How optimal foragers should respond to habitat changes? On the consequences of habitat conversion.

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Abstract

The Marginal Value Theorem (MVT) provides a framework to predict how habitat modifications related to the distribution of resources over different patches should impact the realized fitness of individuals (their long term rate of gain acquisition) and their optimal rate of movement through the habitat. In earlier articles we provided a general treatment of how habitat alterations involving changes in the gain function of patches would impact optimal residence times, and thus movement rate. However an alternative sort of habitat modification consists in habitat conversion, whereby patches are converted from one type to another. In such a case the set of gain functions existing in the habitat remain unchanged, but their relative frequency is modified. Habitat conversion has received very little attention in the context of the MVT. One expects that different ways to alter the distribution of patch qualities should yield consistent results, but this remains to be shown. Here we complement earlier analyses with a treatment of habitat conversion in the MVT, and compare the predictions obtained with previous results. We find that similar results can be rederived in the context of habitat conversion, indicating that MVT predictions are robust to the exact scenario of habitat modification considered. We suggest taking into account behavioral responses may help better understand the ecological consequences of habitat conversion.

1 Introduction

In most analyses of the Marginal Value Theorem [4, 11], including recent re-analyses [1–3], emphasis is on understanding how changes in the shape of gain functions in patches impacted the optimal residence times. Yet an alternative form of habitat alteration is to change the relative frequency of different patch categories, without modifying the categories themselves. For instance one might increase the quality of habitat not by making individual patches richer, but rather by making the richest patches more frequent (and the poorest patches rarer). In the context of the MVT, this corresponds to a situation where the travel time and the gain functions are unchanged, but the frequency distribution of the different patch categories does vary. Whereas changes in the individual gain functions can readily describe scenarios of habitat enrichment [2], modifications of the relative patch frequencies more aptly capture scenarios of habitat conversion (transformation of patches from one category to

another). This form of habitat change is illustrated in Fig. 1. For instance, one might think of converting patches of closed habitat (e.g. forest) into open habitat (e.g. clearings or crop) in a landscape mosaic, or changing the relative frequency of disturbed versus undisturbed feeding sites [8, 10, 12]. Habitat conversion is actually one pervasive aspect of the current global biodiversity crisis, impacting many different types of natural ecosystems [7]. Nonetheless, scenarios of habitat conversion have not received much attention in the MVT literature, probably in part because it requires considering entire habitats, and prevents focusing on individual patches. Also, it renders the graphical arguments historically used to think about the MVT of little help.

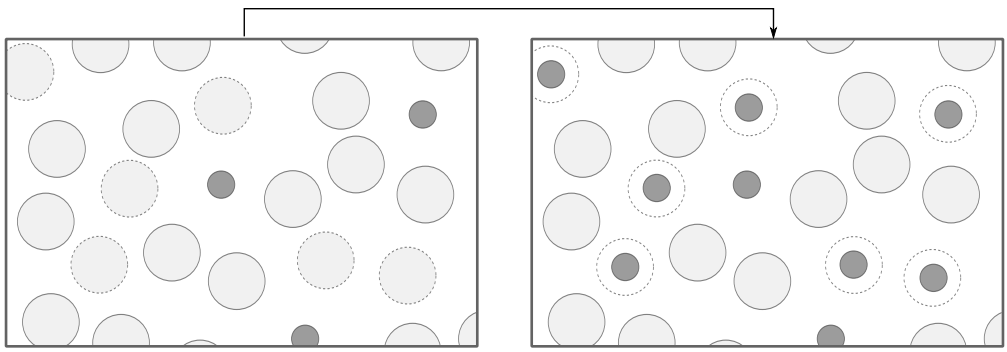

Figure 1. Habitat conversion in the MVT. A patchy habitat containing two sorts of patches is illustrated: large light disks represent pristine patches, small dark disks disturbed patches. Starting form the situation on the left, with disturbed patches in frequency 1/10, some pristine patches are converted into disturbed patches, resulting in the habitat shown on the right, where disturbed patches are in frequency 3/10.

In a previous mathematical reanalysis of the MVT [3], we only briefly mentioned the effect of changing the relative patch frequencies p_i (Section 5.2). We remarked that following changes in the frequency distribution of patch types, all optimal residence times should vary in the same direction, determined by how the long-term realized rate of gain, E_n^*, varies. If the distribution of patches is altered in a way that makes the overall habitat better (higher E_n^*), all residence times decrease, and vice versa.

However we did not analyze further how the average residence time $\langle t_j^* \rangle$, that controls the overall rate of movement in the habitat, would respond to such changes in the frequency of different patch types. We simply observed that "*improving habitat quality by manipulating relative patch frequencies decreases all patch residence times, i.e. increases the movement rate*". The last part of the sentence is actually an abusive simplification. Indeed, the fact that the optimal residence time decreases for each individual patch type is true, but does not guarantee that the average residence time also decreases, since the relative frequencies of different patch types was changed. For instance, if residence times are longer on the best patches, then increasing the frequency of the latter mechanically increases the average residence time, and this might counteract the previous negative effect observed on any particular patch. In subsequent publications [1, 2] we paid special attention to predicting the impact of the resource distribution (i.e. the mean resource level in patches and its variance over patches) on the average rate of movement. Again, this was achieved by considering modifications of the gain functions, rather than changing the relative frequency of the patch types already present.

For consistency, one would expect these two ways of manipulating the resource distribution to yield similar conclusions, but this remains to be established. In this article we complement our previous reanalyses with a treatment of the effects of changing the relative abundances of different patch-types, with the aim of determining the consistency (or lack thereof) of the insights obtained from the two alternative approaches.

2 The MVT and notations

We build on [2,3] and consider the general (heterogeneous) marginal value theorem according to which the optimal residence time t_i^* on patches of type i is defined implicitly by

$$\begin{cases} \left.\frac{dF_i(t_i)}{dt_i}\right|_{t_i=t_i^*} = \frac{\langle F_j(t_j^*)\rangle}{\langle T_j+t_j^*\rangle} & i \in \Omega \\ t_i^* = 0 & i \notin \Omega \end{cases} \tag{1}$$

where F_j is the gain function in patches of type j, T_i is the average time to reach a patch of type i (travel time, usually regarded as the same for all patches) and Ω refers to the set of patches that are effectively exploited in the habitat. Brackets are used to denote spatial averages over the entire habitat ($\Omega \cup \Omega^{\mathbf{C}}$), i.e.

$$\langle y_j \rangle = \sum_{j=1}^{s} p_j y_j$$

with p_j the frequency of patches of type j, $j \in (1, s)$.

Quantity $\langle F_j(t_j^*)\rangle / \langle T_j + t_j^*\rangle$ is the long term average rate of gain realized in the habitat (called E_n^* for short), and is thus also the quitting rate in exploited patch, i.e. the instantaneous rate of gain in a patch at the time the individual leaves it. A well-known consequence of eq. (1) is therefore that all exploited patches should be left at the same quitting rate, equal to the long term average rate of gain in the habitat E_n^*.

Following [2], we remark that unexploited patches can be gotten rid of by restricting the system to the $\tilde{s}$ patches that are effectively exploited. This implies rescaling the p_j to new $\widetilde{p}_j$ accordingly and increasing the travel times to some effective values $\widetilde{T}_j$, given by

$$\widetilde{p}_j = \frac{p_j}{\sum_{k\in\Omega} p_k} \tag{2}$$

and

$$\tilde{T}_j = T_j + \frac{\sum_{k\notin\Omega} p_k T_k}{\sum_{k\notin\Omega} p_k} \frac{\sum_{k\notin\Omega} p_k}{\sum_{k\in\Omega} p_k} = T_j + \frac{\sum_{k\notin\Omega} p_k T_k}{\sum_{k\in\Omega} p_k} \tag{3}$$

In these conditions, instead of (1), we can study the slightly simpler equation

$$\left.\frac{dF_i(t_i)}{dt_i}\right|_{t_i=t_i^*} = \frac{\langle F_j(t_j^*)\rangle}{\left\langle \tilde{T}_j + t_j^*\right\rangle} \tag{4}$$

where there are only $\widetilde{s} = \mathrm{card}(\Omega)$ patch-types to consider, all effectively exploited (i.e. $t_i^* > 0$ for all i).

For clarity we will henceforth drop the tildes and ignore Ω, but one must remember that T_j, S and p_j are intended as their modified values introduced above.

3 Habitat conversion: manipulating the patch frequency distribution p_j

3.1 Which are the best patches?

We first compute the (partial) effect of changing one p_i on the realized fitness (E_n^*). Differentiating (4) with respect to p_i we get

$$\frac{\partial E_n^*}{\partial p_i} = \frac{1}{\langle T_j + t_j^*\rangle^2} \left(\langle T_j + t_j^*\rangle F_i(t_i^*) - \langle F_j(t_j^*)\rangle (T_i + t_i^*) \right)$$

or, isolating E_n^*:

$$\frac{\partial E_n^*}{\partial p_i} = E_n^* \left(\frac{F_i(t_i^*)}{\langle F_j(t_j^*) \rangle} - \frac{T_i + t_i^*}{\langle T_j + t_j^* \rangle} \right)$$

Requiring this to be positive, we get the definition of a "good" (or "better than average") type of patch as one that, if made more frequent in the habitat, contributes to increase the realized fitness. This yields the condition

$$\frac{F_i(t_i^*)}{T_i + t_i^*} > \frac{\langle F_j(t_j^*) \rangle}{\langle T_j + t_j^* \rangle} = E_n^* \tag{5}$$

Note that this criterion to be a good patch is close to the criterion to be effectively exploited (i.e. in Ω). Indeed, only patches such that $F_i(t_i^*)/t_i^* > E_n^*$ should be exploited and the others should be entirely disregarded [6]. This condition to be an exploited patch is, as expected, less stringent that the condition to be a good patch (remark that the value of T_i does not appear at the denominator, in contrast to eq. (5)).

From (5), the good patches are characterized by a large $F_i(t_i^*)$ and/or a small $T_i + t_i^*$. Two scenarios can thus be distinguished regarding the identity of those patches. First, they can have both shorter exploitation time and greater absolute gains, in which case the two effects described above work jointly, and the best patches are unambiguously the best.

Alternatively, the best patches can have greater absolute yields, but longer exploitation time, or smaller yield and shorter exploitation time. In this case the two effects work against one another, and the best patches are not the best in all aspects. In this situation their identity will depend quantitatively on the relationship between absolute yield and exploitation time.

Omitting, as is usual, any systematic variation of travel time over patches, exploitation time boils down to residence time. Therefore the two situations can be discriminated from the association of patch absolute yields ($F_i(t_i^*)$) and residence times (t_i^*) within the habitat. The first occurs when a negative correlation of absolute gains over patches and residence time within a habitat, a definite possibility, though perhaps not the most common expectation. The second corresponds to a positive correlation, which is a very common expectation, since the richest patches would often be exploited for longer times. The two possibilities are illustrated in Figure 2.

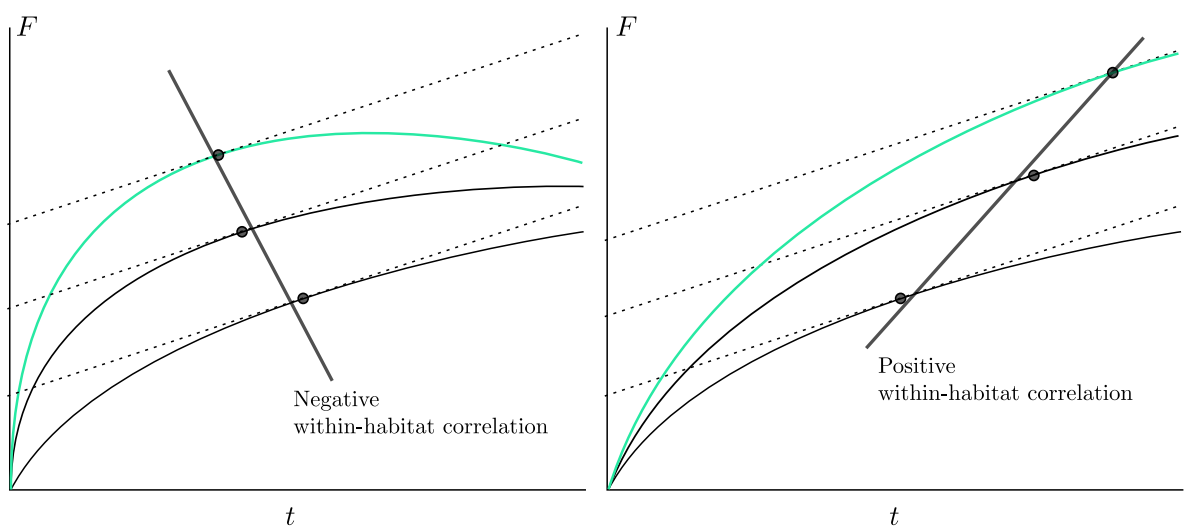

Figure 2. Two possibilities regarding the identity of the best patches. In both cases the best patch is shown in green. *Left*: Best patches are the best in all aspects, as they have both greater absolute yield and shorter residence time. This corresponds to a negative correlation of patch yield and residence time within the habitat. *Right*: Best patches are not the best in all aspects. In the example shown they exhibit greater absolute yield but longer residence time (the symmetric case is also possible). This corresponds to a positive correlation of patch yield and residence time within the habitat.

3.2 Variation of the realized fitness E_n^*

Of course, in practice we cannot vary one p_i alone since the following constraint must hold:

$$\sum_{j=1}^{s} p_j = 1$$

We therefore introduce some dummy habitat variable x to represent the effect of habitat conversion: we let all p_j be functions of x, under the constraint

$$\frac{d}{dx}\sum_{j=1}^{s} p_j = \sum_{j=1}^{s} \frac{dp_j}{dx} = 0$$

The total variation of E_n^* with respect to x is thus

$$\frac{dE_n^*}{dx} = \sum_{j=1}^{s} \frac{dp_j}{dx}\frac{\partial E_n^*}{\partial p_j}$$

Since we are at an optimum with respect to all residence times, we can omit any variation in the t_j^* from the derivative of E_n^* (see [3]), and we have

$$\frac{dE_n^*}{dx} = E_n^* \left(\frac{1}{\left\langle F_j(t_j^*)\right\rangle} \sum_{j=1}^{s} \frac{dp_j}{dx} F_j(t_j^*) - \frac{1}{\left\langle T_j + t_j^*\right\rangle} \sum_{j=1}^{s} \frac{dp_j}{dx}(T_j + t_j^*) \right)$$

which we may want to rewrite as, in terms of relative variations:

$$\frac{d\ln E_n^*}{dx} = \frac{\partial \ln\left\langle F_j(t_j^*)\right\rangle}{\partial x} - \frac{\partial \ln\left\langle T_j + t_j^*\right\rangle}{\partial x}$$

Here, and throughout the rest of the paper, partial derivatives indicate direct variation through the p_j, omitting the indirect variation occurring through changes in the optimal residence times, i.e. $\partial/\partial x = \sum dp_j/dx\ \partial/\partial p_j$.

As a consequence, an alteration of the frequency distribution of patches through an increase in x will increase realized fitness, and thus x will be a metric of habitat quality (see [3]), if and only if

$$\frac{\partial \ln\left\langle F_j(t_j^*)\right\rangle}{\partial x} - \frac{\partial \ln\left\langle T_j + t_j^*\right\rangle}{\partial x} > 0 \tag{6}$$

Quite intuitively, this shows that increasing the quality of a habitat rests on a balance between increasing the absolute gains extracted from patches and shortening the average time it takes to exploit them. First, if the patches that provide the greatest absolute gains become more abundant (positive first term in (6)), realized fitness increases. Second, if the patches that take a long time to exploit become more abundant (long to reach and/or long residence times; positive second term), realized fitness decreases.

3.3 Variation of the average movement rate

We now consider the average residence time $\left\langle t_j^*\right\rangle$, that is inversely related to the average rate of movement [2]. Obviously, the total variation in $\left\langle t_j^*\right\rangle$ can be separated into two components. First, there is the direct effect of changing the relative frequency of the different patches, which mechanically alters the average (see above). This effect can be expressed as

$$\frac{\partial \left\langle t_j^*\right\rangle}{\partial x} = \sum_{j=1}^{s} \frac{dp_j}{dx} t_j^*$$

Second, there is an indirect effect whereby the resulting change in E_n^* (see previous section) impacts all individual optimal residence times. From [3], we know that for all j

$$\frac{dt_j^*}{dx} = \frac{dE_n^*}{dx}\left(\frac{d^2F_j(t_j^*)}{dt_j^2}\right)^{-1}$$

It follows that

$$\frac{d\left\langle t_j^*\right\rangle}{dx} = \sum_{j=1}^{s}\frac{dp_j}{dx}t_j^* + \sum_{j=1}^{s}p_j\frac{dt_j^*}{dx}$$

$$\frac{d\left\langle t_j^*\right\rangle}{dx} = \sum_{j=1}^{s}\frac{dp_j}{dx}t_j^* + \frac{dE_n^*}{dx}\sum_{j=1}^{s}p_j\left(\frac{d^2F_j(t_j^*)}{dt_j^2}\right)^{-1}$$

Introducing as in [3] the harmonic mean H of the second time derivatives ($H < 0$) this is

$$\frac{d\left\langle t_j^*\right\rangle}{dx} = \sum_{j=1}^{s}\frac{dp_j}{dx}t_j^* + \frac{dE_n^*}{dx}\frac{1}{H}$$

As detailed in Appendix, some calculations yield the following criterion for the average residence time to increase with x:

$$\frac{\partial \ln\left\langle F_j(t_j^*)\right\rangle}{\partial x} < \frac{\partial \ln\left\langle T_j + t_j^*\right\rangle}{\partial x} + \frac{\partial\left\langle t_j^*\right\rangle}{\partial x}\frac{|H|}{E_n^*} \tag{7}$$

This is very similar to eq (6), with one term added on the r.h.s. The latter has the same sign as $\partial\left\langle t_j^*\right\rangle/\partial x$. Therefore the condition is more stringent if the direct effect of habitat conversion is positive, i.e. if patches with longer residence times become more frequent.

If we further make the common assumption that all patches have on average the same travel time T, or equivalently that travel times show no consistent trend with habitat conversion, we can express the criterion as (see Appendix):

$$\frac{\partial \ln\left\langle F_j(t_j^*)\right\rangle}{\partial x} < \frac{\partial \ln\left\langle T_j + t_j^*\right\rangle}{\partial x}\left(1 + \frac{\left\langle T_j + t_j^*\right\rangle|H|}{E_n^*}\right) \tag{8}$$

Remark that the parenthesis in (8) is always greater than one.

4 Discussion

4.1 Variation of realized fitness

Comparing eq. (6) with the condition for E_n^* to increase obtained when manipulating patch characteristics (equation (6) in [3]), we see that it is almost identical: the first term is the same, and the second is similar, only lacking the penalty term $\langle T_j \rangle / \langle T_j + t_j^* \rangle$. This is because when varying T_j as a patch attribute, we operated on a fraction of the entire time it takes to exploit one patch (while the optimal residence time itself is out of external control). Here, in contrast, when we convert patches from one type to another, the entire duration of one cycle (travel and residence time) is impacted, and the penalty factor therefore vanishes to unity.

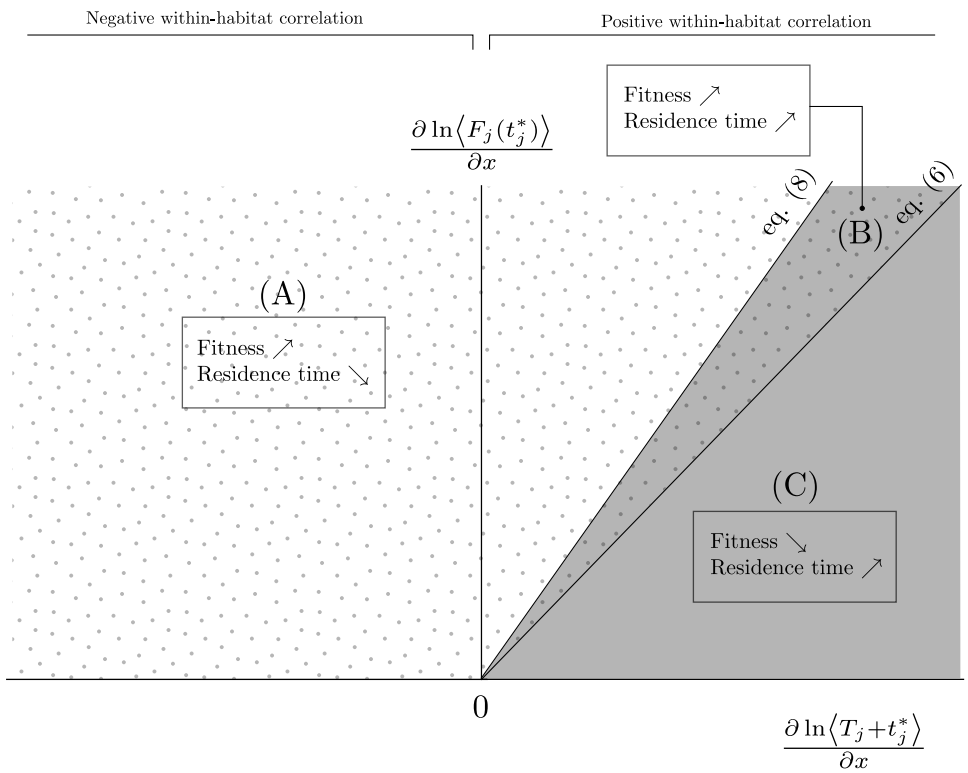

Figure 3. The impact of habitat conversion. The graph predicts the effect of changes in the relative frequency of different types of patches on the realized fitness (E_n^*) and on the average optimal residence time $\langle t_j^* \rangle$. The left half of the graph corresponds to cases where there is a negative correlation between patch yield and residence time within a habitat, whereas the right half corresponds to a positive correlation (see Figure 1). Three areas (A,B,C) can be distinguished. Note that E_n^* and $\langle t_j^* \rangle$ can vary in the same direction only between the two lines (gray dotted area; B).

4.2 Impact of habitat quality on average residence time (movement rate)

Combining (6) and (8), we obtain that habitat quality (E_n^*) and average residence time will both increase if:

$$\frac{\partial \ln \langle T_j + t_j^* \rangle}{\partial x} < \frac{\partial \ln \langle F_j(t_j^*) \rangle}{\partial x} < \frac{\partial \ln \langle T_j + t_j^* \rangle}{\partial x} \left(1 + \frac{\langle T_j + t_j^* \rangle |H|}{E_n^*} \right) \tag{9}$$

Therefore, an increase in habitat quality increases average residence time only if

$$\frac{\langle T_j + t_j^* \rangle |H|}{E_n^*}$$

is large enough, i.e. if the gain functions are curved enough. These results are summarized in Figure 3. Predictions are in full agreement with the ones derived in our previous re-analyses of the MVT [1, 3]. Specifically:

- An increase in habitat quality may have any (negative, null or positive) impact on average residence time.
- The correlation between residence time and patch yield within a habitat partly informs us on the impact of changing habitat quality. While a negative correlation of patch yield and residence time within a habitat ensures that an increase in habitat quality will shorten average residence time (leftmost half of Fig. 2, a positive correlation (rightmost half) does not guarantee an increased residence time (it does so only in area B). Therefore, a decrease in average residence time with habitat quality can be regarded as requiring less stringent conditions [1, 3].
- An increase in average residence time with habitat quality necessitates that residence times increase sufficiently steeply with patch quality in a habitat (area B in Fig. 2). This is equivalent to the result in [3] stating that an increase of residence time with habitat quality requires a "strong direct effect", i.e. a strong increase in the slope of the gain functions with patch quality. A strong increase in the slope of the gain functions with patch quality does generate a steep increase of residence time with patch quality in a given habitat.
- Unless there is a negative correlation of residence time and patch yield in the habitat (left parts of Figures 1 and 2), we cannot predict the response of average residence time to habitat quality based on average quantities only (average patch yield, average residence time, and therefore average rate of gain E_n^*). We further need to know the harmonic mean of the gain function second-time derivatives ($|H|$; see eq. (9)). The greater $|H|$, i.e. the more curved the gain functions, the more likely it is to observe an increase in average residence time with habitat quality. The same results were obtained with the other form of habitat change (see Theorem 3 and eq. (17) in [3]).

4.3 Conclusions

We compared two ways of envisioning habitat changes in the Marginal Value Theorem: on the one hand, changes in the shape of the gain functions [2, 3] and on the other hand, habitat conversion, i.e. changes in the relative frequencies of the different categories of patches (this article). Both were shown to yield equivalent predictions. We can therefore safely transpose results obtained with one approach to the other. This is fortunate, considering that the habitat conversion approach is rather less amenable to mathematical analysis (e.g. one has to consider heterogeneous habitats) and is more remote from usual MVT geometrical arguments [11]. Therefore, we can expect existing predictions regarding the consequences of changing the resource distribution in a habitat that were derived from changing the gain functions [1–3, 5, 14] to extend to scenarios of habitat conversion as well. In other words, MVT predictions appear robust to the specific scenario of habitat modification considered (e.g. patch enrichment versus habitat conversion), which is a satisfying property.

While the theoretical consequences of habitat conversion are usually considered at the scale of population and communities [9, 13], we suggest the MVT can offer a framework to apprehend these questions at the individual and behavioral scales. For instance, dynamic changes in the movement strategies of individuals on the short-term may change the relative exploitation of different parts of the habitat, as well as the realized level of migration and connectivity. Depending on their sign, behavioral

responses might mitigate, or on the contrary amplify, the population and community responses expected under the assumption of static migration rates and connectivity levels. A better integration of the behavioral and population scales might therefore improve our ability to predict the ecological consequences of habitat change in general, and habitat conversion in particular.

Acknowledgments

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Appendix

We here provide the derivation of eq. (7) and (8).

From (6) we can express the total derivative of $\langle t_j^* \rangle$ with x as

$$\frac{d\langle t_j^* \rangle}{dx} = \sum_{j=1}^{s} \frac{dp_j}{dx} t_j^* + \frac{E_n^*}{H} \left(\frac{1}{\langle F_j(t_j^*) \rangle} \sum_{j=1}^{s} \frac{dp_j}{dx} F_j(t_j^*) - \frac{1}{\langle T_j + t_j^* \rangle} \sum_{j=1}^{s} \frac{dp_j}{dx} (T_j + t_j^*) \right)$$

We can directly identify the partial log derivative of $\langle F_j(t_j^*) \rangle$ and $\langle T_j + t_j^* \rangle$ in the parenthesis. Factoring $E_n^* / |H|$ out:

$$\frac{d\langle t_j^* \rangle}{dx} = \frac{E_n^*}{|H|} \left(-\frac{\partial \ln \langle F_j(t_j^*) \rangle}{\partial x} + \frac{|H|}{E_n^*} \sum_{j=1}^{s} \frac{dp_j}{dx} t_j^* + \frac{\partial \ln \langle T_j + t_j^* \rangle}{\partial x} \right)$$

Introducing the partial log derivative of $\langle t_j^* \rangle$ and the absolute value of H, and requiring the parenthesis to be positive yields eq. 7.

Now, if all patches have on average the same travel time T, or if variation in travel time shows no consistent trend with habitat conversion, we have $d\langle T_j \rangle / dx = 0$. Note that under the second scenario (i.e. if all travel times are not equal), achieving a null derivative would in practice requires specific forms of habitat conversion, owing to the constraint that the sum of the p_j is constant. The constraint gradually vanishes as the number of patch-types (s) gets large. From $d\langle T_j \rangle / dx = 0$ it follows:

$$\frac{\partial \langle T_j + t_j^* \rangle}{\partial x} = \frac{\partial \langle t_j^* \rangle}{\partial x}$$

i.e.

$$\frac{\partial \langle t_j^* \rangle}{\partial x} = \frac{\partial \ln \langle T_j + t_j^* \rangle}{\partial x} \langle T_j + t_j^* \rangle$$

We can thus factor $\partial \ln \langle T_j + t_j^* \rangle / \partial x$ out to obtain

$$\frac{d\langle t_j^* \rangle}{dx} = \frac{E_n^*}{|H|} \left(-\frac{\partial \ln \langle F_j(t_j^*) \rangle}{\partial x} + \frac{\partial \ln \langle T_j + t_j^* \rangle}{\partial x} \left(1 + \frac{\langle T_j + t_j^* \rangle |H|}{E_n^*} \right) \right)$$

Requiring the parenthesis to be positive yields eq. (8).