Aquatic Ecosystems and Environmental Frontiers, Volume 4, Issue 4, December 2026 *ISSN: 3049-186X*
DOI: https://doi.org/10.70102/AEEF/V4I4/AF260403

Effects of Wetland Vegetation Fragmentation on Aquatic Invertebrate Dispersal and Colonization

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Abstract: Aquatic invertebrates rely on wetland vegetation as the physical structure on which they live, disperse and persist, but the wetland vegetation is being fragmented into smaller and more isolated patches, through drainage, land conversion and altered hydrology. This study focuses on the effects of fragmentation of the wetland vegetation, rather than the overall quantity of the vegetation, on the dispersal and colonization of aquatic invertebrates. A spatially explicit metapopulation simulation was a landscape of 100 × 100 units with a fixed 30% of landscape vegetated in 1 to 64 circular patches. Weak, moderate and strong dispersal were simulated on 300 different landscapes for each fragmentation level (dispersal distances of 5, 15 and 40 units). Patch connectivity was positively correlated with colonization, patch area negatively correlated with extinction, and metapopulation persistence and patch occupancy were observed at the end of 60-time steps. Occupancy of weak dispersers was sharply reduced (51% to 1%) and persistence of weak dispersers was reduced (58% to 10%) in the 64-patch landscapes compared to the 2-patch landscapes. Moderate dispersers exhibited a "hump" centered at four patches, while strong dispersers had little effect on occupancy, ranging above 76% at all fragmentation levels. The results show that fragmentation effects are not consistently negative and that the dispersal ability of a wetland species helps to determine whether fragmentation results in a fragmented wetland as a connected network of habitats or as a series of isolated habitats. Large patches of vegetation and stepping stone connections should therefore be retained in conservation planning, especially for those poorly dispersing taxa. The results are simulation-derived and offer predictions for field validation.

Keywords: Wetland Vegetation; Habitat Fragmentation; Aquatic Invertebrates; Dispersal; Colonization; Metapopulation.

(Submitted: August 18, 2026; Revised: September 22, 2026; Accepted: November 04, 2026; Published: December 30, 2026)

I. Introduction

Vegetation (emergent reeds and sedges, floating mats, submerged macrophytes) of wetlands offer oviposition sites, predator protection, food resources, and structural complexity that supports a variety of aquatic invertebrate communities. The middle of wetland food webs consists of invertebrates; beetles, bugs, dragonflies, caddisflies, midges, snails and crustaceans are all important in linking aquatic production to birds, amphibians and fish, and are also widely used to evaluate ecological condition. However, many of these taxa require particular vegetation structure and therefore the spatial distribution of vegetation is a direct determinant of the distribution of invertebrates and their access to new habitat.

This spatial pattern is changing on a worldwide scale. Experiments and syntheses with fragmentation demonstrate that the fragmentation of habitat has long-term impacts on biodiversity and ecosystem function, regardless of biome type (Haddad et al., 2015). Wetlands are particularly vulnerable: the long-term estimates indicate that between 64% and 71% of the world's wetland area was lost since 1900 and that the remaining wetlands are often degraded into fragments in an agricultural or urban landscape (Davidson, 2014). In the remnants, vegetation is fragmented by a variety of factors, including channelization, grazing, mowing, nutrient enrichment, invasive plants and water regime changes.

But the ecological significance of fragmentation is disputed. Many landscape-scale studies have been discussed in the context of the broad picture that the majority of significant responses to fragmentation (in addition to habitat amount) were positive, and that small patches should not be given lower conservation values than an equivalent area of a large patch (Fahrig, 2017). A direct rebuttal was provided that this is based on a narrow and possibly biased subset of evidence, and cannot be used to inform conservation decisions (Fletcher et al., 2018). The disagreement has relevance for wetlands because it poses a practical

issue: when the total amount of vegetation is fixed, does a large number of small patches benefit, harm or have no effect the invertebrates that are required to travel between the patches?

In this paper, the answer to this question is explored for aquatic invertebrate dispersal and colonization. Two aspects of the problem are singled out. First, the capacity to disperse is very variable among invertebrates, from highly mobile adult insects to those that are passively dispersed or mainly sedentary, and therefore the impact of fragmentation will probably vary by traits. Second, fragmentation affects multiple components of the landscape simultaneously: its patch size and number, its patch isolation, and the continuity of populations across patches. A single, clear model can cleanly divide these pathways more often than can field data. The aims are thus to (i) measure the effect of patch number on the occupancy and persistence of populations at a constant vegetation cover and (ii) to determine if there are differences between weak, moderate and strong dispersers and (iii) to develop management implications and testable field hypotheses.

II. Literature Review

Metacommunity Theory and Dispersal in Aquatic Systems

Metacommunity ecology identifies groups of local communities that are connected by dispersal and provides a framework to distinguish three types of species sorting: species sorting by local environment, mass effects from high dispersal, and dispersal limitation where suitable habitats are unoccupied due to the inability of colonists to arrive to it. The balance between species sorting and dispersal limitation strongly depended on connectivity and spatial scale in an analysis of observational data from aquatic systems, where species sorting was more dominant in streams and lakes while dispersal limitation was more influential in isolated lakes and ponds (Heino et al., 2015). The main reason for the importance of vegetation fragmentation is for the small, isolated wetland waterbodies—the invertebrate communities are most likely to be limited by colonists' arrival.

Measuring and Interpreting Dispersal

Dispersal is a hard-to-measure process in multispecies systems. A synthesis of the freshwater literature they reviewed identified organismal, genetic, physical and transport-geography proxies for dispersal and they argued that they should be incorporated into a range of bioassessment, conservation planning and restoration research activities, where recolonisation is a key issue (Heino et al., 2017). A complementary synthesis of river-network metacommunities revealed that multiple pathways are involved in dispersal and that organismal traits and landscape structure cooperate to shape dispersal (Tonkin et al., 2018). However, care should be taken with the use of proxies as dispersal traits can provide evidence of potential dispersal distances, but dispersal does not necessarily represent demographic connections as arrival does not necessarily lead to establishment (Lancaster & Downes, 2017). Here, the distinction between movement and effective colonization is embedded in the model used for the simulation, in which a propagule needs to arrive and survive in a patch.

Vegetation Structure, Patch Properties and Invertebrate Assemblages

It has been demonstrated in the field from ponds that there is a relationship between local vegetation and landscape context. The best macroinvertebrate community diversity and conservation value were associated with ponds having complex stands of macrophytes and floating vegetation, low nutrient levels and limited urban development in the surrounding landscape, and a landscape scale influence that was often eclipsed by local-scale influences on conservation value (Thornhill et al., 2017). The result is consistent with two possible mechanisms modeled below: richer and more abundant vegetation means larger number of local populations (smaller extinction), and the landscape determines the ease with which patches are reached.

Connectivity, Dispersal Ability and Community Assembly

In river networks, both habitat connectivity and dispersal ability are found to influence the assembly mechanisms of macroinvertebrate communities (Sarremejane et al., 2017). While patches of wetlands are not arranged as a dendritic network, the same spatial arrangement can be dynamically linked for one species and isolated for another. This trait dependence is the foundation of the contrasting dispersal classes in the present study and is a reason to consider fragmentation as a property of the pair of organism and landscape, instead of being a property of the landscape alone.

Knowledge Gap

The literature thus confirms three points: 1) the role of dispersal in structuring aquatic communities; 2) the trait dependence of dispersal; and 3) the influence of vegetation quality on aquatic invertebrate communities. It is still unknown how the pattern of vegetation (with the same overall amount of vegetation) affects dispersal ability and colonization and persistence. This is because the contribution of this study is to isolate that interaction.

III. Materials and Methods

Simulated Landscapes

The landscapes consisted of square arenas of 100 × 100 arbitrary spatial units. Wetland vegetation was represented as circular patches of equal size (30% of the arena total) which varied in number of fragments independent of the amount of habitat. This area was divided into 6 levels of fragmentation with N = 2, 4, 8, 16, 32 or 64 patches, corresponding to mean patch area 1,500 to 47 units² as well as into a single patch landscape as an unfragmented reference (N = 1). The patch centres were randomly positioned with a minimum separation of one unit between each centre and no centres were in the same position. At each fragmentation level 300 independent random landscapes were created and the mean nearest-neighbour edge-to-edge gap was used as a measure of isolation.

Colonization and Extinction

For each landscape, a discrete-time stochastic metapopulation model was used. An occupied patch j successfully colonizes an empty patch i with probability: $S_{ij} = m \cdot \exp\left(-\frac{d_{ij}}{\alpha}\right) \cdot \sqrt{\frac{A_j}{A_{\text{ref}}}}$ where d_{ij} is the distance between the two patches, α is the average dispersal distance, A_j is the area of the source patch sending colonists, A_{ref} is a reference area of 375 units^2, and $m = 0.25$ is the maximum colonization probability. The overall probability of colonization of an empty patch was calculated as $1 - \prod(1 - S_{ij})$ for all occupied patches. Thus, the larger the size of the source patch, the more colonists are provided, and colonization decreases exponentially with distance as determined by dispersal. Three dispersal classes were simulated: weak ($\alpha = 5$), moderate ($\alpha = 15$), and strong ($\alpha = 40$).

If a patch was occupied, the extinction probability was: $E_i = \min\left[1{,}0.06 \cdot \sqrt{\frac{A_{\text{ref}}}{A_i}}\right]$ meaning that smaller patches where fewer individuals occur and there is less "vegetative refuge" were more likely to lose their individuals. This area-dependence is based on a common assumption that small patches of habitat have smaller population sizes and that these are more susceptible to stochastic loss.

Simulation Protocol and Response Variables

One time step was used as the initial patch to be occupied at each replicate, with each replicate being executed for 60-time steps. Two response variables were taken. Occupancy was the proportion of patches occupied, averaged over steps 41 to 60 (replicates in which the invertebrate population went extinct from every patch contributed an occupancy of zero). Persistence was the proportion of replicate landscapes with a patch occupied at step 60. Reported results are the mean of 300 landscapes with the standard deviation of occupancy. All simulations were coded in Python using a fixed seed for random numbers (42) to ensure reproducibility. The values for all parameters were selected to be realistic values within a wide range of behaviours and not to represent a specific species, and so absolute values should be interpreted as relative comparisons between scenarios.

IV. Results

Landscape Structure

The mean patch area was reduced from 1,500 units (N = 2) to 47 units (N = 64) while the total vegetation cover remained constant. The average distance between patches in the mean nearest-neighbour gap was greatest at four patches (7·0) but reached a minimum of 2·3 at 64 patches, because there were more patches of small size packed into the same arena, giving a closer average of distance between patches between the four and the 64 patch levels (Table 1).

Occupancy and Persistence

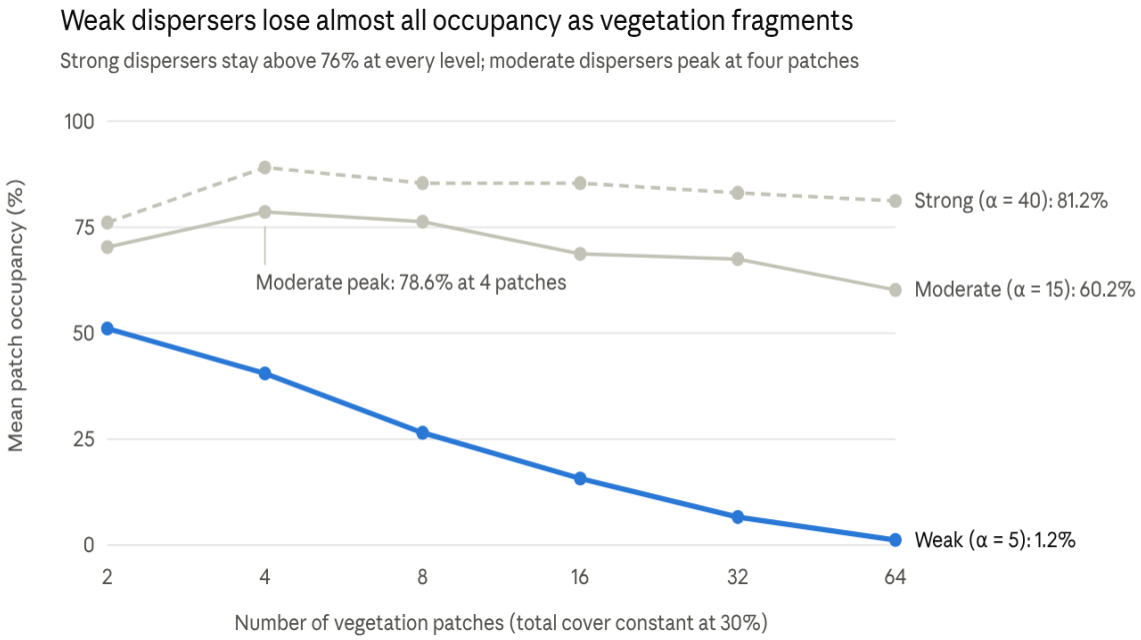
Table 1 and figure 1 reveal a strong dependence of the response to fragmentation on dispersal ability. For weak dispersers, occupancy declined steadily from 51.1% at two patches to 40.5% (4 patches), 26.5% (8), 15.7% (16), 6.6% (32) and 1.2% (64). Persistence decreased as well, from 58% to 10% of landscapes. Moderate dispersers had an occupancy of 70.3% at two patches, peaked at 78.6% at four patches, then dropped slowly to 60.2% at 64 patches; persistence ranged between 77% and 90% across all patches. There was no response to fragmentation for strong dispersers; occupancy was 76.1% to 89.1% at all fragmentation levels, and persistence was 94% to 98% at four or more patches.

Table 1: Simulated Invertebrate Occupancy Across Landscape Structures

Patches (N)	Mean patch area (units²)	Mean nearest-neighbour gap (units)	Weak dispersers (α = 5)	Moderate dispersers (α = 15)	Strong dispersers (α = 40)
1 (reference)	3,000	–	100 (100)	100 (100)	100 (100)
2	1,500	6.2	51.1 ± 44.7 (58)	70.3 ± 39.4 (77)	76.1 ± 37.2 (81)
4	750	7.0	40.5 ± 36.1 (60)	78.6 ± 27.9 (90)	89.1 ± 16.6 (97)
8	375	5.0	26.5 ± 30.2 (49)	76.3 ± 25.8 (90)	85.4 ± 22.4 (94)
16	188	3.9	15.7 ± 20.6 (44)	68.7 ± 29.2 (85)	85.4 ± 17.6 (96)
32	94	2.9	6.6 ± 11.3 (30)	67.5 ± 25.1 (88)	83.1 ± 17.0 (96)
64	47	2.3	1.2 ± 4.3 (10)	60.2 ± 27.0 (83)	81.2 ± 12.6 (98)

Variability among Landscapes

Standard deviations of occupancy were high at low patch numbers (36 to 45 percentage points at 2 to 4 patches) because the outcomes of landscapes with a limited number of patches are all-or-nothing. The variability of the landscapes was lowest for strong dispersers (64 patches, SD = 12.6), when there was a high density of patches that minimized local losses.



Simulation output · mean of 300 landscapes per point (values as in table 1)

Figure 1: Invertebrate Patch Occupancy by Dispersal Ability

V. Discussion

Fragmentation Effects are Trait-Dependent

The most critical finding is that there is no single "fragmentation effect" – the same landscapes were detrimental to weak dispersers, moderately detrimental to moderate dispersers and nearly neutral to strong dispersers. This provides a means to balance the claims of both sides in the fragmentation issue. For most taxa in a data set, if patch spacing is not a factor of high importance, fragmentation per se will seem neutral, or even positive, as found in a large synthesis of significant responses (Fahrig, 2017). The negative consequences highlighted by the critics of that synthesis gain the upper hand (Fletcher et al., 2018) if the focal taxa are poor dispersers. The observed difference is not the difference in the evidence, but rather the difference in the ability of the organisms to disperse and the difference in the scale of measurement for the spacing of the patches.

Why weak Dispersers Collapse Even as Gaps Shrink

The counter-intuitive aspect of the landscapes was that the mean gap between patches decreased with increasing fragmentation because with constant cover in many small circles the arena is more evenly filled. Nevertheless, the number of weak dispersers fell off dramatically. The reason for this is that the model has two processes that depend on the area. Smaller patches showed higher extinction probabilities (0.17 per step when compared to 0.04 when four patches were used) and fewer colonists, making it more likely for the metapopulation to lose patches than colonist patch colonization by individuals that were weakly dispersing could restore them across even narrow gaps. However, the result was influenced by patch size and population viability as opposed to the distance for weak dispersers. This is consistent with field data showing that the condition of local vegetation is a more important driver of invertebrate assemblage richness and conservation value than landscape position (Thornhill et al., 2017) and suggests that local habitat condition and landscape configuration are not separable.

The Intermediate Optimum for Moderate Dispersers

Moderate dispersers reached maximum number of patches at four patches and patches were large enough to support populations and close enough to others to allow the exchange of colonists based on the dispersal distance. More patches decreased patch area and the extinction resistance, while fewer patches (two) increased the risk of total loss by one stochastic extinction event. Intermediate optimum of this type suggests that risk-dispersion and connectivity benefits of subdivision, if any, are bounded; some subdivision may be beneficial in terms of risk dispersion and connectivity, but not beyond a threshold that is dependent upon the dispersal ability.

Dispersal Ability, Connectivity and Restoration

The simulation is similar to simulations of dendritic stream channels where the strength of dispersal was found to impact metacommunity structure (Cañedo-Argüelles et al., 2015). Same applies with restoration. There is a prediction from metacommunity theory that the isolation of communities can influence responses to restoration, in that restored habitat can be recolonized rapidly only when there is a nearshared source population within an effective dispersal range (Swan & Brown, 2017). For wetland managers it also means that beneficial results for poor dispersers may not result from planting or reinstating vegetation in an isolated location without source patches or stepping stones being provided. For strong dispersers, management can focus on improving local habitat quality and on the overall extent of vegetation.

Management Implications

There are three practicable suggestions to be followed next. First, emphasis should be placed on maintaining large vegetation patches, as patch area both increases population size and colonist output. Second, when subdivision of this vegetation is required, ensure patches are not too small and preserve stepping stone vegetation whose inter-patch spacing reflects that of a limiting guild of invertebrates that are weakly dispersed, for instance, by identifying a limiting guild of invertebrates that are weakly dispersed. Third, pay attention to colonization, not to richness, as colonization in newly restored or newly isolated patches should provide an earlier signal of the effect of fragmentation than changes in community composition.

Limitations and Future Research

Results are obtained from a simulation that makes many simplifications: the patches are all the same size, the matrix is evenly populated and not a habitat, there is a single colonising species, the dispersal kernel is exponential, and no seasonal or hydrological changes are included. In reality, hydroperiod-driven drying, variability in wetness, predator-prey relations, and matrix permeability can impact dispersal and survival in real wetlands. Field tests could involve the planting of standardized artificial vegetation substrates at various distances and patch sizes and could link taxon-specific dispersal traits with the results of occupancy. Future models should include temporal dynamics, species interactions and patch size heterogeneity.

VI. Conclusion

The effects of fragmentation of wetland vegetation, while keeping the overall vegetation cover constant, were examined on invertebrate dispersal and colonization using a spatially-explicit metapopulation simulation. Three conclusions emerge. First, fragmentation will depend on how easily the plants can be dispersed. Weakly dispersing invertebrates experienced a significant drop in occupancy from 51% to 1% with an increase in the number of patches (from 2 to 64), and remained in only 10% of the most fragmented landscapes, while strongly dispersing invertebrates occupied over 76% of the landscapes across all fragmentations. Second, moderate dispersers had an intermediate optimum, suggesting that the subdivision of vegetation, although tolerated, can only be done up to a certain point, depending on dispersal distance and patch size. Third, patch area was as influential as distance between patches, via effects on extinction and colonist supply, and was seen as a source of influence even as gaps decreased with a decrease in

dispersal. The results provide information for conservation and restoration that can be used to include the protection of large vegetation patches, addition of stepping stone vegetation of a size suitable to the dispersal ability of target taxa, and monitoring colonization as an early indicator of fragmentation. The results are simulation-generated and are only hypotheses that should be tested by colonization experiments conducted in field wetlands and by occupancy surveys of traits in real wetlands. These tests would help to determine the extent of the trait-dependent pattern observed here to other wetland types, regions and invertebrate groups.

References

[1] Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

[2] Davidson, N. C. (2014). How much wetland has the world lost? Long-term and recent trends in global wetland area. *Marine and freshwater research*, *65*(10), 934-941. https://doi.org/10.1071/MF14173

[3] Fahrig, L. (2017). Ecological responses to habitat fragmentation per se. *Annual review of ecology, evolution, and systematics*, *48*, 1-23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

[4] Fletcher Jr, R. J., Didham, R. K., Banks-Leite, C., Barlow, J., Ewers, R. M., Rosindell, J., ... & Haddad, N. M. (2018). Is habitat fragmentation good for biodiversity?. *Biological conservation*, *226*, 9-15. https://doi.org/10.1016/j.biocon.2018.07.022

[5] Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S., & Bini, L. M. (2015). Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, *60*(5), 845-869. https://doi.org/10.1111/fwb.12533

[6] Heino, J., Alahuhta, J., Ala-Hulkko, T., Antikainen, H., Bini, L. M., Bonada, N., ... & Soininen, J. (2017). Integrating dispersal proxies in ecological and environmental research in the freshwater realm. *Environmental Reviews*, *25*(3), 334-349. https://doi.org/10.1139/er-2016-0110

[7] Tonkin, J. D., Altermatt, F., Finn, D. S., Heino, J., Olden, J. D., Pauls, S. U., & Lytle, D. A. (2018). The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology*, *63*(1), 141-163. https://doi.org/10.1111/fwb.13037

[8] Lancaster, J., & Downes, B. J. (2017). Dispersal traits may reflect dispersal distances, but dispersers may not connect populations demographically. *Oecologia*, *184*(1), 171-182. https://doi.org/10.1007/s00442-017-3856-x

[9] Thornhill, I., Batty, L., Death, R. G., Friberg, N. R., & Ledger, M. E. (2017). Local and landscape scale determinants of macroinvertebrate assemblages and their conservation value in ponds across an urban land-use gradient. *Biodiversity and conservation*, *26*(5), 1065-1086. https://doi.org/10.1007/s10531-016-1286-4

[10] Sarremejane, R., Mykrä, H., Bonada, N., Aroviita, J., & Muotka, T. (2017). Habitat connectivity and dispersal ability drive the assembly mechanisms of macroinvertebrate communities in river networks. *Freshwater Biology*, *62*(6), 1073-1082. https://doi.org/10.1111/fwb.12926

[11] Cañedo-Argüelles, M., Boersma, K. S., Bogan, M. T., Olden, J. D., Phillipsen, I., Schriever, T. A., & Lytle, D. A. (2015). Dispersal strength determines meta-community structure in a dendritic riverine network. *Journal of Biogeography*, *42*(4), 778-790. https://doi.org/10.1111/jbi.12457

[12] Swan, C. M., & Brown, B. L. (2017). Metacommunity theory meets restoration: isolation may mediate how ecological communities respond to stream restoration. *Ecological Applications*, *27*(7), 2209-2219. https://doi.org/10.1002/eap.1602