# Assessing Kettle Holes Habitat Connectivity

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Kettle holes are hotspots of biodiversity that provide suitable conditions for wildlife species (i.e., amphibians, insects, aquatic plants) and contribute to landscape heterogeneity. They are also considered to function as stepping stone habitats that contribute to habitat connectivity.

Keywords: pothole ; wetland ; functional connectivity ; stepping stone biotope ; ecosystem service

## 1. Introduction

The area of kettle holes is usually smaller than 0.01 ha; however, it can also reach sizes of up to 3–15 ha [1]. These pond-like depressions (i.e., kettle holes) in young moraine landscapes [2] formed 10,000–12,000 years ago in the Pleistocene [3]. They are mainly located in agricultural areas [1] and are characterized by strong wet–dry cycles [4]. Some are filled with water throughout the year and potentially flood the surrounding areas during wet periods; others are drying up completely for extended periods of time. The habitat heterogeneity hypothesis states that habitats with small sizes but high intrinsic heterogeneity correspond to a wider range of niches and species [5]. Not only does the ecological role of kettle holes support this hypothesis, but kettle holes are also considered to be keystone structures [6] that determine plant and animal species diversity by their presence.

The intensification of agriculture during the last few decades has caused the loss, degradation, and fragmentation of habitats, which all pose a major threat to the survival of populations and species communities [7][8]. In particular, the loss of wetlands has led to a reduction in the supply of specific ecosystem services, with negative consequences for the multifunctionality of agricultural landscapes [9]. According to Fahrig [10], habitat fragmentation is characterized by a decrease in the total amount of habitat and sizes of habitat patches, as well as by an increase in the number of habitat patches and patch isolation. For species such as amphibians that populate isolated habitats in highly diverse agricultural landscapes, the properties of ecological systems (e.g., habitat connectivity) are more likely to affect species diversity, abundance, and composition than habitat size [11]. As amphibians are characterized by the highest rates of overall endangered species worldwide (41%) [12], they should be considered a focal organism group for biodiversity conservation in agricultural landscapes that are able to provide suitable habitats. Moreover, measures for improving habitat connectivity and foraging opportunities, as well as for reducing disturbance intensity in agricultural landscapes, are of high relevance for preserving populations in isolated amphibian habitats [13]. According to Hamm and Drossel [14], sufficient connectivity and dispersal allows for more species to coexist in a heterogeneous environment than in a homogeneous system. Increasing connectivity, both structural and functional, has gained importance as a strategy for biodiversity conservation [15]. The structural habitat connectivity represents the physical relationship between landscape elements, whereas the functional connectivity represents the degree to which the landscape facilitates or impedes the movement of organisms and matter between natural resource fields [15][16][17]. Multiple tools exist to assess the connectivity or fragmentation of natural habitats [16], such as graph theory [18], circuit theory [19], or modeling of potential organism movements [20].

Kettle holes support biodiversity in agricultural landscapes in two ways: (1) by providing valuable habitats and (2) by acting as stepping stone biotopes, connecting other wetland habitats and enabling genetic exchange [1]. In this way, kettle holes complement the habitat provision by other aquatic or semi-aquatic habitats, as well as the connecting role of other corridor habitats. While this dual role of kettle holes is well-recognized in academia, society, and environmental legislations [1], to the best of our knowledge, no attempt has yet been made to quantify the contributions of kettle holes to habitat provision and habitat connectivity, which both are regulation and maintenance ecosystem services.

# 2. Kettle Holes and Connectivity

## 2.1. Amphibians and Functional Connectivity

Amphibian community structure is strongly related to habitat features and habitat connectivity [21]. Therefore, habitat loss and fragmentation are among the largest threats to amphibian populations [13][22]. If the current trends of landscape homogenization continue, it is likely that only mobile and opportunistic species will be able to persist. In order to understand population- and species-level implications, it is necessary to shift from site-specific analyses to assessments at the landscape scale. For example, in an empirical movement study in Northern France, the dispersal of amphibians was strongly influenced by the loss of grassland habitats that served as priority movement corridors [23]. A better understanding of amphibian movement ecology is a missing component for counteracting population declines [24].

## 2.2. Methods for Measuring Functional Connectivity

Several other methods exist for assessing functional connectivity in complex landscapes. Least-Cost Path (LCP) analysis (e.g., [25][26]), Circuit Theory (CT) (e.g., [27]), and Graph Theory (GT) (e.g., [28]) are among the most common ones. Both LCP and CT are based on assigning each habitat type a so-called "resistance value", representing the difficulty or danger associated for a target species with traveling through it. The distance traveled through a habitat is multiplied by its resistance value, and the sum of all weighted segments of a path is recorded in LCP. GIS-based optimization is then used to identify the pathways between habitats that have the lowest cost. Instead of identifying the optimal pathway, CT assesses multiple pathways in parallel. Just as the strength of electrical flow through a heterogeneous surface will depend on the resistance values of the respective locations, the intensity of movement of organisms through a landscape is considered to be determined by the habitat's resistance value. LCP and CT analyses are powerful tools to predict the locations of movement corridors and to assess the relative importance of patches and landscape connectivity patterns. Using both methods together has been suggested as a comprehensive approach for corridor identification [29]. Such an identification of movement corridors is well suited for animals moving in herds or creating tracks. Individuals may explore to determine the optimal route, which other animals follow. However, the approach may be less fitting for amphibians who move individually. Under real-life conditions, amphibians cannot recognize the shortest route but will appropriate habitats such as kettle holes if they are within their movement range.

GT uses an abstracted model of the landscape where the habitats relevant for a species are interpreted as "nodes". These nodes are either isolated or connected by "edges" (vertices) to their nearest neighbor. Whether or not a connection exists depends on the movement range of the target species and may be based either on Euclidean distances or, as in LCP or CT, resistance values for different habitats (e.g., [30]). Connectivity is assessed based on the resulting network or networks, particularly by considering the number of connected nodes. Compared to our method, GT has the advantage of directly showing which habitats are connected, but it does not show by what route they are connected, i.e., what areas may be traversed. Our clustering approach, on the other hand, gives detailed information on the areas through which movement may occur.

Approaches based on assigning resistance values to all habitat types require detailed knowledge of species behavior and critical threshold values, which is not always available. Ideally, resistance values should account for obstacles (roads, settlements, etc.) and site-level environmental inputs (i.e., relief classes, topography) insofar as they affect the movement of the species [31]. In this regard, our method constitutes a simplified approach with a binary weighing system. We set the resistance value for reproduction habitats, kettle holes, and corridor habitats to zero, while all other habitats received a resistance value of one. Unlike LCP or CT, our method resets the travel cost once an individual reaches one of the zero-resistance habitats. This reflects amphibian habitat requirements, as amphibians can live and forage indefinitely in these habitats and require open water bodies only for their reproduction. Our method provides an overview of connectivity with modest requirements for species data, expertise in landscape ecology, or computing. One of the strengths of this approach lies in its flexibility. It can readily be transferred to other species and landscapes as long as habitat needs and species ranges are adapted accordingly. Identifying areas suitable for improving connectivity is another strength of the approach since this task is far more complex with alternative methods. Where more precise calculations are required, our method can be modified to account for obstacles to movement, such as roads, wide rivers, or steep slopes, or to limit the distance that animals can travel through corridor habitats. A digital elevation model should be included in areas where the terrain is very uneven, such as mountainous regions. However, all this would come at the price of higher data and computing requirements. For this study, the precision of the current approach was considered sufficient.

## 2.3. Contribution of Kettle Holes to Habitat Provision and Habitat Connectivity

The dataset we used only includes kettle holes that are classified as perennial water bodies. Therefore, our calculations could not account for the contribution of kettle holes that are filled with water in some years but dry in others (ephemeral kettle holes), and our results should thus be interpreted as a conservative estimate.

### *2.3.1. Habitat Provision*

Within our research areas, kettle holes play a highly important role for habitat provision. Their small average size is compensated by their high number. Furthermore, a small size also indicates a high shoreline to water ratio, which is favorable for amphibians. Overall, the contribution of kettle holes in our research areas is on par with, or even exceeds, that of other reproduction habitats, such as lakes or reed beds.

However, it is important to note that their smaller relative size also makes them more susceptible to pollution or drying up, which reduces their ability to provide reproduction habitats for amphibians. In many regions, climate change is likely to increase the frequency and duration of this drying up, potentially resulting in a permanent loss of some kettle holes [1]. Perennial kettle holes may become ephemeral. Accordingly, in a study on 75 kettle holes in Märkisch-Oderland, Hoffmann et al. [32] found that most of the kettle holes classified as perennial in 1993 had to be classified as temporarily water-filled in a very dry year (2020).

### *2.3.2. Habitat Connectivity*

We found that the current state of functional connectivity depended strongly on species' range. While for the short-range species garlic toad the landscape presented itself as highly fragmented, for the long-range species European green toad all reproduction habitats were part of a single cluster. The effect of range dependency of connectivity is well known and has already been discussed in earlier studies, such as the one by Bunn et al. [18]. However, we found that also the relative importance of kettle holes for habitat connectivity depends on a species' range. For the short-range species, kettle holes were by far less important for functional connectivity than corridor habitats, which are more numerous and have a larger total area. For the long-range species, kettle holes were able to function as connectors of wetland habitats. Even in the scenario where corridor habitats were removed, the total number of clusters was two or lower in all research areas. The contributions of kettle holes and corridor habitats to the functional connectivity of the long-range species were mostly redundant. This redundancy can be interpreted as a safeguard against future fragmentation, as the loss of individual habitats (kettle holes or corridor habitats) would not automatically reduce functional connectivity.

We were able to show how our clustering approach can be applied to identify areas where the creation of stepping stone habitats would connect clusters and thereby improve functional connectivity. However, it is important to note that locations need to fulfill multiple requirements in order to be suitable for the creation of artificial stepping stone habitats. While our approach can help to focus the investigation for possible sites, it must be complemented by further local assessments.

### 2.3.3. Ecosystem Services

While kettle holes provide multiple ecosystem services, a review by Vasić et al. [1] shows that the service most often addressed in journal articles is their supply of nursery populations and habitats. This service also includes the protection of gene pools. However, the positive contributions of kettle holes are frequently overlooked by farmers, since small wetlands are often considered problematic in terms of agricultural productivity [33][34]. Negative effects of crop management on farmland biodiversity have been noted, as farmland intensification has led to a severe decline in the diversity of amphibians in the vicinity of kettle holes [13].

The supply of habitats for amphibians provided by kettle holes is determined by water availability and by wet and dry cycles. Therefore, any disturbances that affect water availability or lead to longer dry cycles may endanger the supply of this ecosystem service. Conversely, improving functional connectivity may support its supply.

## 2.4. Climate Change in Relation to Habitat Provision and Connectivity by Kettle Holes

Amphibians are extremely sensitive to climate change, mostly because of their low mobility and strict physiological constraints [35][36]. Habitat loss and fragmentation combined with recent climate change have endangered many amphibian species [22][35][37], while various studies predict further huge habitat losses under climate projections [38][39]. Additionally, future climate changes connected to warming and an increase in the intensity and duration of drought periods may have strong negative impacts for amphibians through creating less suitable environmental conditions [35][40].

Therefore, conservation needs to include climate change adaptation. The connectivity of suitable habitat for species migration and dispersal is critical for successful adaptation to climate change through shifting species range boundaries [41][42]. This is consistent with findings by Hodgson et al. [43], who state that increasing connectivity through increasing habitats should be the most recommended option for conservation in the face of climate change. Furthermore, Heller and Zavaleta [44] highlight maintaining connectivity as an important strategy for conserving species diversity in a changing climate. Consequently, it is important to focus on habitats that create a diversity of microclimates (such as kettle holes), as they can buffer the effects of climate change, giving species more possibilities and time to adapt to the changing climate [45][46].

Considering the effects of climate change, the size and depth of kettle holes are likely to play a significant role. Kettle holes with a smaller surface will probably dry out sooner than those with a larger surface and longer dry cycles [3]. This further indicates the importance of kettle holes with a larger area, as they will be able to provide favorable habitat conditions for a longer time. In this regard, it is desirable to connect potential kettle holes of smaller sizes with larger ones, since, in accordance with the predicted climate changes, this may provide a “safe road” for amphibians to migrate from smaller to larger kettle holes during unfavorable conditions.

### 2.5. Decision Support for Landscape and Spatial Planning

Environmental and spatial development based on an ecosystems approach facilitates finding more feasible biodiversity protection strategies where desired land use and required ecosystem services are combined [47]. Regarding potential improvements of ecosystem service supply, mapping and prioritizing areas for conservation strategies would allow the negative impacts of land use and climate change to be minimized [48]. The clustering approach used in this paper enables the identification of areas where the creation of stepping stone biotopes would decrease habitat fragmentation and improve the functional connectivity of target species. Our results show that only a small share of the landscape would be suitable for this purpose. Hence, the identification of such areas is crucial for environmental protection authorities in order to facilitate spatially targeted environmental restoration and protection measures. Where biotope mapping is available, this approach can be implemented at various scales across various landscapes.

Likewise, mapping priority areas for biodiversity conservation would facilitate a better understanding of decision-making processes, hence, contributing to an open dialogue among stakeholders [49][50]. The mapping approach used in this study could be integrated into decision-making processes. However, participatory ecosystem-based wetland landscape and spatial development still lacks a conceptual model for spatially explicit, monetary or non-monetary valuation of ecosystem services and their trade-offs, which is an obstacle to stakeholder cooperation.

Result-based payments for amphibian populations on farms could be a way to motivate farmers to not only apply measures for improving connectivity, but also to adapt their management in favor of amphibian biodiversity [1]. Monitoring and assessment tools should aim for minimal financial and bureaucratic requirements [1] in order to achieve a high degree of farmers’ participation. Furthermore, integrated and participatory stakeholder activities for the identification of suitable policy measures based on the mapping of ecosystem services are desirable. Such measures could make a significant contribution to sustainable land management and the sustainable use of natural resources.

## 3. Conclusions

In agricultural landscapes that are characterized by a high number of kettle holes, kettle holes play a highly important role for the provision of amphibian habitats. This contribution is on par with, or even exceeds, the contribution of other reproduction habitats, such as lakes or reed beds. In our research areas, the high number of kettle holes more than compensated for their small average size, while their high shoreline to water ratio was considered favorable for amphibians.

The importance of kettle holes as stepping stones, i.e., for functionally connecting other reproduction habitats, strongly depended on species’ range. For the short-range amphibian species garlic toad, the contribution of kettle holes to functional connectivity was much lower than the contribution of corridor habitats. For the long-range species European green toad, the contributions of kettle holes and corridor habitats were equally strong, though mostly redundant.

The clustering approach applied in this paper was suitable to assess the current state of functional connectivity for three amphibian species with different movement ranges and to quantify the contribution of kettle holes. We demonstrated how the approach can be used to identify locations suited to improving functional connectivity. As our method has low data and computing requirements and can easily be transferred to other species, it could be a valuable tool for landscape planners and environmental protection agencies.

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