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Review

Gradients of microclimate, carbon and nitrogen in transition zones of fragmented landscapes – a review

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ABSTRACT

Fragmentation of landscapes creates a transition zone in between natural habitats or different kinds of land use. In forested and agricultural landscapes with transition zones, microclimate and matter cycling are markedly altered. This probably accelerates and is intensified by global warming. However, there is no consensus on defining transition zones and quantifying relevant variables for microclimate and matter cycling across disciplines. This article is an attempt to a) revise definitions and offer a framework for quantitative ecologists, b) review the literature on microclimate and matter cycling in transition zones and c) summarise this information using meta-analysis to better understand bio-geochemical and bio-geophysical processes and their spatial extent in transition zones. We expect altered conditions in soils of transition zones to be 10–20 m with a maximum of 50 m, and 25–50 m for above-ground space with a maximum of 125 m.

Contents

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1. Introduction

Most landscapes are composed of different kinds of ecosystems, which are nested but also often physically separated into fragments (Ries et al., 2004). Fragmented forested and agricultural landscapes are characterised by the occurrence of discontinuities or variations in prevalent or native land cover and habitat properties (Strayer et al., 2003).

In quantitative terms, they differ from other landscapes by having a lower average size of the fragment, a lower interior-to-edge ratio (see Section 2.3 for definitions) and an increase in isolation and distance to each other for patches of similar properties (Mitchell et al., 2014; Saunders et al., 1991).

Fragmented landscapes are not static *per se* but are rather in a continuous natural process of fragmentation. Drivers of fragmentation act on various spatio-temporal scales: geogenic (e.g. differing parent rock), topographical (relief), geomorphological (e.g. kettle holes), pedogenic (e.g. climate), hydrological (e.g. groundwater or rivers), and phytological (e.g. seed dispersal or succession) (Cadenasso et al., 2003a; Wu and David, 2002). Moreover, landscapes are fragmented by sudden events, such as wind throw, erosion (water or wind), volcanic eruptions, earthquakes, pests and diseases, fires or floods (e.g. Braithwaite and Mallik, 2012; Laurance and Curran, 2008).

The total area of forest has been decreasing for millennia (probably for more than 6000 years) due to deforestation and the intrusion of agricultural land (FAO, 2012; Williams, 2006); currently, the area of contiguous intact forest is decreasing twice as quickly as the total area of forest (Riitters et al., 2015). Fragments of native vegetation are often surrounded by managed land (Saunders et al., 1991). This anthropogenically driven fragmentation of landscapes largely changes the land's properties and functioning by mixing zones of different habitat quality and ecological features. The main man-made drivers are agriculture and forestry (e.g. horizontal expansion, logging), urbanisation (Liu et al., 2016), rural development (e.g. road construction) and energy production (e.g. dams). In addition to natural sudden events, man-made disasters such as fires or pollution (e.g. chemical spill, nitrogen deposition, acid rain) also cause fragmentation.

Fragmentation leads to biome patches with zones of transition in between them. These transition zones are characterised by active and passive exchange of matter, energy and information – their properties differ from native forest, plain pasture and agricultural land (Gosz, 1992; Wiens et al., 1985). In fact, 74% of the total forest area in England (Riutta et al., 2014), 74% of semi-deciduous savanna forest in north-east Ivory Coast (Hennenberg, 2005; Hennenberg et al., 2008), almost 50% of all Brazilian Atlantic rainforests (Ribeiro et al., 2009), 44% of continental United States forest (Riitters et al., 2002) and 40% of the total forest area in Bavaria (Germany) (Spangenberg and Kölling, 2004) have been defined as being located within a transition zone of 90–100 m from the forest edge. Globally, Haddad et al. (2015) calculated that 20% of forested land was located in a 100 m transition zone within forests.

Fragmentation affects the local climate. For example, the air within and above cropland is warmer and drier than the moister and cooler air in adjacent forests (Ewers and Banks-Leite, 2013; Laurance et al., 2011). The different microclimate which evolves within the fragments fosters the establishment of differently adapted plant communities, which in turn also influence the microclimate (Chen et al., 1992; Laurance et al., 2011; van Rooyen et al., 2011; Saunders et al., 1999). Some taxa clearly respond positively or negatively to changes in microclimate caused by fragmentation (Godefroid et al., 2006; Heithecker and Halpern, 2007; Magnago et al., 2015). Research on edges conducted in recent decades mainly described them as hot spots for biodiversity and evolutionary processes (Kark and van Rensburg, 2006; Lidicker, 1999 see Ries et al., 2004), which will not be addressed in this review.

Within transition zones, microclimate alters matter cycling (Laurance et al., 2007, 2011; Nascimento and Laurance, 2004). In forested transition zones, above-ground carbon storage capacity has been found to be as little as half that of the forest interior (Paula et al., 2011). Pütz et al. (2014) calculated a total of 200 Tg carbon gas emissions per year due to forest degradation (fragmentation) in tropical forests; this is one-fifth of all emissions caused by deforestation. Moreover, in addition to the carbon gas emissions caused by deforestation, simulations by Laurance et al. (1998) suggest that another 22–149 Tg C loss per year is caused by fragmentation of tropical forests worldwide. Due to altered decomposition rates and primary production (Chen et al., 1992) within these transition zones, Ewers and Banks-Leite (2013) hypothesise that, as global climate change take place, transition zones will increasingly gain in importance.

The relevance of transition zones is thus substantially increasing. However, up to this point, there is no consensus among scientists with respect to definitions and investigation strategies. A synthesis of the existing knowledge on matter dynamics and the connection to microclimate in transition zones is currently lacking. This review provides a first attempt to fill this gap.

The aim of this review is to a) address the various definitions of 'edge effects', b) review the literature on microclimate and matter cycling in transition zones and c) summarise this information using meta-analysis to better understand bio-geochemical and bio-geophysical processes in transition zones (Fig. 1).

The meta-analysis consisted of a literature search for the expressions 'edge effect', 'forest', 'microclimate', 'ecotone', 'transition zone', 'pasture', 'agriculture', 'carbon', 'nitrogen', 'matter and nutrient dynamics' and 'cycling'. To define the spatial extent of the influence of transition zones, the maximum distance had to be stated as measured from the zero line (see Fig. 2 or Table 1) perpendicularly in one direction. If a range was given, both values were used. Although the magnitude of variables has not been taken into account, studies that reported no significance were omitted.

2. Definitions – gradients in fragmented landscapes

2.1. Structural traits in fragmented landscapes

Ecosystems are usually understood as complex systems: they are nonlinear, emergent, self-organised and self-regulated, interrelated, open and agent-based; they also have attractors (Gosz, 1992; Müller and Kroll, 2011; Wu and Loucks, 1995). In order to understand them better, humans tend to structure things when investigating units of a system. In ecology, patches are often used as such a concept for structuring a system (see Wu and Loucks, 1995 for a review). The characteristic feature of patches is a delineation from their environment in which patches can be seen as physical systems. As such, a system boundary must be identified, which is a question of definition and scale. Delineation is usually considered

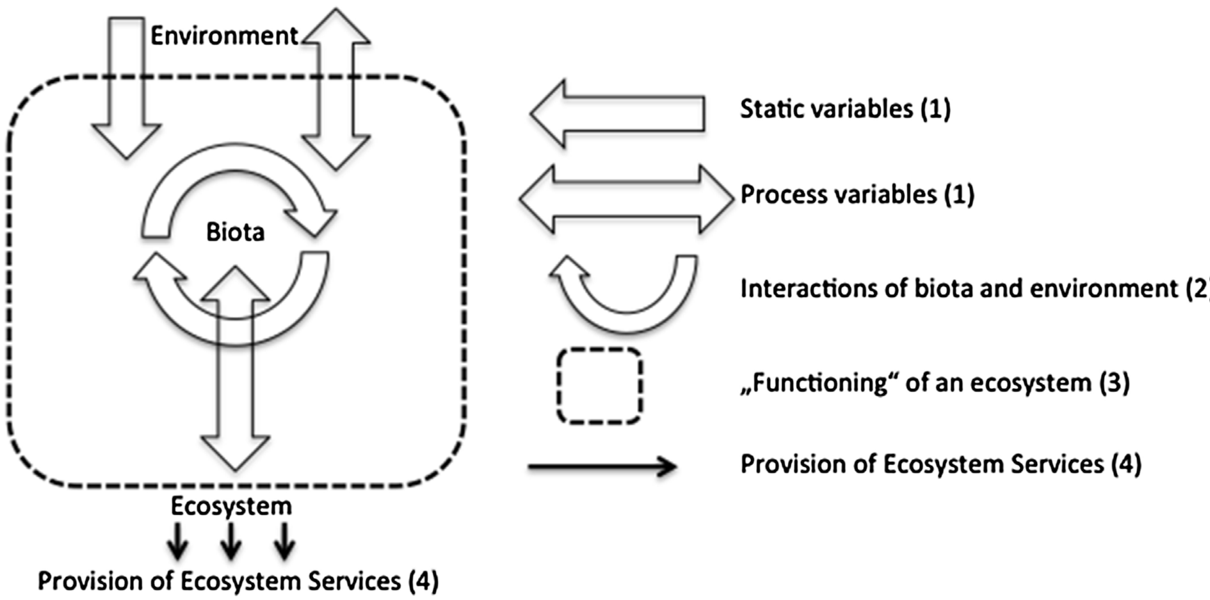

Fig. 1. Breakdown of *functions* concerning ecosystems according to Jax (2005).

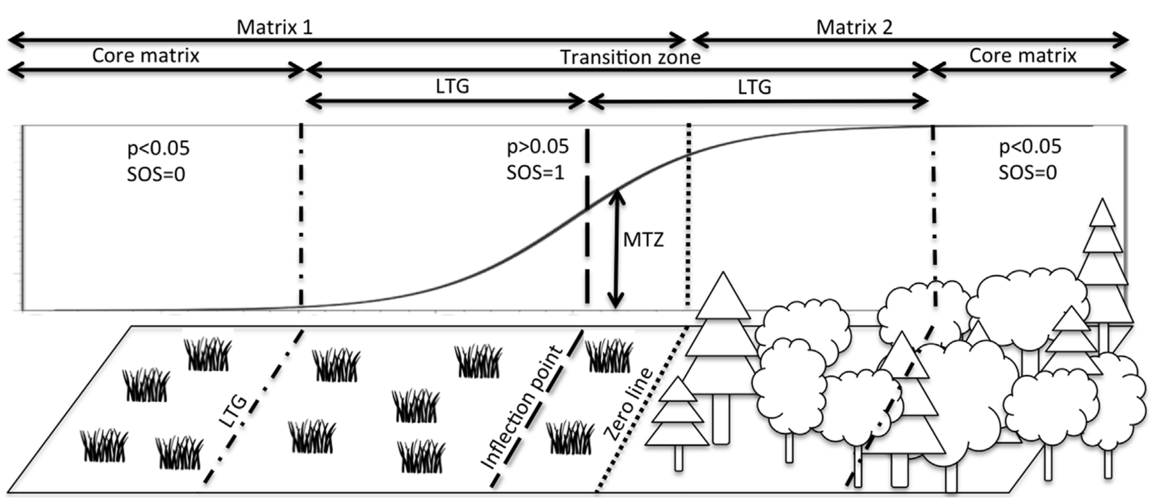

Fig. 2. Example of the application of the definitional toolbox for the quantitative distinction of components of fragmented landscapes; here, for an agricultural field (left) and a forested area (right).

to be worthwhile when within-patch heterogeneity is substantially less than that of between patches. The scale is always a challenge, as a patch can be a leaf, a group of plants, an ecosystem, a landscape or a continent (Wu and David, 2002; Wu and Loucks, 1995; Yarrow and Salthe, 2008). Scale is apparently also a problem in transition zones: whereas both Gosz (1993) and Peters et al. (2006) suggest plants, populations, patches, landscapes and biome levels with transition zones, Erdős et al. (2011) exclude elements such as hedgerows, fences and roads from being 'landscape elements'. Despite in-depth discussion, the tenor in the literature is a multiple scales approach (Kark and van Rensburg, 2006).

Another approach to the structuring of complex ecosystems is the hierarchy theory (Wu and Loucks, 1995). This concept assumes that higher levels involve larger entities and bigger units, which makes them slower. Thus they can be seen as static for subsystem investigations. In contrast, the high-frequency processes of subsystems can be averaged at higher levels, with the exception of highly non-linear systems (Wu and David, 2002; Wu and Loucks, 1995). Depending on the scale of the research question, variables at higher levels or lower levels can be more manageable for the purpose of analysis and interpretation.

In the hierarchy patch dynamics paradigm, both concepts are merged (Wu and Loucks, 1995). Landscapes can be seen as hierarchical mosaics of nested patches (ecosystems), while these ecosystems "correspond to land cover types" with "homogenous vegetation-soil complex" (Wu and David, 2002). This is in line with Yarrow and Salthe (2008), who defined land cover type as "surface-type". Examples of application aaare classification into biomes (e.g. temperate broadleaf forest), biographic regions (e.g. continental or boreal) or soil types (e.g. Podzol or Stagnosol). Cadenasso et al. (2003a) also distinguished patches "compositionally and structurally". A broadly applicable approach to define structural traits for vegetation is the Land Cover Classification System (Di Gregorio, 2005). Besides structural traits for identifying patches, an article by

Table 1
Toolbox for a quantitative description of transition zones in fragmented landscapes.

Term	Definition	Synonyms used in literature
Landscape	A scale- and system-neutral conglomeration of matrices and their transitions, differentiated by land use and type of vegetation (Cadenasso et al., 2003a)	
Matrix	"Spatial domain where processes, properties or magnitudes" of physical, chemical or biological "variables are sufficiently distinct from those of its neighbors to warrant their segregation" (Woo, 2004)	Patch, fragment, ecosystem, biome, habitat (Fagan et al., 2003), exterior, environment, borders, biome ecotone, 'island'
Core matrix	Area in which biotic and abiotic properties do not change significantly over mesoscale (relative homogeneity; depends on research question)	Interior, 'end states' (Peters et al., 2006), core area (Fagan et al., 2003), remnant area, climax state
Transition zone[a]	Spatio-temporal variable entity with functional and structural gradients in between adjacent core matrices	Boundary, edge, corridor, ecotone, ecocline, ecological ecotone, buffer zone, interference zone, hybrid zones, space-segment, (see Hufkens et al. (2009) for an overview of ecocline and ecotone and Kark and van Rensburg (2006) for a history of ecotones)
Solitary matrix	Matrix which – owing to its small size – consists of only a transition zone without a core matrix	Solitary fragment
Zero line[a]	The structural boundary of matrices; a point or line of edge creation and edge maintenance (Murcia, 1995), or land use change and its maintenance ("last unharvested tree trunk" Baker et al. (2016)); static or dynamic	Boundary, edge, barrier, delimitation, interface, border, demarcation line, delineation, borderline
Inflection point[a]	The functional boundary of matrices; defined as the line of maximum gradient in a transition zone	
Magnitude of variables in the transition zones (MTZ)	Physical property of a physical object, state variable, process variable or system which can be quantified (measured)	Magnitude of edge influence (MEI), steepness, intensity, degree, contrast
Transitional gradient (TG)	Vector of physical quantities (e.g. concentration of matter or density of population) in space describing the direction and magnitude of change in physical quantities for every point in a vector field $TG = \frac{\Delta MTZ}{L}$, where L is the distance perpendicular to the zero line	Edge influence (EI) according to Harper et al. (2005), edge effect, interference, transition, causal ecotone, complex gradient, factor-gradient (see Erdős et al. (2011) for a distinction between environmental gradients and community gradients)
Significance in slope (SOS)	Significant difference ($p > 0.05$) of the slope of the transitional gradient compared to the related core matrix in the same matrix	Significance of edge influence (Chen et al., 1995)
Length of significant transitional gradient (LTG)	Linear spatial extent (distance) perpendicular to the zero line where SOS is given	Depth of edge influence (DEI), extent, distance, edge-effect penetration distance
Permeability[a]	Reciprocal rate of space-filling vegetation Vertical: sparse (20–10% to 1% canopy cover), open (70–60 to 20–10%), closed (>70–60%) Horizontal (stratification): open (only tree layer), semi-open (dominant herb layer, less shrub), semi-closed (dominant shrub layer), closed (fully developed stratification)	According to the Land Cover Classification System by FAO (Di Gregorio, 2005)

[a] Further explanations of these definitions are given below.

Wu and David (2002) and a study by Cadenasso et al. (2003a) also named functional units, which can be problematic (see Section 2.2).

2.2. From functional traits to functional gradients in fragmented landscapes

The word *function* has several implications. Jax (Jax, 2005) suggested differentiating between at least four kinds of *functions*: "1) Processes and the causal relations that give rise to them, 2) the role of organisms within an ecological system, 3) overall processes that sustain an ecological system (functioning), and 4) services a system provides for humans and other organisms." We suggest using the following terms to make a precise distinction in *functions*:

Point 1 by Jax (2005) is split into static variables (e.g. energy, population size) and process variables (e.g. heat, work). Static and process variables are thus the functional traits of a certain system. Process variables as such are mathematical functions, which would be another *function*. For quantitative analyses, it is important to differentiate between both, as well as other *functions*.

In point of fact, functional traits are gradients and "symbolize the spatial, functional, or temporal differences of structures or energetic and material units in ecological systems or subsystems" (Müller, 1998). In sum, functional gradients are *based* on functional traits (static and process variables) and are *influenced* by structural traits. A combination of hierarchy theory and a functional and structural nesting leads to a hierarchical "system of gradients" (Müller, 1998).

Functional gradients are measureable and quantifiable, and are therefore a better basis for the understanding of interactions in and the functioning of ecosystems, as well as for evaluations of ecosystem services.

2.3. Quantification of structural and functional nesting in landscapes – the transition zone

In most papers, the line between at least two adjacent types of land or land use (structural traits) with a certain difference has been referred to as the *edge* (Murcia, 1995). However, the term *edge* implies a sharp and defined structure, which in many cases is only an adequate description for structural traits (Kark and van Rensburg, 2006). Cadenasso et al. (2003b) used the term 'ecological boundary', but this tended to describe an ecosystem boundary. In their review, Yarrow and Marín (2007) found boundaries described as two- or three-dimensional with a bordering line (the *real* 'edge'; abrupt change in land cover) and an edge (the patch area; influenced zone). Dialectically, none of the three terms – edge, ecocline and ecotone – are broadly applicable.

In addition, a number of terms in articles on transition zones were used synonymously or were applied without an explicit definition (Erdős et al., 2011). For this reason, we (and others: Hufkens et al., 2009) feel that there is a need to propose a set of terms and definitions related to fragmented landscapes so as to establish a well-founded basis for further research on these increasingly important transition zones (Table 2).

The following table combines ecological features with algebraic and geometric components to summarise existing definitions. This appears to be necessary because most frameworks focused on biotic factors, but neglected the role of microclimatic properties and matter cycling. Moreover, functional and structural traits were often investigated separately (Wu and Loucks, 1995). We believe that the revised definitions we propose in Table 1 are more suitable for quantitative studies and metric assessments.

These definitions and terms represent a basic toolbox for the quantitative description of transition zones in fragmented landscapes. The intention is to establish a relatively straightforward general system of concepts that quantitative ecologists can use; as a result, it will be broadly applicable as well as unambiguous (according to Erdős et al., 2011). The following section depicts a sample area (Fig. 2), introduces a workflow chart (Fig. 3), and explains some parts of the toolbox in greater detail to more clearly describe the terminology.

Transition zones include other concepts, such as 'ecotone', 'ecocline', 'interface', 'edge', 'system of gradients', 'ecological boundary' and 'border' (Cadenasso et al., 2003a; Müller, 1998; Yarrow and Marín, 2007). The biotic transition by Peters et al. (2006) can also be adopted, but without taking matrices as 'end states'. Furthermore, taking transition zones and their gradients as autonomous entities in landscapes emphasises their importance and makes them quantifiable (Müller and Kroll, 2011; Yarrow and Salthe, 2008). As such, they fit into the concept of hierarchy theory as well as the patch dynamics paradigm (Wu and David, 2002). The twofold approach – using structural and functional traits – may help tackle the problems due to the larger number of variables with a lower scale in modelling (Gosz, 1993).

The zero line is a result of a structural distinction of matrices, whereas the inflection point is the result of a functional analysis. In other words: the zero line exists for the detection of boundaries in fieldwork or on maps (visible discontinuity), while the inflection point is a result of measurements and mathematical analysis (Post et al., 2007; see Hufkens et al. (2009) for an overview of methods of detection). This is in line with the idea proposed by Kolasa (2014) for boundary detection recognising: a) "steepness of a gradient and a variable", b) "the amount of contrast between adjacent patterns", and c) "entities as 'owners' of boundaries". This differentiation is necessary to enable an initial, easy and practical solution to be found for structural matrix distinction, while leaving open the possibility to predict the extent and magnitude of transition zones.

Boundaries are "signal processors" (Yarrow and Salthe, 2008). Wiens et al. (1985) describe boundaries as membranes, Naiman and Décamps (1997) compare them with semi-permeable membranes of cells. Their permeability (or their resistance, reciprocally) depends on the characteristics of the patches (structural traits) and of the observed gradients (functional traits) (Gosz, 1992). Out of 52 studies considered to review the spatial extent (length) of gradients in transition zones, 30 used the terms 'open' (26), 'closed' (13) or both to describe structural characteristics. Thirty studies referred to canopy cover, 14 to land use, eight to age of vegetation, and three to history of management. In addition to underlining the need for a common definitional framework, it became the basis for the framework according to the appearance of authors' terms. We therefore decided to use the Land Cover Classification System (Di Gregorio, 2005) to define structural traits for vegetated areas. Horizontal permeability (e.g. horizontally open) is described by vertical stratification of herb, shrub and tree layers and their relative quantities. It affects physical processes that are vectored horizontally, such as wind. The higher the manifestation of stratification (e.g. a fully developed shrub layer and herb layer in addition to trees), the lower the horizontal permeability for a certain distance. For example, a forest with no shrub and herb layer has a higher depth of penetration of wind than a forest with full stratification. This is critical if the kinetic energy of the wind, which has to be processed, is the same, but needs to go a longer distance into the forest to be transformed (Maurer et al., 2013). Vertical permeability (e.g. vertically open) also depends on stratification. The permeability for solar radiation, for example, depends on the development of the stratification: if the tree layer and the shrub layer are fully developed, the herb layer receives less radiation, which affects its biomass or ecological strategy (florescence), for instance. Moreover, the temperature of the soil is mainly driven by radiation and is therefore also influenced by vertical permeability, which influences soil microbial activity (see Sections 3.1.1 *Solar radiation*, 3.2 *Carbon compounds and cycling* and 3.5 *Correlation of matter cycling and microclimate in transition zones*).

To achieve interdisciplinary conformity, we further suggest the following expressions and definitions to enable a comparison of different transition zones: transition zones are four-dimensional with respect to time and their occurrence as three-dimensional physical bodies (Hufkens et al., 2009). They are clearly temporally variable (e.g. Chen et al., 1995; Saunders et al., 1999; Young and Mitchell, 1994). The general term *transition zone* can be specified by prefixes such as *terrestrial*, *aquatic*, and so on. Following Hufkens et al. (2009), Jax (2005), Yarrow and Marín (2007) and , this approach helps to a) include all terms used in the past, b) encourage further development of operational terms, c) satisfy policymakers' needs for one simple term, d) satisfy the need for precision in science by using prefixes and e) bring ecological approaches in line with modelling. Finally, suffixes specify the ecological or local conditions or the reference system itself.

3. Gradients of matter cycling and microclimate in forested transition zones

In addition to soil and hydrology, other key drivers influence processes and conditions of transition zones in forests. These include age, structure, fragment size, distance to next fragment, forest type, weather, climate and latitude. These transition zones are located in the forest, but have an adjacent matrix of different land use or cover. Most measurements were only conducted for gradients into forests – a fact which is reflected by the literature in this section.

The structure of transition zones depends on the age of the vegetation (Camargo and Kapos, 1995; Chabrerie et al., 2013; del

Table 2
Generic classification of transition zones.

Prefix	Second prefix and recommended application	General term	Sample suffixes
Terrestrial	Biotic (according to Peters et al., 2006; e.g. abundance and diversity of fauna and flora) Abiotic (according to Peters et al., 2006; e.g. microclimate, matter dynamics, geology)	Transition zones	Vegetation zones according to Whittaker (1970) • of tropical rainforests • of temperate deciduous forest • of cool-temperate sphagnum bog • of savanna • of temperate grasslands Land use type according to Anderson et al., (1976) • of urban areas • of agricultural land
Aquatic	Biotic (abundance and diversity of fauna and flora) Abiotic (e.g. microclimate, matter dynamics, hydrology)		

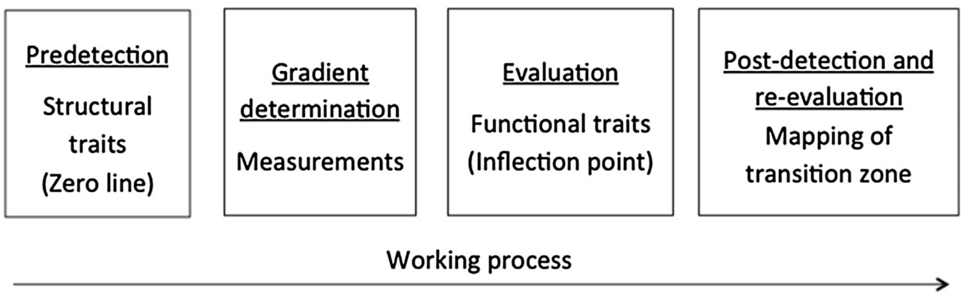

Fig. 3. Workflow chart for mapping transition zones in fragmented landscapes (also works for other approaches such as populations, see Kolasa, 2014).

Castillo, 2015; Matlack, 1993). Successive stages and the degree of maintenance lead to more open or closed transition zones. While aging, gradients weaken (Camargo and Kapos, 1995; D'Angelo et al., 2004; Didham and Lawton, 1999; Wicklein et al., 2012) but may increase when aging proceeds (Laurance, 2004). If they are not maintained, transition zones exhibit higher spatial variability (Saunders et al., 1999). As proposed by Chabrerie et al. (2013), the age of a transition zone can be indexed by comparing old and new maps. Didham and Lawton (1999) found that properties change if the character of the fragment remains the same, but the size of the fragment changes. Moreover, the interconnection of fragments plays a crucial role, as the impacted areas overlap (Porensky and Young, 2013).

3.1. Microclimatic factors

The predominant vegetation (forest type) of a given area has an influence on the spatial extent and magnitude of effects in transition zones. Values for the spatial extent of altered microclimate in transition zones have been found for boreal (Redding et al., 2003), temperate (Chen et al., 1995; Didham and Ewers, 2014; Dovčiak and Brown, 2014) and tropical forests (Hennenberg et al., 2008; Kunert et al., 2015; Patten and Smith-Patten, 2012). The microclimatic patterns established by Young and Mitchell (1994) for more closed transitions differed to those found by Chen et al. (1995) for more open transition zones. Didham and Lawton (1999) found the spatial extent of altered microclimate in transition zones to be two to five times higher at open transition zones compared to closed ones, suggesting the following rank order for the spatial extent of the influence of transition zones: closed continuous < closed fragmented < open continuous < open fragmented forests.

Microclimatic effects were highest on sunny and windy days (Wicklein et al., 2012), so there is a direct dependence on weather, but also on the time of the day (Chen et al., 1995; Davies-Colley et al., 2000; Meyer et al., 2001). Orientation perpendicular to the zero line is reported to be influential in most studies (Cadenasso et al., 1997; Dignan and Bren, 2003; Gehlhausen et al., 2000; Heithecker and Halpern, 2007). In contrast, Voicu and Comeau (2006) found air temperature to be independent of orientation. Furthermore, altitude is reported to have less influence on the magnitude of alteration of microclimate in transition zones (Lippok et al., 2014). This might be in contrast to Wicklein et al. (2012) because wind speed is altered in areas with hills and mountains, which function as obstacles that cause upwind and downward areas.

Obviously, the corresponding latitude of the site also has an impact in terms of climate (Matlack, 1993; Murcia, 1995; Williams-Linera, 1990; Young and Mitchell, 1994). In higher latitudes, seasons influence the magnitude of the effects in transition zones (Chen et al., 1995; Ewers and Banks-Leite, 2013; Kunert et al., 2015; Ritter et al., 2005). In this context, north-facing transition zones in the Southern Hemisphere are comparable to south-facing transition zones in the Northern Hemisphere, which is why Dignan and Bren (2003) deem the expression 'towards the equator' to be more coherent.

3.1.1. Solar radiation

Solar radiation is a key driver of altered microclimates in transition zones. Different wavelength ranges were used in the literature, depending on the research question. Nevertheless, radiation from the most influential spectrum for microclimate (250–3000 nm) decreased rapidly (Fig. 4) within 10–60 m (Chen et al., 1995; Davies-Colley et al., 2000; Young and Mitchell, 1994) and nearly vanished within 100 m (Dignan and Bren, 2003). Denyer et al. (2006) highlighted the fact that different intensities of solar radiation had a shorter penetration distance in transition zones than was the case with temperature. The intensity of solar radiation penetration was also influenced by vertical density of foliage (Mourelle et al., 2001; Parker et al., 2004). In light of this finding, Didham and Ewers (2014) therefore divided the space into bright, transition and dim zones. This enabled them – and Dignan and Bren (2003) – to detect a

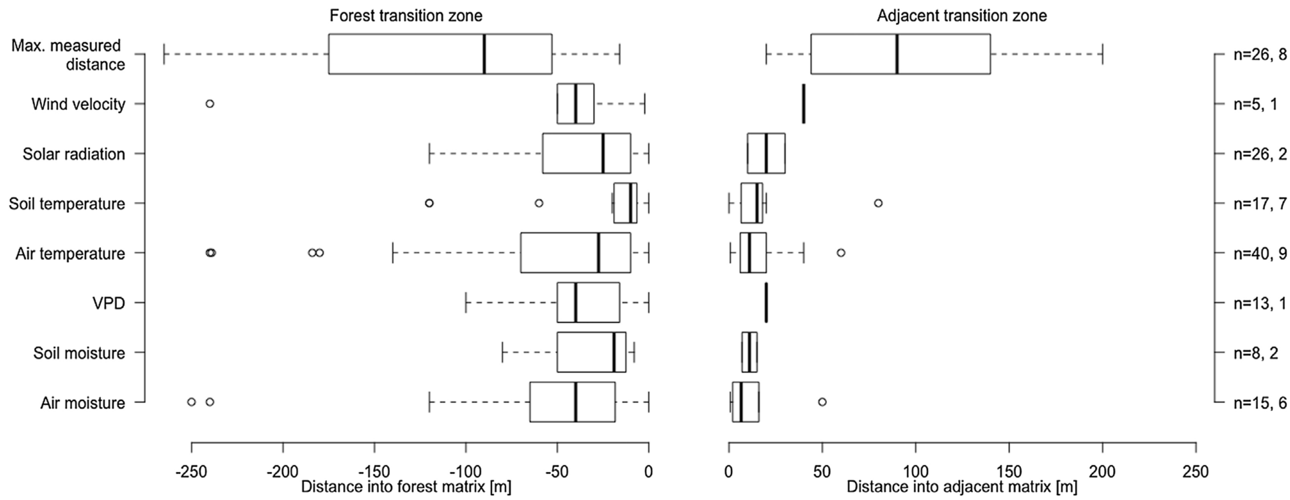

Fig. 4. Quartiles of influence in transition zones from the zero line between adjacent matrix and forest (left), and vice versa (right). Out of 76 studies concerning microclimate, 33 stated a distance. n = number of values reported for forest transition zones and adjacent transition zones. VPD = vapour pressure deficit. The box denotes 25–75% of the values with the median (bold) in it. The dashed bars are areas without outliers (small circles).

vertical gradient. The orientation and canopy height of transition zones also affected the penetrability of solar radiation (Dignan and Bren, 2003). The biggest effects were reported for equator-facing transition zones (Dignan and Bren, 2003).

3.1.2. Wind

Wind velocity was higher in transition zones (Cienciala et al., 2002). It decreased to about 20% of the wind in a non-forested matrix within approximately 60–240 m (Fig. 4), and changed directions (turbulences) (Chen et al., 1995; Davies-Colley et al., 2000; Raynor, 1971).

3.1.3. Temperature

Most authors argued that temperature effects penetrated 50–100 m into the forest (Fig. 4; Heithecker and Halpern, 2007; Meyer et al., 2001; Newmark, 2001), while heat flux was modelled to reach 100–200 m into the forest core matrix (Malcolm, 1998). Air and soil temperatures increased at night and decreased during the day from the zero line to the forest core matrix (Chen et al., 1995). There was also a significant vertical gradient of temperature (Didham and Ewers, 2014). Ritter et al. (2005) suggested that soil temperature is influenced by shading (Wright et al., 2010), higher evaporation and the isolating effects of a lower canopy height. This is in line with the findings by Giambelluca et al. (2003), which suggest that evapotranspiration is greatest when high positive heat flux is induced by high heat advection from clearings.

As air temperature was often lower in forests (Davies-Colley et al., 2000), Ewers and Banks-Leite (2013) argued that tropical forests reduced the surrounding temperature (if the maximum temperature outside the forest increased by 1 °C, temperature inside the forest increased by just 0.38 °C or 0.69 °C for the minimum temperature). Due to a higher heat capacity of forest and soils compared to air, transition zones and forest core matrices typically had a microclimatic lag time compared to non-forested matrices (Ewers and Banks-Leite, 2013).

3.1.4. Humidity and vapour pressure

Humidity increased from the zero line into forest core matrix (Fig. 4; see also Wicklein et al., 2012; Williams-Linera et al., 1998). Dodonov et al. (2013) found the same at some sites, but also a decrease at other sites. Chen et al. (1995), Heithecker and Halpern (2007) and Mendonça et al. (2015) found no significant relationship. A vertical gradient in the vapour pressure deficit was found by Camargo and Kapos (1995) as well as by Didham and Ewers (2014), although its magnitude does not seem to be generalis able, as the figures were contradictory and were measured in different regions of the world. Didham and Ewers (2014) argued that vertical stratification of air layers was disrupted in transition zones.

Compared to forest core matrix, a higher wind velocity in transition zones increased conductivity for heat and gases and therefore, again, transpiration was higher (Cienciala et al., 2002).

3.1.5. Soil moisture

Tree water use was greater in forest transition zones than in forest core matrix (Cienciala et al., 2002; Herbst et al., 2007; Kapos, 1989; Taylor et al., 2001); this is because advection (Giambelluca et al., 2003) and convection (Klaassen et al., 1996) were higher. Gehlhausen et al. (2000) postulated that the spatial extent of soil water showing changes was greater than that of canopy openness in transition zones, which means that wind could also affect soil moisture. Farmilo et al. (2013) found that an increased canopy cover and decreased air temperature were responsible for a higher level of soil moisture in small forest fragments compared to continuous forest, in contrast to the results of Kapos (1989) and Gehlhausen et al. (2000). The reason might be a problem of scale, as the fragments analysed by Farmilo et al. were solitary, having no core matrix (Farmilo et al., 2013). Kapos (1989) determined lower soil matric potential (up to −1.5 MPa) within 20 m of a small patch of rainforest (Fig. 4). Others found the spatial extent of changes in soil moisture in transition zones to be between 20 and 40 m to the zero line (Davies-Colley et al., 2000; Ewers and Banks-Leite, 2013). In winter, more open stands (Mellander et al., 2005) and lee sides of forests (Hiemstra et al., 2006) can facilitate a deeper layer of snow in transition zones. Zakrisson (1987) reported snow accumulation in non-forested transition zones of up to 40 m, with less snow in forested transition zones – up to 15 m. This might lead to changes in soil moisture and soil temperature as well as in carbon and nitrogen dynamics (Groffman et al., 2001). This phenomenon is attributed to possible changes in water uptake and carbon assimilation of trees (Mellander et al., 2005). Otherwise, it is almost impossible to distinguish between measureable parameters leading to a given desiccating microclimate because microclimatic effects in transition zones tend to be cumulative (Godefroid et al., 2006; Laurance et al., 2011).

3.1.6. Spatial extent of altered microclimate in transition zones

In a review for forest microclimate (n = 35), Broadbent et al. (2008) determined a mean distance of alteration in transition zones into the forest core matrix of 191 m and a median of 60 m. Dodonov et al. (2013) recommended considering at least 60 m for transition zones in microclimate for savanna; this is similar to the average of 50 m reported by Hennenberg et al. (2008). Mosquera et al. (2014) recommended considering 10–20 m.

To our knowledge, three-dimensional (vertically and horizontally) studies have only been conducted by Camargo and Kapos (1995), Delgado et al. (2007), Didham and Ewers (2014), Dignan and Bren (2003) and Ewers and Banks-Leite (2013); findings from these studies showed that effects were higher in elevation, suggesting that near-ground measurements underestimate the influence of transition zones.

3.2. Carbon compounds and cycling

In tropical forest transition zones, mature stands of trees are replaced by pioneer trees (Laurance et al., 2006) within 300 m into the interior (Laurance et al., 2000). Dantas de Paula et al. (2016) found a lower tree cover within 50 to 100 m five years after fragmentation. In contrast, Williams-Linera (1990) reported a value of only 15 m. This replacement led to a decrease in biomass (Nascimento and Laurance, 2004), as well as a decrease in above-ground carbon storage (Laurance et al., 2007, 2011), although Ziter et al. (2014) argued that this is not valid for temperate forests. As bigger and older trees die faster after fragmentation (Laurance et al., 2000), they are displaced and replaced by younger trees that have a lower carbon storage capacity (Laurance et al., 2006). In contrast, Voicu and Comeau (2006) found that higher light transmittance was positively related to annual stem increment. Furthermore, Remy et al. (2016) found that stem density, wood volume and C stock of wood are lower towards the forest interior. It is hypothesised that less biomass production is directly connected with less leaf litter production (Farmilo et al., 2013), speeding up organic carbon decomposition (Nascimento and Laurance, 2004). Other than this, Remy et al. (2016) found no differences in C sequestration in transition zones.

Stanton et al. (2013) reported a higher soil total carbon stock in forest transition zones, while Johnson and Wedin (1997) detected a 17% lower soil organic matter content in a transition zone compared to in the core matrix. Remy et al. (2016) also reported a higher below-ground C stock for the transition zone (see Fig. 5).

Decomposition is driven by microorganisms, climate (temperature and moisture) and litter quality (CoÛteaux et al., 1995), and declines with fragment size independent of location in a fragment or the interactions among fragments (Moreno et al., 2014). Decomposition was found to be faster in the forest core matrix than in the transition zone (see Fig. 5). Riutta et al. (2012) ascribed this to higher soil moisture, but see Section 3.3 Soil moisture on that topic. In contrast, neither Rubinstein and Vasconcelos (2005) nor Vasconcelos and Laurance (2005) found any differences. Nevertheless, others even reported distances of the influence of transition zones, as Fig. 5 shows.

3.3. Nitrogen compounds and cycling

Forested transition zones have been described as 'hotspots' for nitrogen deposition and acidification (see Fig. 6) because of local advection, turbulent wind flow and inflow (De Schrijver et al., 2007; Devlaeminck et al., 2005). Atmospheric deposition has been reported to be higher in transition zones (Wuyts et al., 2008) and can reach approximately 100 m into the forest (Ould-Dada et al., 2002). Weathers et al. (2001) measured 50% higher concentrations of ammonium and nitrate in throughfall compared to the core matrix. Ion deposition was three times higher (up to 15 times) in transition zones (Weathers et al., 1995). Stanton et al. (2013) reported higher total soil nitrogen contents for transition zones. Dissolved organic nitrogen leaching was also found to be higher, as well as nitrogen stocks (Wuyts et al., 2011). Remy et al. (2016) detected higher N stocks in the wood as well as in the mineral soil of transition zones. In contrast, Wicklein et al. (2012) argued that transition zones had no significant effect on nitrate and ammonium concentration in soil. Furthermore, Johnson and Wedin (1997) found that mineralised nitrogen in transition zones was one-third of that at the core matrix. Net nitrogen immobilisation and microbial nitrogen were lower in forested transition zones (Toledo-Aceves and García-Oliva, 2007).

3.4. Gradients of matter cycling and microclimate in non-forested transition zones

Although Tuller (1973) maintained that the adjacent matrix to forest is also a zone of transition, only a few researchers have investigated effects for both the forest and the adjacent matrix (e.g. Baker et al., 2014; Davies-Colley et al., 2000; Dodonov et al., 2013). The evaluated literature includes studies on pasture land (Davies-Colley et al., 2000; Didham and Lawton, 1999; Williams-Linera et al., 1998), cropland (Hernandez-Santana et al., 2011; Williams-Linera, 1990), recently harvested forest or clear cuts (Baker et al., 2014; Dovčiak and Brown, 2014; Heithecker and Halpern, 2007; MacDougall and Kellman, 1992; Redding et al., 2003), savanna (Dodonov et al., 2013; Hennenberg et al., 2008) and plantations (Denyer et al., 2006; Farmilo et al., 2013). Studies have also been conducted on linear elements, such as roads, power lines and similar anthropogenic structures (Delgado et al., 2007; Kunert et al., 2015).

In agricultural transition zones with adjacent forest, the matrix is shaded by trees. The shading effect might cause lower rates of evapotranspiration (Laurance et al., 2011) and lower temperatures for both air and soil, which depend on incoming direct radiation (Gray et al., 2002). Voicu and Comeau (2006) found a spatial extent of shading of 0.3 times the height of aspen on adjacent spruce. The magnitude of alteration of microclimate in transition zones decreases as the age of the adjacent regenerating forest increases (Farmilo et al., 2013) and depends on the distance from the adjacent forested matrix, short-term and medium-term time scales, and climatic scales (Baker et al., 2014). Clearings – interpreted here as temporally non-forested to stress initial fragmentation effects – were usually hotter and drier compared to forest core matrix (Laurance et al., 2011), but this only seems to be true for tropical forests. Mixing of air led to lower air temperatures in clear cuts (Chen et al., 1993). The centres of gaps have been reported to have higher soil moisture than the transition zones in adjacent forest, at least initially (Gray et al., 2002). In a temperate forest gap, soil water content reached the level of the adjacent beech forest within two years (Ritter et al., 2005).

For the adjacent matrix (pasture land), lower total carbon stocks in soil and litter have been reported (Stanton et al., 2013; Toledo-Aceves and García-Oliva, 2007), although Farmilo et al. (2013) determined no significant differences. Johnson and Wedin (1997) did not differentiate between quantitative differences, but an altered quality of carbon compounds. These differences are likely to occur because of a lower rooting depth of plants and a lower leaf area index (Laurance et al., 2011), resulting in less leaf litter mass (Farmilo et al., 2013). Stanton et al. (2013) found lower total nitrogen levels in the adjacent matrix, which is in line with Toledo-Aceves and García-Oliva (2007), who reported lower total nitrogen and soil microbial nitrogen levels in pasture land.

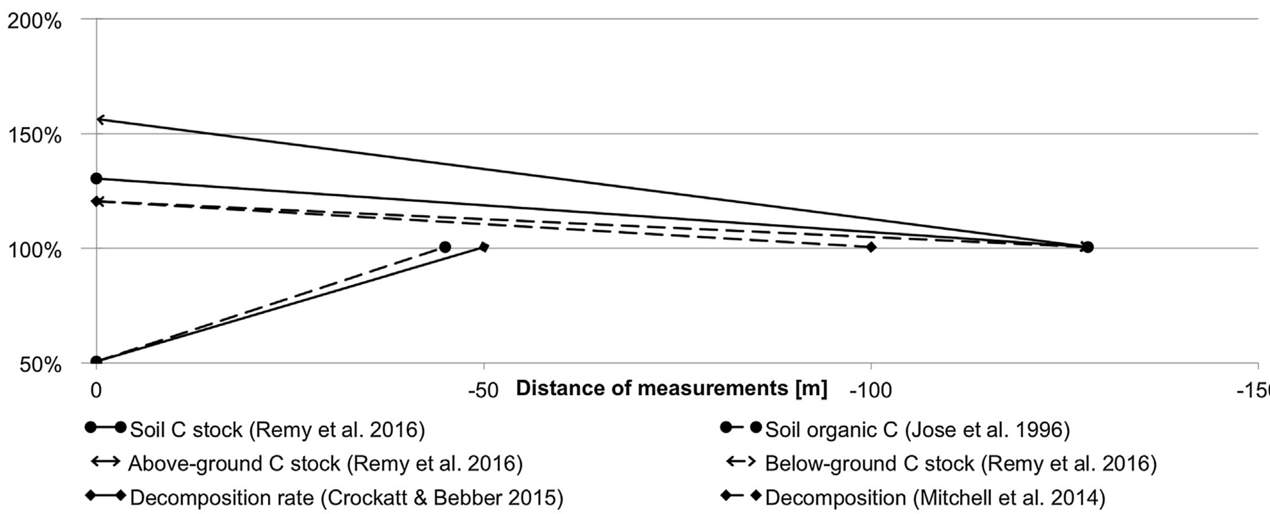

Fig. 5. Relative changes in the amount of carbon compounds and rates of related processes with respect to distance to the zero line (0 m) into forest transition zones.

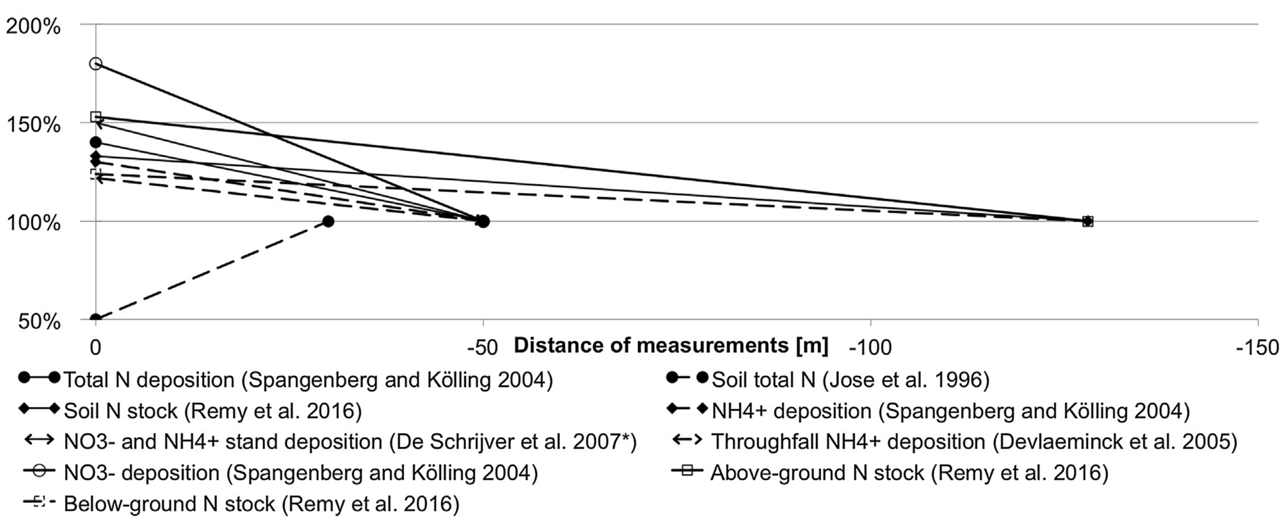

Fig. 6. Relative changes in the amounts of nitrogen compounds in soils in forest transition zones with respect to distance to zero line (0 m). *Median of reviewed articles.

3.5. Correlation of matter cycling and microclimate in transition zones

Both Hastwell and Morris (2013) and Simpson et al. (2012) found a correlation between microclimate and matter cycling in transition zones; Jose et al. (1996) was unable to detect any regularities; and Didham (1998) found no correlation whatsoever. Crockatt and Bebber (2015) reported that altered microclimate in transition zones of forests hampers decomposition. The findings of Riutta et al. (2012) outlined a correlation with soil moisture and temperature as key drivers influencing the metabolism of microorganisms, increased soil erosion and lower productivity (Trnka et al., 2013). As temperature is driven by radiation, Hastwell and Morris (2013) argued that canopy light transmission has a greater influence on litter decomposition than fragmentation-related features. The importance of microorganisms for matter cycling is well known and the correlation with temperature is evident (Moyano et al., 2008). The comparison of Figs. 4–6 does not negate the idea that there might be a general correlation, but it does suggest that there is a site-dependent relationship of matter cycling to microclimate. Furthermore, the *matter cycling* system reacts much more slowly to microclimatic changes. Simple and short measurements that did not find a correlation may be inaccurate as the correspondence is time-shifted. Microclimate, especially radiation with soil moisture as the thermal storage system and temperature as its expression, was correlated with the activity of microorganisms. Hence, conditions for altered matter cycling in transition zones – as radiated areas – change temporally and spatially.

Despite radiation, wind shadows and vertical and turbulent wind dynamics foster the penetration of fertilisers in forest transition zones (Draaijers et al., 1988). Higher nitrogen availability enhanced wood and leaf litter decomposition (Bebber et al., 2011). On the other hand, depending on the orientation of the transition zone, wind can blow out the litter, which leaves less biomass for soil carbon sequestration (Hastwell and Morris, 2013) in the forest stand, but creates an additional input in the adjacent land use system. Thus, it has an effect on soil water storage capacity, and therefore heat storage capacity, which again influences the activity of soil microbial biomass. Transpirational stress increases by one-third in transition zones caused by radiation and wind (Riutta et al., 2014), which may lead to less leaf litter production and therefore less source material for decomposition.

4. Conclusions

It can be gathered from the considerations above that the rapidly increasing total area of forested transition zones (Riitters et al., 2015) may be so relevant that it influences processes at the global scale. Tropical rainforests take up the largest amount of atmospheric carbon over the course of a year, followed by savannas (Beer et al., 2010). At the same time, these are the areas that are most threatened by deforestation and degradation, causing the formation of new transition zones. Fragmenting these highly vulnerable ecosystems – as a form of degradation – will increase the rate of carbon dioxide emissions, and therefore accelerate global warming (Ewers and Banks-Leite, 2013; Haddad et al., 2015). For boreal forests, Baltzer et al. (2014) reported a higher fragmentation caused by thawing, which possibly adds to the emissions. This is a correlating feedback to global warming and affects an even bigger storage of carbon: frozen soils in boreal forests thaw and increase respiration; this releases large amounts of greenhouse gases (Koven et al., 2011). Hence, further fragmentation of landscapes leads to an additional acceleration of global warming. Moreover, the accompanying feedback effects foster fragmentation. Together, climate change and fragmentation decrease actual net carbon sequestration, and thereby endanger one of the most important regulating ecosystem services (Riutta et al., 2012).

The relevance of transition zones is not only justified by their global importance and extent: the current imbalance of research on forested versus non-forested transition zones is reflected in this review. A much larger section addresses forested areas, revealing a noticeable knowledge gap with respect to non-forested transition zones. However, with respect to microclimate, these transition zones in ecosystems also influence each other: higher temperatures in forested transition zones compared to forest core matrices, for example, lower the soil's moisture content, but increase the rate of chemical processes. With respect to organic matter decomposition, these effects act antagonistically, and it is up to simulation models and field observations to determine whether decomposition is slowed down or accelerated at specific locations. The opposite may then occur in the adjacent non-forested area, where the cooling effect of forest on adjacent non-forested areas might reduce evapotranspiration and hence increase soil moisture. This example demonstrates the mutual dependencies of ecosystems' transition zones, and almost suggests addressing them as ecosystems in their own right (according to the definition by Jax, 2006). Improved insights into the complexity of ecosystems' transition zones could emphasise the hot spot character attributed to them – not only in terms of biodiversity: since forest transition zones are often subject to higher deposition by winds and surface water, such as of nitrate (De Schrijver et al., 2007; Devlaeminck et al., 2005), they could serve as an "early warning system" for critical loads (Kark and van Rensburg, 2006).

Modelling ecosystems' transition zones and the effects of fragmentation in landscapes could provide more insights: for example, linking adjacent matrices or landscape elements via the soil water fluxes within and between them may reveal different mechanisms to explain observations, rather than simply comparing the soil water regimes of two ecosystems. The use of plant growth models for different adjacent matrices and their transition zones may change the accuracy of predictive models for large-scale evapotranspiration, which could then refine watershed models for fragmented landscapes (Wright et al., 2012). To facilitate this approach, state-of-the-art remote sensing should be used to image transition zones: for example, the resolution of satellite images of 30 m some years ago was improved to less than 5 m. This now enables transition zones to be detected that are most likely to be smaller than 30 m. The possibilities offered by state-of-the-art computing – for example, the ability to realise non-linear and high-dimensional modelling in a reasonable time – can be used to analyse and upscale information from these combined landscape models with their transition zones to a global level. The theoretical techniques for detecting transition zones already exist: the most common ones are wombling (identifying zones of rapid changes, Fitzpatrick et al., 2010) and moving split windows (see Hufkens et al., 2009 for an overview). Nevertheless, a common framework must be established to enable a comparison of results – this review offers such as framework.

In order to increase our knowledge of ecosystems' transition zones, we evaluated the literature concerning the significance of the values under review: it was not possible to validate the spatial extent of altered conditions of 100 m perpendicular to the zero line, which is suggested (see Section 1 *Introduction*) as being universally applicable. It is most likely that transition zones have spatio-temporal differences and must therefore be adjusted for the research question and the region under investigation. However, they are important and should be considered. Our review of the literature suggests that we can expect altered conditions in soils of transition zones to be 10–20 m with a maximum of 50 m, and 25–50 m with a maximum of 125 m for above-ground space. Nevertheless, further insight is necessary in order to enable us to understand the global influence of fragmented landscapes, especially for non-forested matrices and in terms of ecosystem services to humans (Mitchell et al., 2015). Furthermore, the difference – if any – between natural and anthropogenic transition zones deserves a thorough investigation in this context (Kark and van Rensburg, 2006).

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