

# Landscape connectivity

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## Introduction: movement success and population persistence

The concept of landscape connectivity arose from three interconnected ideas that took root during the 1970s and 1980s. First, populations of many species are distributed across disjunct patches of habitat (den Boer 1968). Second, the persistence of such populations depends not only on reproduction and survival but also on movement of individuals between the patches of habitat (Levins 1969). And third, there are features of landscapes – both natural and human-made – that can help or hinder movements between the patches (Merriam 1984). A landscape with high connectivity is one that facilitates movement of organisms among habitat patches (Taylor et al. 1993). Movement success is thus central to the concept of landscape connectivity.

Organisms move for different reasons: to search for food, mates, or nesting sites, to avoid danger from predators or bad weather, to disperse to new sites, and to make annual migrations. Not all organisms make all of these movement types; for example, plants move only for dispersal. Movements vary from passive (via wind or currents) to active locomotion, and different life stages of a species can move for different reasons and in different ways. For example, in many aquatic insects, immature stages swim, walk, or move via water currents, whereas mature stages fly. Here, we use the term ‘movement’ to refer to any type of movement, for any motivation, by any type of organism, including its gametes or propagules.

Irrespective of the proximate reason for moving, the ultimate reason is to increase individual fitness by increasing reproduction. Not all individual movements are ‘successful’, i.e. not all movements increase fitness. Some even lead to the death of the moving individual, e.g. when passive dispersers such as seeds land in non-habitat or when the moving individual is taken by a predator. Movements not leading to death can also be unsuccessful if, for example, the energy used during movement is not outweighed by energy acquired during foraging movements. In other words, movements entail both benefits and costs. Movement is successful when an individual who moves reaps the benefit of that movement, such that the benefit is higher than the cost, and the individual’s reproductive success is increased. As such, movement success is a per-individual concept.

Although movement success is defined at the level of the individual, it has implications for population persistence (Fahrig 2007). Natural selection works to increase movement success of individuals, and an increase in average movement success across individuals in a population will lead to an increase in population abundance and distribution, and thus, population persistence

(Bowne and Bowers 2004). Species vary in the importance of movement success to population persistence relative to other population processes. For example, for species that depend on ephemeral habitats, such as dung beetles, movement success is a driving factor in population dynamics and population persistence. For species inhabiting more stable habitats, local factors affecting reproduction and mortality may play a larger role in population dynamics than movement success. Therefore, individual movement success and population persistence are linked, but they are not equivalent.

## Movement success and landscape structure

Given the link between movement success and population persistence, and given the ongoing human alteration of landscapes, it is important to know whether there are any general relationships between landscape structure (e.g. forest cover or fragmentation, landscape heterogeneity, edge density, etc.) and movement success. The most obvious landscape alteration is the ongoing conversion of natural covers to human land-uses, such as agriculture and development. The amount of habitat is trivially related to the total number of moving individuals of a given species that is associated with that habitat. More habitat leads to a larger population, which increases the sheer number of individuals moving.

However, opportunities to increase natural habitat as a way of increasing the number of movements (i.e. by increasing the population size and thus, the number of emigrants) are increasingly limited by the growing demand for land area to feed and house the human population. This leads to the question of whether we can increase population persistence by increasing individual movement success by landscape management, such as through the judicious addition of small bits of habitat (e.g. corridors, stepping stones), or by changing other aspects of landscape structure, such as matrix quality or landscape heterogeneity. As noted by Baguette et al. (2013), ‘The *best* way to curb such extinctions would be to increase the carrying capacity ... by increasing either the habitat area or the habitat quality. ... An *alternative* (or complementary) strategy would be to increase the exchange of individuals among local populations, to reduce their functional isolation’ (our italics).

Much of the landscape connectivity literature implies, explicitly or implicitly, that movement success is tightly linked to habitat configuration, on the assumption that movement is highly constrained by habitat, i.e. organisms are reluctant to leave habitat and venture into the matrix (non-habitat), and that organisms will cross only small distances between habitat patches. This assumption has led to the dominant emphasis in connectivity application on habitat corridors, stepping stones, and between-patch distances.

The assumption that movements are constrained by habitat may be valid for organisms that are physiologically restricted to a certain habitat type, such as many aquatic species that simply cannot survive out of water and so cannot cross the aquatic–terrestrial boundary. However, both theory and empirical work suggest that this model of highly constrained movement is much less general than is often assumed (see later). Theory indicates that a species’ movement attributes can evolve such that the risk associated with moving through the matrix is reduced, thus increasing the benefit/cost ratio of such movements. In particular, theory consistently predicts the evolution of straighter, faster movement trajectories through more risky cover types, reducing the time spent there and thereby, increasing movement success (Bartoń et al. 2009, Travis et al. 2012, Martin and Fahrig 2015). If movement cost is reduced by the evolution of straighter, faster movement trajectories in the matrix than in preferred habitat, this increases the benefit/cost ratio of making these movements through the matrix (Martin and Fahrig 2015).

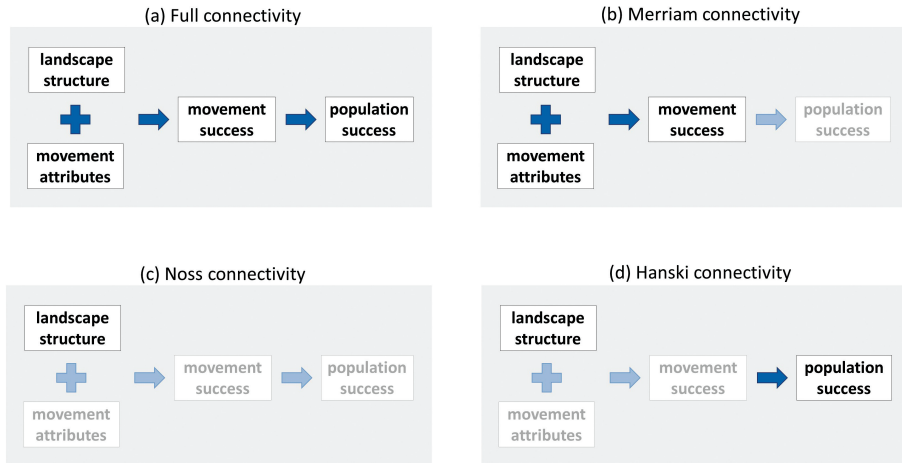
Many empirical studies have challenged the notion that habitat boundaries strongly limit movements (reviews in Harrison 1991, Bowne and Bowers 2004). Animals make frequent movements into and through the matrix, including not only dispersal movements but also seasonal movements and even daily movements (e.g. butterflies – Baguette et al. 2000, Schultz et al. 2012, birds – Fraser and Stutchbury 2004, turtles – Roe et al. 2009, and forest primates – Arroyo-Rodríguez et al. 2017, Galán-Acedo et al. 2019). In a global synthesis, Tucker et al. (2018) showed that movement distances of mammals are actually longer in resource-poor environments. Similarly, wind-dispersed plants move farther across openings than in forests (Nathan et al. 2002), and depending on pollinator behavior, gametes of forest plants can travel faster across open areas than within forests (Kam et al. 2010). Even many habitat specialists can readily cross the habitat boundary into the matrix during regular movements. For example, tracking data on the fisher, a forest-specialist mammal, show that home ranges can contain multiple forest patches with regularly used movement routes between them through cropland, developed open spaces such as golf courses and cemeteries, and pastures (LaPoint et al. 2013). The same is true for some forest small mammals; Bowman and Fahrig (2002) found that chipmunks, a forest specialist, crossed at least 600 m over open spaces between forest patches to return to their home territories following translocation. As predicted by theory, empirically documented movements through the matrix are typically straight and fast in comparison to movements through habitat (Schultz et al. 2012, LaPoint et al. 2013), reducing the amount of time spent in the matrix. Note that the idea that the edges of habitat patches do not represent movement boundaries is consistent with a view of the landscape as a gradient of use or movement rather than discrete patches. This more nuanced view of the landscape has not yet been widely incorporated into the concepts and application of landscape connectivity (see next section), which generally divide the landscape into habitat and matrix.

## Connectivity concepts

There are over 3,000 papers on habitat connectivity. Searches conducted on 14 January 2019, using the search terms ‘landscape connectivity’ OR ‘habitat connectivity’ OR ‘patch connectivity’, returned 3,580 items on Google Scholar and 3,212 items on Web of Knowledge. The initial concept of landscape connectivity (Merriam 1984) was developed to capture the notions discussed earlier: depending on the movement attributes of a species, some landscape patterns will have high benefit/cost ratios of between-patch movements, i.e. high movement success, and therefore, will have high population abundance and population persistence. Such landscapes are said to have high connectivity (Figure 4.1a). However, practical difficulties in estimating connectivity according to this initial concept have led to a divergence in the ways that researchers measure and even conceptualize connectivity (Figure 4.1b–d). Each of these concepts has its uses and limitations. Here, we describe the three main connectivity concepts, in chronological order, and we label them according to their originators: *Merriam connectivity*, *Noss connectivity*, and *Hanski connectivity*. We focus mainly on describing the concepts as they were defined by their originators and as they are generally applied today. We also include some discussion of ongoing modifications to these original concepts.

### *Merriam connectivity: emphasis on movement success*

Merriam (1984) first introduced the concept of landscape connectivity as the interaction between movement attributes and landscape structure that influences between-patch movements and ultimately, population persistence. Merriam specified that connectivity is ‘defined not just by environmental features but also by species behaviour’, i.e. ‘functional connectivity’



**Figure 4.1** Illustration of the full concept of connectivity (a) and three major variants on this concept (b–d). Boxes in dark text represent components that are explicitly included, while boxes in light text represent components that are either ignored or implicitly assumed. We label the three main connectivity concepts for their originators, Gray Merriam, Reed Noss, and Ilkka Hanski, but note that a variety of alterations have been proposed by later authors.

sensu Tischendorf and Fahrig (2000). This initial concept explicitly linked movement success to population size and population persistence (Fahrig et al. 1983, Fahrig and Merriam 1985) (Figure 4.1a). A subtle shift in Merriam connectivity occurred when Merriam and co-authors simplified the definition to ‘the degree to which a landscape facilitates or impedes movement of organisms among resource patches’ (Taylor et al. 1993). Here, the emphasis became limited to movement success, while the link between movement success and population success became implicit (Figure 4.1b).

Empirical estimates of Merriam connectivity focus on estimating individual movement success in response to landscape structure. There are two main approaches to doing this. In the first approach (Figure 4.2a; e.g. Goodwin and Fahrig 2002b, Cline and Hunter 2016, Fletcher et al. 2019), one begins by making detailed field studies to estimate individual movement attributes – boundary-crossing tendency, movement speed and step lengths, movement tortuosity, and mortality during movement – in all possible cover types and boundary types (e.g. Ricketts 2001, Goodwin and Fahrig 2002a, Mueller et al. 2014, Tucker et al. 2018). These movement attributes are then scaled up to infer between-patch movement success in the landscape for a variety of different landscapes that vary systematically in their structures. The results are then summarized into relationships between movement success and metrics of landscape structure (e.g. landscape heterogeneity, edge density, percentages of different cover types, etc.).

In the second approach to estimating Merriam connectivity (Figure 4.2b), between-patch movement success is estimated directly at the landscape scale rather than by scaling up from individual movement attributes. Movement success is measured in many different landscapes, varying widely in landscape structure, and the results are again summarized into relationships between movement success and metrics of landscape structure. In principle, this approach could be followed by conducting mark-recapture experiments in all resource patches in all the landscapes. While in many situations, this would require a sampling effort far greater than would be possible, there are some situations where it may be possible. These include cases where the

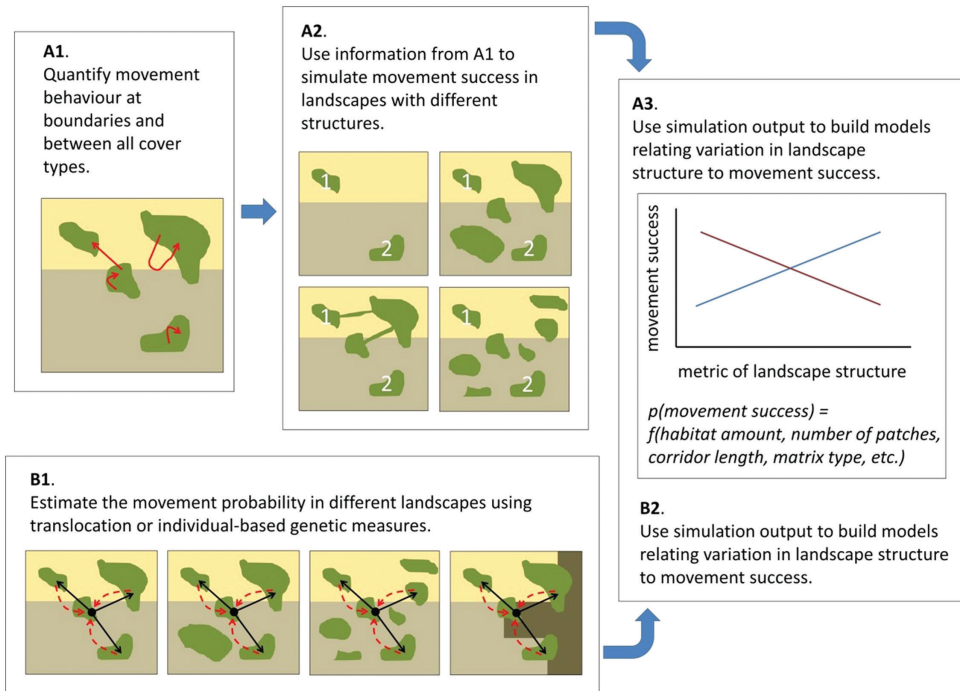


Figure 4.2 Illustration of two methods (A and B) for estimating landscape connectivity as originally defined (see Figure 4.1a).

provenance of very many individuals can be determined over very large areas, as can sometimes occur for genetic tagging (Lamb et al. 2019), parentage analysis of seeds (Aufrett et al. 2017), or stable isotope labels (Herrmann et al. 2016). For example, Flores-Manzanero et al. (2019) related genetic distance to landscape structure variables in order to estimate the determinants of connectivity in a species of small mammals. It may also be possible to estimate movement success across multiple landscapes for large, collared mammals, where huge quantities of movement data can be collected and analyzed over very large regions. Finally, it may be possible in situations where homing animals can be translocated within multiple landscapes with different structures (shown in Figure 4.2b; e.g. Bender and Fahrig 2005, Geoffroy et al. 2019).

We also note that estimating Merriam connectivity may be more feasible for largely one-dimensional systems. In rivers and streams, for example, movements can be in primarily up- and down-stream directions, especially for species that move long distances along channels, such as some fish (salmon, eels, lamprey) and snails (Schneider and Lyons 1993). Estimating movement success in such one-dimensional systems is more straightforward than in two-dimensional systems, because in one-dimensional systems, there is only one possible movement axis, i.e. up and down stream or along the coast. This simplifies the task of identifying landscape elements that help or hinder movement, in comparison to two-dimensional systems, where movements can go in any direction, making the role of landscape features in movement success much more difficult to estimate. Many features can influence movement success along a river, e.g. natural features such as riffles, pools, and waterfalls, and anthropogenic features such as dams, weirs, and road culverts. These features typically span the entire channel width, so the structure of these landscapes can be depicted as a linear sequence of different patch types that may allow or hinder

movement. Movement success of aquatic organisms has been measured directly over short river lengths (Erman 1986, Hayashi and Nakane 1989, Bubb et al. 2004) and across individual structures or patch types (Belford and Gould 1989, Jackson et al. 1999, Lancaster et al. 2011, Thiem et al. 2013, Brooks et al. 2017). Such direct measures may be suitable for estimating movement success in larger landscapes with multiple patches, i.e. whole rivers or watersheds (analogous to Figure 4.2a). The movement success of individuals in rivers with different landscape structures can be estimated also from the densities and life stages of individuals along migration paths (Tamario et al. 2019). Alternatively, movement success could be measured directly for multiple linear landscapes using mark-recapture, genetic tagging, radio telemetry, or radio transponders attached to large-bodied aquatic organisms (analogous to Figure 4.2b). For example, PIT tags (Passive Integrated Transponder devices) are routinely used to monitor movements of individual fish in rivers and often over long distances. Thus, river systems may be more amenable to estimating Merriam connectivity than many two-dimensional terrestrial systems.

### Limitations of Merriam connectivity

While measuring Merriam connectivity is sometimes possible, it is often, perhaps usually, impossible due to the challenges of estimating individual movement success for many species in many cover types. This problem has been noted before. Brooks (2003) stated: ‘Traditional studies of landscape connectivity have attempted to discern individual behavioral responses to landscape features, but this methodology is intractable for many species’. Tischendorf and Fahrig (2000) were even more blunt: ‘The effort required to estimate connectivity empirically likely exceeds any feasible project’. In addition to the difficulty of empirically measuring movement attributes or movement success, Merriam connectivity requires modelling to extrapolate these empirical results to a landscape scale (rightmost panel in Figure 4.2; e.g. Hauenstein et al. 2019). Such extrapolation involves assumptions and errors (Fahrig et al. 2019). Even if it is possible to estimate Merriam connectivity for a few species or in a few environments, deriving cross-species generalities about the relationships between landscape structure and Merriam connectivity is likely close to impossible.

### *Noss connectivity: emphasis on habitat and corridors*

Not long after Merriam (1984) introduced the concept of connectivity, Noss (1987) suggested a different definition: ‘the extent to which patches are connected to one another by similar habitat or corridors’ (Figure 4.1c). Noss connectivity is entirely about landscape structure; no information on animal movement success is necessary here, because animals are assumed to move only or mainly through their preferred habitat. While this may be an appropriate assumption for some species, it appears to be inappropriate for many species, with significant practical consequences (see ‘Limitations of Noss connectivity’ later). However, due to its ease of measurement, Noss connectivity is by far the most commonly used concept of connectivity in applied situations. In its simplest applications, it only requires land cover maps. In species-specific applications, it also requires information about species habitat associations and limited assumptions about the species’ ability to cross gaps in its habitat. Using this information, connectivity tools (see later) are used to prioritize habitat for preservation. Because Noss connectivity assumes that movement is constrained by habitat, large-scale maps of Noss connectivity generally look a lot like habitat maps (e.g. Pelletier et al. 2017).

Others have noted that Noss connectivity is fundamentally different from Merriam’s original concept. Baudry and Merriam (1988) called Noss connectivity ‘connectedness’, noting that it ‘refers to structural links between elements of a landscape’, and differentiating it from Merriam

connectivity, which '[is] a parameter of landscape function', i.e. individual movement success. To avoid confusion with Merriam connectivity, Tischendorf and Fahrig (2000) called Noss connectivity 'structural connectivity' as opposed to Merriam connectivity, which they called 'functional connectivity', again referring to the lack of explicit estimation of individual movement success in Noss connectivity. Finally, Fischer and Lindenmayer (2007) referred to Noss connectivity as 'landscape connectivity' to highlight that it does not consider individual movement success.

It is important to note that the use of Noss connectivity in single-species applications typically involves implicit assumptions about animal movement, i.e. that animals move only or mainly through the habitat and that they can only cross small gaps in habitat. For this reason, it is often assumed that when estimated for a single species, Noss connectivity is a measure of functional connectivity (i.e. Merriam connectivity). This assumption is evident in a review of connectivity applications (Ayram et al. 2016), which concluded that most such studies are about functional connectivity, because these studies refer to particular species. However, these studies are in fact using Noss connectivity, because most of them identify only the distribution of the species habitat and do not include or measure movement or movement success in response to landscape features.

Noss connectivity includes a strong emphasis on corridors. The review by Ayram et al. (2016) found that '[n]early half of the articles explicitly raised the issue of identifying or proposing potential corridors'. In fact, for many researchers and practitioners, connectivity has become essentially synonymous with habitat corridors and therefore, with Noss connectivity. Noss connectivity is not only the most commonly used connectivity concept in applied situations; it is also very prevalent in the scientific literature, on a par with Merriam connectivity. A citations search in Web of Science combining 'Merriam' as author and 'connectivity' as topic resulted in 8 articles, which have been cited 2,084 times, while a search of Noss as author and 'connectivity' as topic resulted in 15 articles, which have been cited 2,224 times.

### Limitations of Noss connectivity

The biggest limitations of Noss connectivity are its inherent assumptions that (i) movements are largely limited to habitat and (ii) when individuals do move through the matrix, their success is lower than when they move through habitat. It is these assumptions that allow estimation of Noss connectivity without measured movement attributes or movement success except for estimation of gap-crossing distances (e.g. Desrochers and Hannon 1997). While these two assumptions are likely valid in some situations, evidence to date suggests that this may not be the norm. Given that Noss connectivity is the primary concept in applied situations, this calls into question the validity of many, if not most, applications of connectivity in conservation planning.

The first assumption inherent in Noss connectivity is that animal movement paths are constrained by habitat; in other words, animals turn back towards habitat when they encounter habitat boundaries. There are several situations in which this appears to be a reasonable assumption. These typically involve a prey species or a microclimate-sensitive species, where the cover type on the other side of the habitat boundary is perceived to lack protection from predators or exposure. For example, Rittenhouse and Semlitsch (2006) found no radio-tagged individuals of a forest-specialist salamander more than a few meters into the adjacent grassland. Several studies have shown that small mammals turn back at boundaries between habitat and roads (Ford and Fahrig 2008, Rico et al. 2007), and Sieving et al. (1996) demonstrated through playbacks that several understory forest birds do not move from temperate rainforests into open matrix. In addition, as mentioned earlier, obligate aquatic species always turn back at the water-land boundary.

However, this behavior, where animals avoid moving from habitat into matrix, may be the exception rather than the rule. Movements of forest-dwelling small mammals are not nearly as constrained by wooded cover (Bowman and Fahrig 2002) as had been assumed by Fahrig and Merriam (1985). The same is true for many large mammals, especially large predators. Based on their studies of individual movement of the fisher, a forest-habitat specialist, LaPoint et al. (2013) advised against using habitat associations to identify corridors, as fishers appear to actually prefer moving through open areas. Vanbianchi et al. (2018) came to a similar conclusion for lynx, another forest specialist, stating that 'maintaining connectivity will require preserving habitats and linkages that would previously have been deemed unsuitable for lynx'. Similarly, Scharf et al. (2018) studied space use by four mammalian predators – black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and wolves (*Canis lupus*) – and concluded: 'We could not find a direct correspondence between corridors chosen and used by wildlife on the one hand, and *a priori* habitat suitability measurements on the other hand ... We suggest future studies to rely more on movement data to directly identify wildlife corridors based on the observed behavior of the animals'. Even the arboreal kinkajou, a tropical forest-specialist mammal, readily moves through farms and pastures during natal and adult dispersal movements: 'farms and pastures did not pose higher resistance to dispersal movements than forests' (Keeley et al. 2017). In other words, for these animals, Noss connectivity does not coincide with animal movements. Worryingly, some large-scale connectivity projects focus on large predators, i.e. species for which Noss connectivity is likely to fail (e.g. 'Yukon to Yellowstone' – grizzly bear; 'Algonquin to Adirondacks' – wolf).

The assumption of habitat-constrained movement is likely inappropriate for other species as well. A global review of primate data indicates movements through various kinds of human-modified covers (Galán-Acedo et al. 2019). Roe et al. (2009) studied turtle movements between wetlands and found that they were completely unrelated to Noss connectivity, stating:

Neither network nor relative connectivity was related to any physical landscape attribute commonly used as a surrogate for actual connectivity,' and 'information [on movement] can potentially yield more important insight on connectivity than measures of landscape structural features alone.

Similarly, for an endangered butterfly, Schultz et al. (2012) found no congruence between habitat distribution and movement, stating: 'The implicit assumption in most other studies is that *a priori* designation of habitat based on physical structure or resources alone will adequately characterize movement.' Noss connectivity may even be inappropriate as an indicator of movement for some plants. Aavik et al. (2014) found no relationship between gene flow and Noss connectivity in a grassland plant. Thus, the assumption of habitat-constrained movement greatly limits the applicability of Noss connectivity. As Cushman et al. (2013) state:

suitability for occupancy and suitability for dispersal may not be driven by the same factors. ... Few studies have formally evaluated the performance of habitat suitability models as surrogates for landscape resistance, but those that have, generally have found them to perform poorly. This highlights the importance of not assuming that habitat relationships optimally reflect the landscape features governing population connectivity.

In general, Noss connectivity is expected to correspond to movement success whenever movement is clearly constrained by habitat. For example, as mentioned earlier, for aquatic species



in linear systems, it is often reasonable to assume that a continuous flow of water along river channels is sufficient to ensure movement. An exception is aquatic species with terrestrial stages that may have very little movement during the aquatic stage (Jackson et al. 1999), and so connectivity may depend on movement of terrestrial stages, which may or may not be constrained by the distribution of terrestrial habitat. Noss connectivity may also correspond to movement success for plant species whose seeds will only germinate in their preferred habitat. For example, Cushman et al. (2014) found a strong relationship between river corridor networks and movement success, as indicated by gene flow, for a species of cottonwood found only in riparian zones. However, for terrestrial animal species, the assumption of habitat-constrained movement is often not met.

Some authors have recognized that the assumption of habitat-constrained movement limits the applicability of Noss connectivity and have made alterations to deal with this. Anadón et al. (2018) studied the separate effects of habitat suitability and connectivity on the spread of ungulates in Spain. They simultaneously estimated a least cost path model along with habitat suitability, thus effectively controlling for habitat availability when estimating the effect of connectivity. McClure et al. (2016) used data from global positioning system (GPS) collared animals to estimate habitat suitability specifically for movement. They then showed that circuit theory and least cost models based on movement-defined habitat suitability (rather than species presence data) performed well in predicting the remainder of the movement data. Similarly, Zeller et al. (2018) showed that resistance maps using species presence data do not correspond to actual movement but that this can be overcome by building resistance maps using actual movement data.

The second inherent assumption in Noss connectivity is that when animals do move through the matrix, their movements are less successful than when they move through the habitat. This is likely true in some situations, e.g. when the matrix cover is particularly deadly, such as a high-traffic road. However, many studies have found that a higher risk in the matrix can be compensated by faster and straighter movements through the matrix, reducing the time spent there for a given distance travelled or equivalently, increasing the distance travelled for a given time spent. This relationship between movement risk per time and movement speed will determine whether movement success is higher through habitat or through matrix and likely explains why some species actually prefer to move through matrix (reviewed earlier). Many species have greater movement speeds and travel longer distances in matrix than in habitat. Nowicki et al. (2014) found a tenfold difference for butterflies. For dragonflies, Chin and Taylor (2009) found that '[l]ong distance movements were more likely, and short-distance movements were less likely, when there were larger amounts of cut matrix between peatlands'. Goodwin and Fahrig (2002b) found that between-patch movements of a beetle were lower in landscapes containing more habitat, because movements were slower in habitat than in matrix. Hass et al. (2018) found that pollinators moved farther along non-vegetated field boundaries than vegetated ones. And Tucker et al. (2019) found that birds move farther in homogeneous than heterogeneous landscapes, likely due to a sparser distribution of resources.

The widespread emphasis on habitat corridors (*sensu* Noss 1987) in conservation planning is particularly worrying if habitat distribution is not a good indicator of animal movement preferences or success. This concern is not new. Franklin (1993) stated: 'While we intuitively expect that corridors are important, their effectiveness has not been proven and there is almost certainly a large proportion of the species for which corridors are not likely to be very useful.' Despite the proliferation of connectivity studies since then, the general conclusion has not changed. Ayram et al. (2016) concluded that 'the empirical validation of corridors is scarce because of the difficulty in obtaining field data with regard to dispersal.' There are counter-examples (e.g. Haddad

and Tewksbury 2005), but the accumulating evidence appears to support the notion that habitat corridors often do not coincide with species movement paths, again calling into question the widespread application of Noss connectivity, at least in its original form. In addition, in discussing corridors, it is important to note that the literature has two distinct meanings of the word. Noss's original definition of 'corridor' was a physical linear strip of habitat connecting patches of habitat. As data have accumulated on actual movement paths of individual organisms, the term 'corridor' has also been used to describe movement routes that are frequently used through the landscape. These movement routes or corridors are often not through the preferred habitat of the species, so this use of the term 'corridor' is very different from Noss's meaning.

Despite the lack of evidence supporting the general application of Noss connectivity, this does not negate the important role of small bits of habitat, including linear strips ('corridors') and small patches ('stepping stones'), for population persistence in human-modified landscapes. For example, this has been shown for reptiles and amphibians (Mendenhall et al. 2014), for plants (Bennett and Arcese 2013, Horskins et al. 2006), and for species richness in general (Wintle et al. 2019). This is because these bits of habitat increase the total amount of habitat in the landscape and therefore, the potential population size of the species in that landscape. This benefit accrues even if these bits of habitat do not increase individual movement success. Protection of all bits of habitat is important for population persistence, irrespective of whether they play a special role in facilitating connectivity (Fahrig 2017).

### *Connectivity tools*

Connectivity tools, as they are currently applied, generally measure Noss connectivity. In their review of applied studies, Ayram et al. (2016) found 23 methods used to measure connectivity. The most common were least cost path analysis, graph theory, and habitat availability from habitat suitability models. They found a striking increase in connectivity studies since 2008, which they linked to software for circuit theory, graph theory, and conservation prioritization. Almost all studies estimated connectivity either directly by habitat suitability or by using habitat suitability as input into connectivity algorithms. Such tools are easy to apply because they only require land cover data; no species movement data are needed except for limited assumptions about species gap-crossing distances.

Least cost path approaches started to be applied in connectivity work after algorithms became available in geographical information system (GIS) software (e.g. Meegan and Maehr 2002). Least cost paths are based on habitat suitability, with the assumption that less suitable habitat is more costly for movement and therefore, movements follow more suitable habitat. An important limitation to this approach is that there is no option to include cases where movement success through unsuitable habitat is high due to faster and straighter movements. As discussed earlier, the assumed equivalency between movement success and habitat suitability is not valid for many species, and so this calls into question the usefulness of least cost path analyses in estimating movement success. The least cost path approach is also problematic because it inherently assumes that the animal has complete knowledge of the landscape between its current location and where it 'wants' to go and that it uses that information to estimate and move along the least costly path. This assumption may be reasonable in some situations, but it is very unlikely to be true for natal dispersal movements, where the animal is moving through novel areas of the landscape. Finally, the parameterization of least cost path models can be problematic; most often, it is based on either expert opinion or habitat suitability modelling, again on the assumption that habitat constrains movement.

Graphs (Fahrig et al. 1983, Lefkovitch and Fahrig 1985, Urban and Keitt 2001) and circuits (McRae et al. 2008) also generally measure Noss connectivity, as applications usually assume that movement between nodes or points is more likely when they are linked by habitat or when they are closer together. For example, the ‘equivalent connected area index’ is built on the ‘probability of connectivity’, which ‘is defined as the probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other’ (Saura et al. 2011, Tarabon et al. 2019). As such, it is similar to the ‘effective mesh size’ of Jaeger (2000). In principle, graphs and circuits could be used to estimate Merriam connectivity if data on boundary responses and individual movement rates through different cover types were incorporated into the graph or circuit structure, but researchers almost always make the same assumptions as are made in least cost path applications, i.e. distance-based and habitat suitability-based movement success. Moilanen (2011) argues that there is currently an over-use or uncritical use of graph-theoretic methods in landscape planning and that their ease of use is resulting in over-confidence in the relevance of the results to conservation. Such over-confidence is particularly problematic because there is a wide array of different metrics for defining connectivity from graphs with different inherent assumptions about movement behavior. These can lead to very different estimates of connectivity (e.g. d’Acampora et al. 2018).

### *Hanski connectivity: emphasis on immigration*

Hanski connectivity emerged from metapopulation theory. In 1994, Hanski introduced a measure,  $S_i$ , which is a user-parameterized negative function of the distances from patch  $i$  to other patches and a positive function of the sizes of those other patches. Hanski did not give  $S_i$  a name in 1994, but later, Moilanen and Hanski (1998) referred to  $S_i$  as ‘isolation (actually connectivity but we use isolation to confer to common practice)’, and then in 1999, Hanski began explicitly referring to  $S_i$  as a metric of connectivity. Originally,  $S_i$  was used to predict patch colonization-extinction dynamics, but its use has broadened to predict species occurrence patterns and patch-level species richness. The spatial scale of the Hanski connectivity function is obtained by fitting the connectivity model with occurrence data (e.g. Ranius et al. 2010). In Hanski’s original function, connectivity was assumed to decrease with between-patch distance according to a negative exponential function. Other functions are possible, and the best function for a given species is assumed to be related to its dispersal biology.

Hanski connectivity has important similarities to and differences from the previous connectivity concepts. Unlike the previous concepts, Hanski connectivity is an attribute of a given focal patch, not a whole landscape; however, a whole landscape measure of Hanski connectivity can be obtained by averaging patch connectivity values across the patches in a landscape. The original Hanski connectivity concept is similar to Noss connectivity and different from Merriam connectivity in that it avoids directly measuring individual movement attributes or individual movement success, and it ignores the effect of matrix quality and spatial pattern on movement success (Howell et al. 2018). However, it is different from Noss connectivity in two important ways. First, it does not consider the particular habitat configurations that dominate the measurement and application of Noss connectivity, namely, corridors and stepping stones. Second, while Noss connectivity simply assumes a relationship between habitat pattern and movement, in the application of Hanski connectivity, this relationship is validated by modelling the relationship between  $S_i$  and patterns of patch occupancy or colonization-extinction events (Figure 4.1d). If there is a strong relationship between  $S_i$  and patch occupancy, one infers that movement is an important, potentially limiting factor for population success. However, it is

important to note that in Hanski’s metapopulation models, connectivity affects patch immigration rate rather than individual movement success. This distinction is important because immigration rate is affected not only by the movement success of individuals but also by the number of individuals that potentially can move, which is affected by population size (Figure 4.3). Note that Calabrese and Fagan’s (2004) ‘potential connectivity’ is conceptually equivalent to Hanski connectivity.

Hanski’s emphasis on distances between the focal patch and other patches rather than on aspects of the matrix that might influence movement success may result from his work with butterflies, where this assumption seems to hold. For example, Moilanen and Hanski (1998) concluded that incorporating matrix type into their Hanski connectivity metric did not improve prediction of patch occupancy by the Glanville fritillary butterfly. Ouin et al. (2008) came to the same conclusion for the meadow brown butterfly, noting that forest cover is the only matrix element that impedes their movement, which is otherwise unaffected by the matrix. The same seems to be true for several other butterflies (Fahrig and Paloheimo 1988, Leidner and Haddad 2010). In regions where forest cover is relatively low, this would lead to generally unconstrained movement across the landscape for butterflies, such that inter-patch movement success is only a function of inter-patch distance, though this would not be the case when the matrix is entirely forest, as in Haddad and Tewksbury (2005).

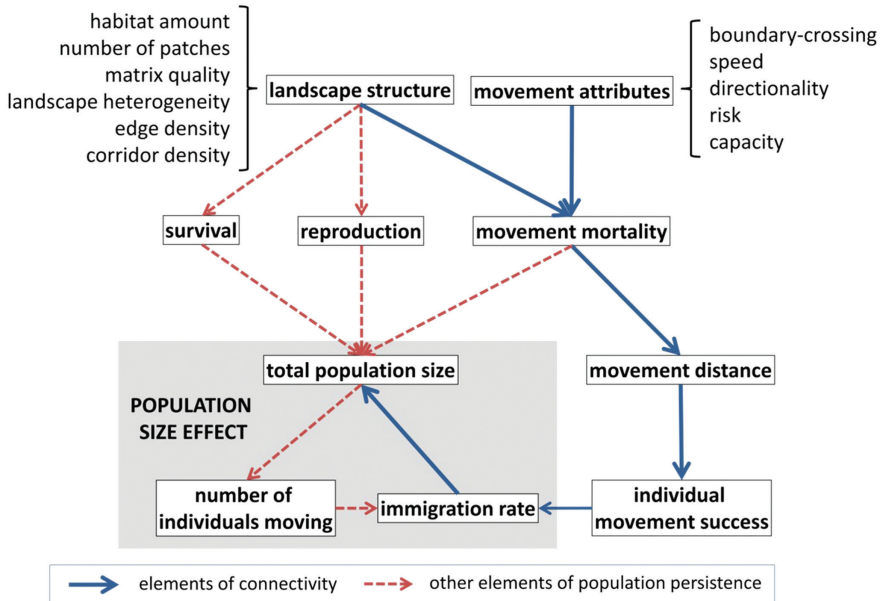


Figure 4.3 The effect of landscape structure on population size (and therefore on population persistence) is only partly determined by connectivity (blue arrows). Landscape structure also affects population size through its effects on reproduction and survival (dashed red arrows). Hanski connectivity estimates patch immigration rate by linking patch isolation to population occurrence or colonization. However, immigration rate is affected not only by movement success but also by population size, which determines the number of emigrants and therefore, the number of potential immigrants to the patch – the population size effect. Therefore, Hanski connectivity combines effects of landscape structure on movement, reproduction, and survival.

## Limitations of Hanski connectivity

Hanski intended his measure of connectivity as an estimate of patch immigration rate, not as a measure of movement success. This creates challenges when trying to understand the role of movement success using Hanski connectivity, because Hanski connectivity inherently confounds movement success with population parameters, i.e. reproduction and survival. This is because patch immigration rate is determined not only by individual movement success but also by population size, which is itself influenced by reproductive success and survival, and reproductive success and survival are also affected by landscape structure (Figure 4.3).

In fact, it is possible to find a strong relationship between Hanski connectivity and population success (occurrence/colonization) even in situations where there is no actual relationship between movement success and Hanski connectivity. To see this, note that measures of Hanski connectivity are strongly correlated with (even redundant with) the amount of habitat surrounding the patch (Moilanen and Nieminen 2002, Bender et al. 2003, Tischendorf et al. 2003, Prugh 2009, Fahrig 2013). This is because the closer other patches are to patch  $i$  and the larger those other patches are (i.e. the higher the Hanski connectivity), the more habitat there is near to patch  $i$  (see figure 7 in Fahrig 2003). This means that Hanski connectivity is strongly related to the total number of potential immigrants to patch  $i$  (more surrounding habitat = higher population = more potential immigrants). The more potential immigrants there are, the more likely they are to land on patch  $i$  by chance, irrespective of individual movement success. Thus, Hanski connectivity confounds movement success with a population size effect (Figure 4.3). To avoid this confounding, Dufflot et al. (2018) included both amount of habitat in the landscape and Hanski connectivity in models predicting the abundance and richness of grassland species. They found no effect of connectivity once habitat amount was accounted for. As Hanski connectivity predicts the immigration rate to a patch and not individual movement success, some authors do not consider Hanski connectivity to be a measure of landscape connectivity, e.g. Tischendorf and Fahrig (2000): ‘Any measure of connectivity must be based on movement of an organism through a landscape. ... demographic indicators, such as species abundance and distribution, while potentially related to connectivity, are not measures of connectivity.’

A second limitation of Hanski connectivity, at least in its original formulation, is that it ignores the effect of matrix pattern and focuses only on inter-patch distances and sizes of patches. While often appropriate for butterflies, this is likely not appropriate for most species. Gilbert and Levine (2013) included a term for matrix quality in a Hanski connectivity model, but the change in quality was applied to the whole matrix uniformly; they did not include spatial variation in the matrix that might influence movement paths. Bender and Fahrig (2005) showed that spatial variation in matrix pattern can greatly obscure or even eliminate the relationship between individual movement success and connectivity measures that are based on patch size and isolation. Note, however, that more recent versions of Hanski connectivity do allow spatial variation in matrix quality. For example, Howell et al. (2018) incorporated least cost path modelling into the estimates of colonization probability in a metapopulation model, and Kärvmö et al. (2016) included variation in matrix quality using multiple Hanski connectivity estimates based on distances not only to habitat but also to matrix covers.

## Aquatic systems: cross-ecosystem contrasts

As an observation (not a criticism), we note that movement and connectivity within marine and freshwater systems seldom feature in the landscape ecology literature, and vice versa. Nevertheless, contrasting systems in the same theoretical framework can sometimes yield fruitful

or unexpected insights. For example, logistical difficulties in one system may be absent in others, and indeed, earlier, we suggest that measuring Merriam connectivity may be relatively straightforward in largely one-dimensional systems such as rivers.

In fact, there is a rich literature from marine systems that aligns closely with the original concept of landscape connectivity (Figure 4.1a). This research focuses on organisms with complex life cycles in which juveniles and adults occupy quite different and often distant habitat patches in naturally fragmented seascapes. Such organisms include barnacles and mussels, with pelagic larvae that live in the open ocean and sessile adults that inhabit rocky shores, and reef fish that also have pelagic larvae while adults are sedentary around reefs. Thus, larvae inhabit and disperse through the matrix that connects patches of sessile adults. Although some self-recruitment does occur (Jones et al. 1999), larval movement from outside the local area is required to sustain many populations; the notion that movement success influences demographic rates of the local population(s) is implicit in these systems (Cowen and Sponaugle 2009) and often assessed directly (Carson et al. 2011).

Although it is virtually impossible to follow movements of individual larvae, geochemical signatures (Levin 2006, Thorrold et al. 2007) can determine the probability that larvae from a particular source population will disperse to different patches of adult habitat within a landscape. Such data can be used to construct a ‘connectivity matrix,’ which describes the probability of movement between source and settlement nodes (Cowen et al. 2006), analogous to the approach suggested in Figure 4.2 b1. It is conceivable that metrics of movement success can be derived from such matrices. However, describing the physical structure of these marine landscapes is unlikely to be straightforward and is difficult to capture by a simple metric (Figure 4.2 a3). Larval dispersal is not determined simply by the distance between adult patches (cf. Hanski’s butterflies), because dispersal distance and direction are strongly contingent upon water currents (Connolly et al. 2001), which are themselves influenced by complex interactions between coastal topography, wind, tidal forces, surface waves, and water stratification. Although models can describe the ocean currents that create transport corridors and influence the dispersal of marine larvae (Werner et al. 2007), deriving a metric of landscape structure or ranking different landscapes with respect to structural complexity has challenges. However, heterogeneity, anisotropy, and advective transport (e.g. wind- and current-assisted movement) are common to other ecosystems, and this is an active area of research (Vandermeer and Carvajal 2001, Shima et al. 2010).

### **SAMC: a hybrid approach**

Recently, Fletcher et al. (2019) proposed a new approach for estimating landscape connectivity. Like circuit theory, their Markov chain-based method (‘SAMC’) is based on resistance maps. However, the SAMC approach incorporates two important additional elements. First, it decomposes landscape resistance into its two components – resistance due to behavioral avoidance of a cover type, and resistance due to mortality of individuals that do enter the cover type. This is particularly important because land cover types with high resistance to movement via behavioral avoidance can in some cases also have low mortality risk (Fletcher et al. 2019). This means that there can be a trade-off between dispersal mortality and avoidance of a given cover type when estimating connectivity. The second important element included in SAMC is that it can incorporate the initial distribution of the population, thus partly accounting for the effect of population size on the number of emigrants and therefore, on immigration.

Conceptually, SAMC is a hybrid approach. Its underlying structure is related to the circuit theory approach to estimating Noss connectivity, as it is based on resistance maps. However, by separating behavioral resistance from mortality resistance, SAMC becomes much more similar to Merriam connectivity. If different cover types can have low behavioral resistance but high mortality resistance, or vice versa, and if this affects the inferred connectivity, the application of SAMC requires detailed species-specific information about animal movement behavior and movement risk across all cover types in the landscape, just as is required for Merriam connectivity. By incorporating the initial distribution of individuals into the estimated movement probabilities, SAMC also becomes related to Hanski connectivity, because it estimates immigration rate, at least over the short term, as in Hanski connectivity. Note, however, that SAMC is not a full demographic model, as it does not include reproduction, and so it only partly includes the population size effect that is implicit in Hanski connectivity (Figure 4.3). Thus, at least in principle, SAMC is an amalgam of aspects of the three connectivity concepts. However, in practice, SAMC relies on the collection of detailed, species-specific information on population distribution and on movement and mortality in all cover types in a landscape. This may make it as data-hungry as a realistic individual-based simulation model of animal movement (e.g. Hauenstein et al. 2019, Trapp et al. 2019). It thus remains to be seen whether the introduction of SAMC will encourage collection of those data or whether in practice, most applications of connectivity will continue to use the basic Noss connectivity concept, where movement success is assumed to be determined by habitat distribution.

## Implications for conservation and future research

Given the large differences among the three major concepts of connectivity, and their various alterations and combinations, it is confusing to both the practitioner and the researcher that they all have the same label. Our main conclusion is that practitioners and researchers should be aware that 'connectivity' is not a single thing but rather, a wide range of concepts that differ in important ways. It is important to be cognizant of which concept (or modified concept) one is using and its aims, assumptions, and appropriate uses. Although Taylor et al. (2006) argued that we should return to the original definition of connectivity, i.e. Merriam connectivity, given that all three concepts are in wide and varied use under the same name, we suggest that this is no longer a realistic goal.

Given the limitations surrounding all three concepts of landscape connectivity, there are clearly many areas needing further research. Noss connectivity and Hanski connectivity are the simplest to apply, because movement success is assumed to be constrained by habitat in the former, and immigration rate is assumed to be determined by patch isolation in the latter. In principle, both of these can be measured using only knowledge of habitat and species distribution and possibly an estimate of the species' gap-crossing ability. In contrast, Merriam connectivity requires information about how the species responds to all cover types in the landscape or its movement success in different landscapes. Research is needed to identify the situations in which the different concepts of connectivity are meaningful and can be applied.

In the applied world, Noss connectivity is ruling the day with the application of least cost path analysis, graph theory, and circuit theory. What are the implications of this for conservation? Conservation policies that increase Noss connectivity by applying habitat-based connectivity metrics for land planning will increase habitat conservation because the dominant assumption in Noss connectivity is that habitat = connectivity. This is usually a good outcome for species conservation, because habitat loss is probably the main threat to species conservation.

However, if the assumptions inherent in Noss connectivity do not apply in a particular situation, this can lead to less-than-optimal and constrained land planning decisions for conservation.

The use of Noss connectivity constrains the prioritization and selection of habitats for preservation/restoration to those that have been identified as important in a connectivity analysis. This limits options and increases cost. For example, Beier and Noss (1998) argued that evidence of animal movements in corridors is the same as evidence that corridors are important for conservation. This is a leap in logic that effectively undervalues the protection of habitat that is not in a habitat corridor (Keeley et al. 2017). The benefit of corridors for conservation needs to be demonstrated and not simply assumed. Second, Noss connectivity is used as a reason to limit conservation to contiguous habitat and to offer little or no protection to small patches of habitat even when they are numerous. This prioritization of large, contiguous habitat areas is not supported by evidence (Fahrig 2017, Wintle et al. 2019). Third, the dominant focus on habitat means that there is too little attention placed on matrix quality and pattern. This is problematic for conservation because many species appear to move preferentially through the matrix (see examples earlier).

The assumed strong linkage between movement and population success that underlies conservation decisions based on connectivity is also risky for conservation in some situations. For example, wildlife overpasses and underpasses have become common approaches to mitigate the impacts of roads on wildlife populations, based on the assumption that the movement barrier effect of roads is critical. However, if the mortality effect of roads on population persistence is larger than the barrier effect, then the emphasis should be on measures that keep animals off roads rather than measures to facilitate movement across them (Teixeira et al. 2020). In general, research is needed to identify the relative importance of barriers to movement versus other landscape impacts for population persistence. For example, fencing likely has large effects on connectivity for many large animals (Jakes et al. 2018), but there is little research that would allow us to understand the situations in which this has, versus does not have, a net negative impact on population persistence. Current connectivity research ignores the fact that the effect of the landscape on population success is not only, or even mostly, determined by movement success (Figure 4.3), because landscape structure influences other processes, e.g. species interactions, that also affect reproduction and mortality.

On the other hand, a benefit of Noss connectivity and Hanski connectivity over Merriam connectivity is that they can be measured with reference only to habitat distribution and without reference to a particular species. Connectivity metrics are assumed to apply to all species associated with a particular habitat type. This is very helpful in the context of landscape management. It avoids the dilemma in applying Merriam connectivity, namely, that connectivity is highly species-specific while land management must be cross-species. To get around this problem, Cushman et al. (2013) suggest selecting a set of umbrella species, doing a Merriam connectivity estimate for each one (Figure 4.1), and combining the results into a cross-species connectivity map. However, research is needed to determine whether this approach can work, as even closely related species can have very different responses to landscape structure (Henry et al. 2019). In addition, it may be difficult to simultaneously maximize connectivity for desirable species without increasing the spread of undesirable or exotic species and without increasing biotic homogenization (Olden and Rooney 2006).

All this begs the question of whether connectivity is an effective paradigm for land management aimed at species conservation. Is there a more practical approach that does not require species-level information about movement success? For example, Gagné et al. (2015) suggest an alternative approach that does not explicitly consider connectivity but rather, involves a prioritized sequence of decisions to maximize conservation of natural habitats, maximize the diversity of natural habitats, minimize impacts on fresh water systems, and minimize the marginal impacts of new human activities. In the meantime, in situations where connectivity metrics are



used to make land management decisions, we recommend that researchers and practitioners be aware of the particular concept of connectivity within which they are working (Figure 4.1) and especially of its assumptions and limitations. Before a particular approach is applied, evidence should be provided demonstrating that the selected approach is actually appropriate in the particular situation.

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