuration was substantially different from geometrical indices' responses, which indicates that patches can exhibit topological patterns that differ from geometrical patterns. Thus, we believe that representing patches as a spatial network offers methodological perspectives, notably because networks are abstract and flexible data structures that can adapt to specific needs. For example, instead of a cell-based patch representation, one could design a network that reflects functional connectivity according to focal species, by accounting for dispersal barriers and corridors within patches (e.g. creeks, elevation, soil). The computation of MDI within such a network would be similar, and so would be its interpretation.

Perspectives for conservation and restoration planning

Ecological connectivity is essential for species persistence and ecosystem functioning (Taylor et al. 1993; Fletcher et al. 2016). Consequently, it must be accurately measured to ensure the success of conservation and restoration planning efforts. The inter-patch component of connectivity has been the most widely studied to date. However, intra-patch connectivity is also an essential overall connectivity and fragmentation component (Tischendorf and Fahrig 2000a, b; Laita et al. 2011; Spanowicz and Jaeger 2019). We have shown that alternative intra-patch connectivity measures to the patch area alone can offer new insights to explore fragmentation and connectivity patterns. In our experiment on the Koniambo massif in New Caledonia, using the probability of connectivity index, our CWA-based intra-patch connectivity measures produced prioritizations that presented strongly monotonic relations with the one obtained using the patch area. This result was not surprising as CWA is proportional to the patch area. However, this monotonic

relation does not imply similar outcomes for management. Indeed, we have shown that all patch complexity measures impacted the ranking for numerous patches ($\approx$42% with MDI, $\approx$51% with FRAC, and $\approx$ 84% with SHAPE). We also observed substantial differences in patch ranking, especially with SHAPE (from -28 to +21), and the large and medium-sized patches were mainly affected. This result shows that when such prioritizations are for the purpose of conservation planning under limited resources, the proper consideration of the intra-patch component of ecological connectivity can substantially impact decisions. We furthermore suggest that, in landscapes with low intra-patch connectivity, investing in intra-patch connectivity restoration might be more beneficial than investing in inter-patch connectivity restoration. Using proper measures of intra-patch connectivity is clearly a prerequisite to addressing such issues. In a conservation and restoration planning context, integrating refined intra-patch connectivity measures could also help identify the best tradeoffs to foster multispecies intra-patch connectivity, as already done for inter-patch connectivity (Dilkina et al. 2017). In conclusion, we hope these new intra-patch connectivity measures will allow a deeper and more comprehensive exploration of potential actions to conserve and restore ecological connectivity.

Author contributions All authors conceived the ideas and methodology; DJ led the writing of the manuscript; DJ, TI, GV, PB prepared the dataset, designed the case study, and analyzed its result; DJ, XL conceived and implemented the algorithms and the software package; DJ, TI, GV, XL, PB contributed critically to the draft and gave final approval for publication.

Data availibility The `intra` R package is available on Github at https://github.com/dimitri-justeau/intra and Zenodo at https://doi.org/10.5281/zenodo.7751397 (Justeau-Allaire et al. 2023b). The R scripts and the data used in this article are available on Zenodo at https://doi.org/10.5281/zenodo.8399767 (Justeau-Allaire et al. 2023a).

Declarations

A Appendix

A.1 Patch complexity indices

We now introduce a set of patch complexity indices that can be used with CWA. While the first two indices are geometrical indices already used in landscape ecology, the third one is a topological index based on a graph representation at the patch level and derived from spatial network analysis.

A.1.1 Shape index (SHAPE)

The shape index (SHAPE) is a geometrical patch complexity index based on the ratio between the perimeter of the patch and the minimum possible perimeter of a patch having the same area (Patton 1975; McGarigal et al. 2012). SHAPE was introduced to correct a problem with the perimeter-area ratio, which decreases with patch area although the shape is maintained constant. For a given patch p, SHAPE is defined as:

$$\text{SHAPE}(p) = \frac{P_p}{\min P_p} \tag{2}$$

With P_p the perimeter of patch p, and $\min P_p$ the minimum possible perimeter for a patch having the same area A_p as p. When the landscape is represented as a raster, with n the side of the largest integer square smaller than A_p and $m = A_p - n^2$, $\min P_p$ is given by (MILNE 1991; Bogaert et al. 2000):

$$\min P_p = \begin{cases} 4n \text{ if } m = 0 \\ 4n + 2 \text{ if } n^2 < A_p \leq n(1 + n) \\ 4n + 4 \text{ if } A_p > n(1 + n) \end{cases} \tag{3}$$

SHAPE is equal to 1 when the patch has the lowest possible complexity and increases without limit with increased complexity. Then we can use 1/SHAPE as the complexity index into CWA:

$$\text{CWA[SHAPE]}(p) = \frac{A_p}{\text{SHAPE}(p)} \tag{4}$$

A.1.2 Fractal dimension (FRAC)

The fractal dimension (FRAC) is a geometrical patch complexity which resulted from the application of fractal theory to landscape ecology (Mandelbrot 1983; Kenkel and Walker 1993). FRAC expresses as a ratio between the logarithm of the patch perimeter and the logarithm of the patch area, it is given by:

$$\text{FRAC}(p) = \frac{2 \ln(0.25 P_p)}{\ln(A_p)} \tag{5}$$

As SHAPE, FRAC is not affected by the perimeter-area ratio problem. It has a predefined range of variation which varies between 1 (lowest possible complexity) and 2 (highly convoluted). The inverse of FRAC can be used as the complexity measure into CWA, as its range of variation, between 0.5 and 1, is included in]0, 1]. However, it is important to remember that the lower bound of CWA[FRAC](p) is $0.5 A_p$ when interpreting the results.

$$\text{CWA[FRAC]}(p) = \frac{A_p}{\text{FRAC}(p)} \tag{6}$$

A.1.3 Mean detour index (MDI)

In landscape ecology, spatial network structures are often used to describe inter-patch connectivity (Galpern et al. 2011). However, to the best of our knowledge, intra-patch connectivity was rarely evaluated with spatial networks. At the patch scale, a cell-based representation of patches is necessary to represent the patch as a spatial network. Some authors relied on such representations to evaluate connectivity as the

immigration rate between patch cells (Tischendorf and Fahrig 2000a), or to represent patches as cell-based spatial networks but only measuring intra-patch connectivity as the number of cells (Wu and Murray 2008). Here, we represent patches with a cell-based spatial network representation (see Fig. 4). Using this representation, we use the *mean detour index* (MDI) which measures the efficiency of a spatial network (Barthelemy 2010). Two distance measures are needed to compute MDI: a "natural" (e.g. euclidean) and a "route" (through the network) distance. The first measure represents the best possible distance and is a reference to evaluate network efficiency. In our case and given a patch p, we use the grid distance d_g as reference (or Manhattan distance), and the patch distance d_p as network distance (see Fig. 5). Given a pair of cells $(i, j) \in p^2$:

- $d_g(i, j)$ is the shortest path length between patch cells i and j in the grid, regardless of the presence of patch cells in the path.
- $d_p(i, j)$ is the shortest path length between i and j without leaving the patch p.

Using these two distance measures and for pairs of cells $(i, j) \in p^2$, the detour index $Q_p(i, j)$ is given by:

$$Q_p(i, j) = \frac{d_g(i, j)}{d_p(i, j)}. \tag{7}$$

We then have $Q_p(i, j) \in]0, 1]$ and $Q_p(i, j) = 1$ when the network is optimal for the pair (i, j). The global efficiency of the network can be assessed by computing the mean value of the detour index for all pairs of distinct cells within the patch:

$$MDI(p) = \frac{1}{N_p(N_p - 1)} \sum_{(i,j)/i \neq j} Q_p(i, j). \tag{8}$$

With N_p the number of cells in the patch p. The mean detour index satisfies the necessary conditions to be used in CWA:

$$CWA[MDI](p) = MDI(p) \times A_p \tag{9}$$

A.1.4 Robustness to changes in spatial scale

Most landscape indices are sensitive to changes in scale. Such behavior is not necessarily problematic

and may even be desirable in some cases (e.g. absolute habitat amount). However, because they aim to reflect spatial patterns per se (i.e. independently of habitat amount), patch complexity indices should, by definition, have a low sensitivity to changes in spatial scale. Both SHAPE Patton (1975) and FRAC Kenkel and Walker (1993) were designed to ensure high robustness to changes in spatial scale. However, how does MDI, as employed in this article, react to such changes? To address this question, we considered four different patch shapes: *perfect circle*, *highly compact*, *moderately convoluted*, *highly convoluted*. From a vector representation of these shapes, we produced a series of raster patches with widths varying from 10 pixels to 300 pixels with a step of 10 pixels (see Fig. 11). Then, we computed 1/SHAPE, 1/FRAC, and MDI for the raster patch series, and evaluated the average index value and the standard deviation along each series.

We summarized the results in Table 4 and Fig. 12. These results clearly indicate that MDI is very robust to changes in spatial scale (even more than SHAPE and FRAC). It is therefore an appropriate patch spatial complexity measure.

A.2 Integration of CWA into the effective mesh size (MESH)

The effective mesh size (MESH) is a fragmentation index based on the habitat patch areas distribution within the landscape, introduced by Jaeger (2000). MESH expresses in area units and describes the probability that two random points are in the same patch. It is given by:

$$MESH = \frac{1}{A_L} \sum_{p \in V} A_p^2 \tag{10}$$

With A_L the total landscape area, V the set of patches, and A_p the area of patch p. Considering A_p as an attribute of the patch p, we can use CWA(p) instead of the area to compute MESH:

$$MESH_{CWA} = \frac{1}{A_L} \sum_{p \in V} CWA(p)^2 \tag{11}$$

As for a given patch p, the complexity-weighted patch area always verifies $CWA_p \leq A_p$, $MESH_{CWA}$ conserves the mathematical properties of MESH described by Jaeger (2000), such as low sensitivity

Fig. 11 Series of artificial patches. From top to bottom: patch shapes, from left to right: scale (width in pixels)
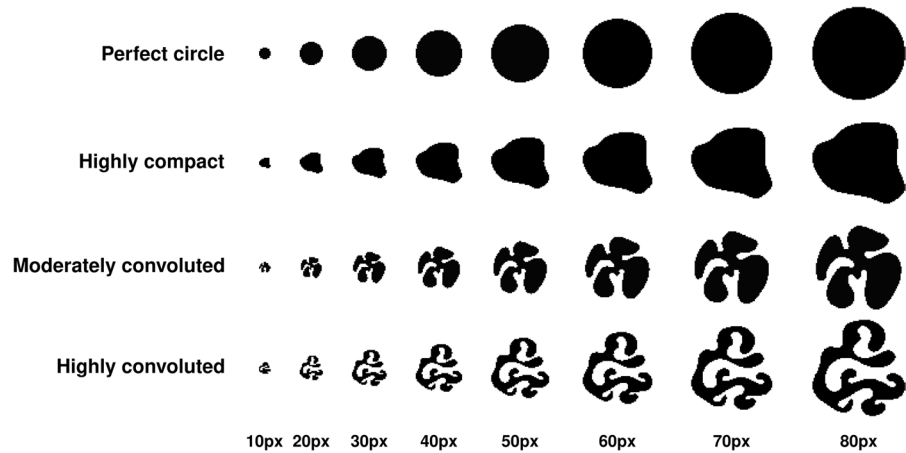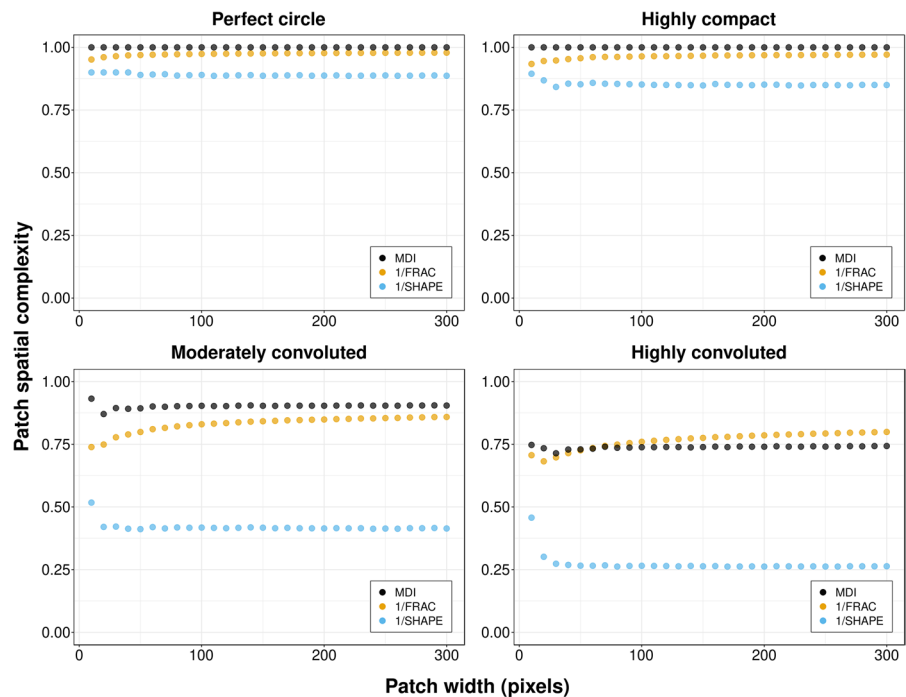

Table 4 Behavior of 1/SHAPE, 1/FRAC, and MDI to spatial scale changes on fixed shapes

For each shape and index, we computed the average μ and the standard deviation σ

	1/SHAPE – μ (σ)	1/FRAC – μ (σ)	MDI – μ (σ)
Perfect circle	0.89 (0.0044)	0.97 (0.006)	1 (0)
Highly compact	0.85 (0.009)	0.94 (0.0086)	0.99 (2.0×10^{-5})
Moderately convoluted	0.42 (0.019)	0.83 (0.032)	0.90 (0.0088)
Highly convoluted	0.27 (0.036)	0.77 (0.033)	0.74 (0.006)

Fig. 12 Behavior of 1/SHAPE, 1/FRAC, and MDI to spatial scale changes on fixed shapes. Shapes were fixed and scale was defined through varying width from 10 to 300 pixels with a step of 10 pixels

to very small patches, or area-proportional additivity. Note that our approach is, to a certain extent, comparable to Petsas et al. (2021) who transformed MESH into the *weighted effective mesh size* by weighting the area component of MESH with D, the component density. Nevertheless, because they used MESH

as a connectivity index instead of a fragmentation index, the integration of D concerns patch components (i.e. groups of interconnected patches) and then only affects the measure of inter-patch connectivity. In their modified version of MESH, the patch area remains the intra-patch connectivity measure. Consequently, our approach is also compatible with the *weighted effective mesh size* described in Petsas et al. (2021). Also, note that our approach can also be used in the CBC variant of MESH proposed by Moser et al. (2007).

A.3 Integration of CWA into the integral index of connectivity (IIC) and the probability of connectivity (PC)

The integral index of connectivity (IIC, Pascual-Hortal and Saura 2006) and the probability of connectivity (PC, Saura and Pascual-Hortal 2007) are two connectivity indices based on a spatial network (or graph) representation of patches. In such a representation, the landscape is modelled as a network $G = (V, E)$, with V the *nodes* and $E \subseteq V \times V$ the *edges*, that is the connections between the nodes in V. Each patch is then associated with a node, and two patches are connected by an edge if they satisfy a condition. It is up to the user of these indices to determine which condition is the best according to their use case (Galpern et al. 2011). In practice, structural (e.g. distance threshold) or functional (e.g. species dispersal capacities) conditions are chosen according to focal species. In Fig. 6, we depict an example of such a network representation with a maximum distance threshold. The main difference between IIC and PC is that PC uses a probabilistic connection model where each edge is labelled with a probability (e.g. probability of dispersal between two patches) whereas IIC uses a binary connection model. These indices are given by:

$$\text{IIC} = \frac{\sum_{p \in V} \sum_{q \in V} \frac{A_p A_q}{1 + l_{pq}}}{A_L^2} \qquad (12)$$

$$\text{PC} = \frac{\sum_{p \in V} \sum_{q \in V} A_p A_q p_{pq}^*}{A_L^2} \qquad (13)$$

With A_L the total landscape area, V the set of patches (or nodes), A_p the area of patch p, l_{pq} the shortest path length (i.e. in the number of edges) between patches p and q, and p_{pq}^* the maximum product probability of all possible paths between patches p and q. In the descriptions of IIC and PC (Pascual-Hortal and Saura 2006; Saura and Pascual-Hortal 2007), the authors suggested that patch area A_p (and A_q) can be generalized to use any other patch attribute instead (e.g. patch quality). The complexity-weighted patch area CWA can therefore be seamlessly used within IIC and PC as a patch attribute to integrate an intra-patch connectivity measure that takes into account both the habitat availability within the patch and its complexity. Given a patch p, Saura and Rubio (2010) proposed a decomposition of its contribution to IIC and PC into three fractions: *intra*, *flux*, and *connector*. The *intra* fraction corresponds to the intra-patch connectivity of the patch p, and the impact of using CWA as the patch attribute is then directly visible. The *flux* fraction corresponds to the area-weighted dispersal flux to and from patch p, and will then be impacted by CWA through a reduction of the perceived habitat area along with increased patch complexity. Finally, the *connector* fraction corresponds to the contribution of patch p as a stepping stone between other patches, and will not be impacted by CWA as its value only depends on the topological position of patch p in the network (Saura and Rubio 2010).

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